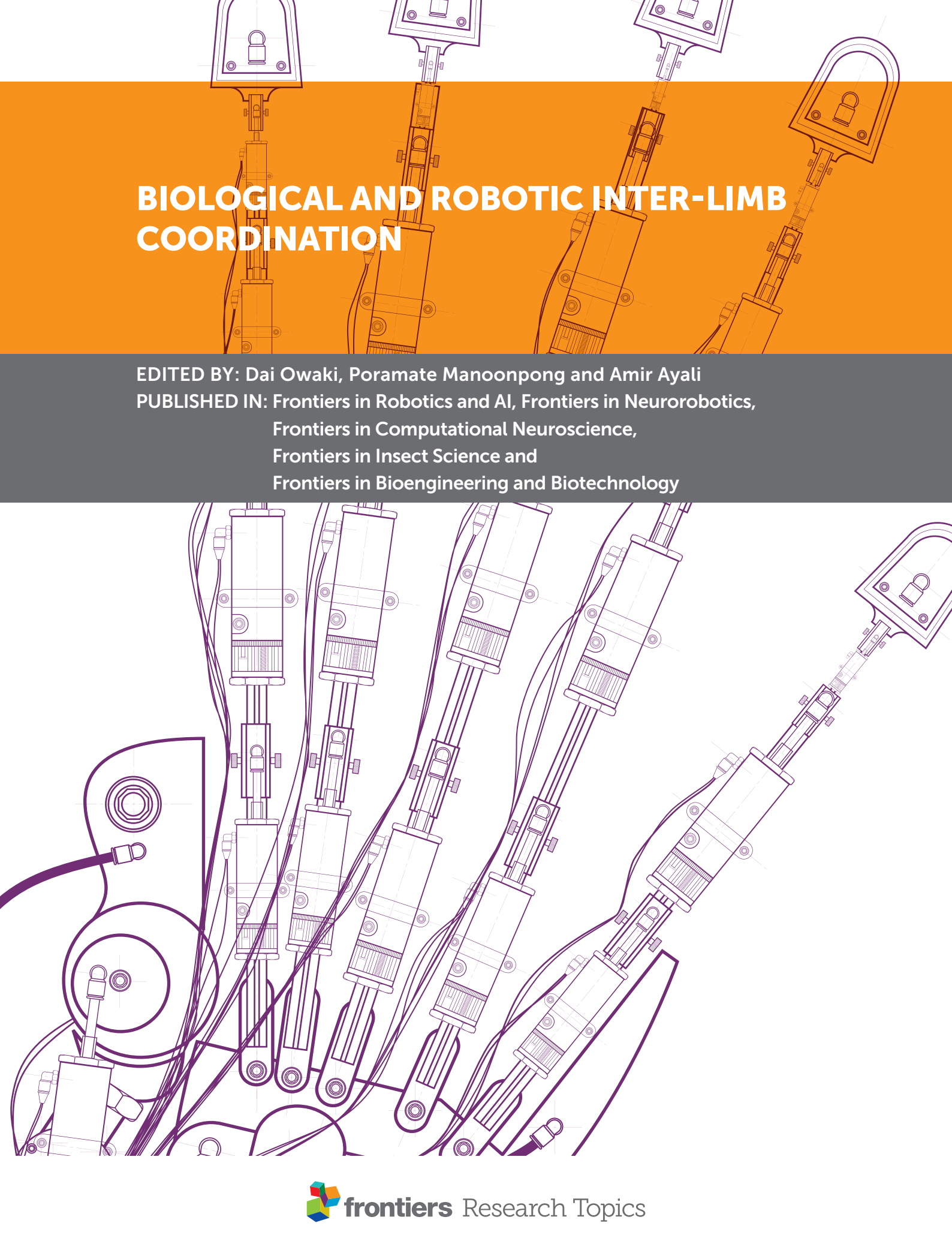




BIOLOGICAL AND ROBOTIC INTER-LIMB COORDINATION

EDITED BY: Dai Owaki, Poramate Manoonpong and Amir Ayali

PUBLISHED IN: Frontiers in Robotics and AI, Frontiers in Neurorobotics,
Frontiers in Computational Neuroscience,
Frontiers in Insect Science and
Frontiers in Bioengineering and Biotechnology



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ISSN 1664-8714

ISBN 978-2-88974-911-9

DOI 10.3389/978-2-88974-911-9

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BIOLOGICAL AND ROBOTIC INTER-LIMB COORDINATION

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Citation: Owaki, D., Manoonpong, P., Ayali, A., eds. (2022). Biological and Robotic Inter-Limb Coordination. Lausanne: Frontiers Media SA.
doi: 10.3389/978-2-88974-911-9

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Editorial: Biological and Robotic Inter-Limb Coordination

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Keywords: locomotion, legged animals, embodiment, bio-inspired robotics, robotics-inspired biology

Editorial on the Research Topic

Biological and Robotic Inter-Limb Coordination

1 INTRODUCTION

Animals on Earth have evolved to counteract the effect of gravity, negotiate terrestrial ground, and locomote efficiently for predation and survival. Locomotion is thus one of the fundamental functions of life. Through many cycles of evolutionary selection, both vertebrates and invertebrates have acquired sophisticated locomotor skills, exhibiting resilient and flexible locomotion in response to changes in body morphology, environment, and context, by coordinating leg movements, i.e., inter-limb coordination. Thus, understanding the inter-limb coordination mechanism is both essential for understanding the locomotive mechanism in legged animals and useful for establishing design principles for legged robots that can reproduce flexible and efficient locomotion resembling that exhibited in animals.

Understanding the principles of legged locomotion is a goal shared among biologists and robotics engineers, who have struggled to build multi-legged robots able to exhibit adaptive locomotion via inter-limb coordination. Although it is now possible to create a high-performance architecture, e.g., CPU/GPU, to control the movement of a robot, robots are still not able to carry out more than a small fraction of the complex and adaptive behaviors found in animals. Given the limited number of neurons that comprise a nervous system (insects for example possess only approximately 10^5 to 10^6 neurons in their nervous system) we must consider the potential role of not only intrinsic neural circuits in adaptations to dealing with unpredictable situations, but also that of the sensory feedback mechanisms that reflect body properties and physical interactions with the environment. Understanding the mechanisms that underlie adaptive locomotion contribute not only to biology but also to the field of robotics, by facilitating the design of durable and resilient legged robots capable of adapting to unpredictable and changing situations, much like animals.

Thus, the goal of this Research Topic is to consolidate topics related to “Biological and Robotic Inter-limb Coordination”, in order to encourage the acceleration of collaborative approaches between the fields of biology and robotics. The topic contains 22 articles, addressing biological and robotic inter-limb coordination mechanisms in different robotic and animal systems (**Figure 1**), as well as the translation of results to real-world applications, such as electromyographic (EMG)-based limb prostheses control.

OPEN ACCESS

Edited and reviewed by:

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The University of Sydney, Australia

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Specialty section:

This article was submitted to
Computational Intelligence in Robotics,
a section of the journal
Frontiers in Robotics and AI

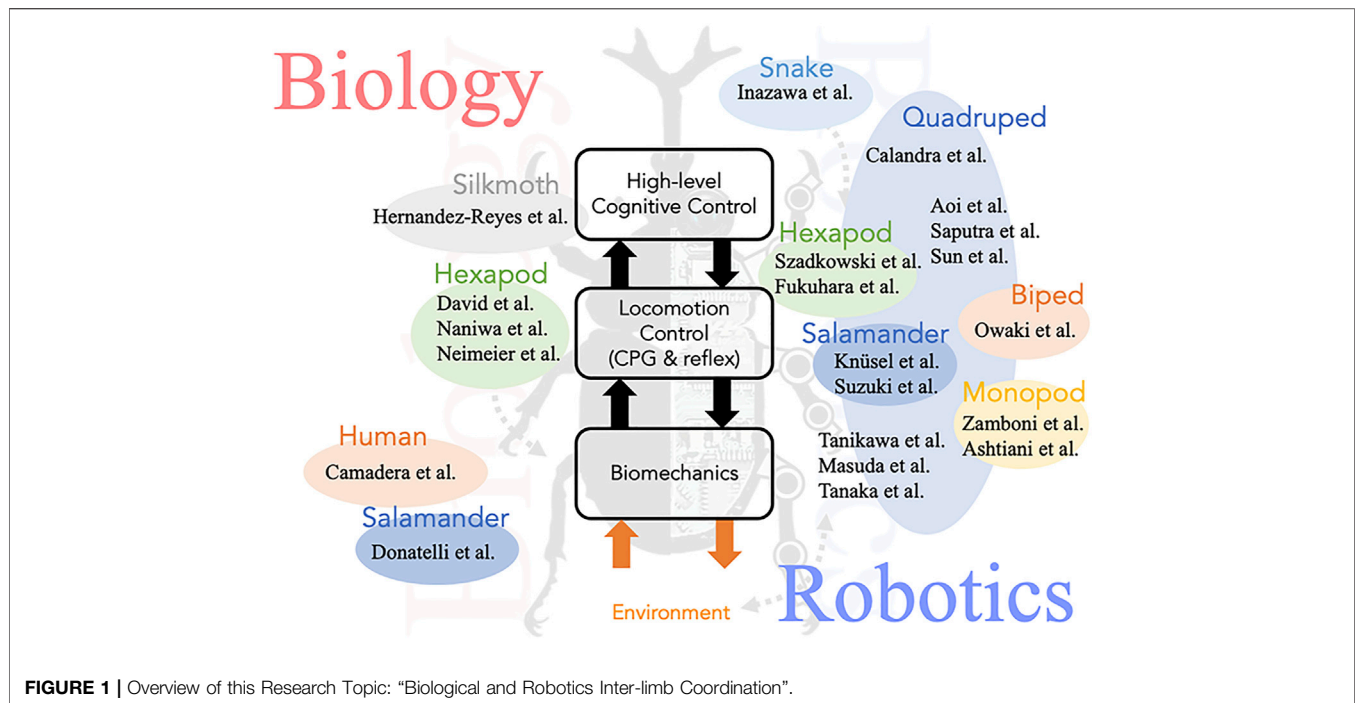
Received: 14 February 2022

Accepted: 22 February 2022

Published: 22 March 2022

Citation:

Owaki D, Manoonpong P and Ayali A
(2022) Editorial: Biological and Robotic
Inter-Limb Coordination.
Front. Robot. AI 9:875493.
doi: 10.3389/frobt.2022.875493



2 BIOLOGICAL INTER-LIMB COORDINATION

A major feature of animal locomotion is that of its flexibility or adaptability, i.e. the capacity of the locomoting animal to maintain robust and consistent movement through a variable and constantly changing environment. This outstanding ability, perfected by a long evolutionary history, is manifested at all levels of control and execution of locomotion: from the central and local neuronal circuits controlling and generating locomotion-related motor patterns, through the complex interactions of the central nervous system with ongoing as well as transient sensory signals, via the interactions of the central and sensory system with the muscular system responsible for executing movement of the body parts (legs, tail, and trunk), and last but not least, the dynamic interaction of these body parts with the physical environment (**Figure 1**, Center). A number of contributions to this special issue have addressed the distinctive plasticity of animal locomotion, focusing on aspects of locomotion and inter-limb coordination related to the different levels noted above (**Figure 1**, Left).

Starting with the central circuits, David and Ayali (2021) present a detailed investigation of the locomotion central pattern generating (CPG) neuronal networks and their underlying connectivity scheme in the cockroach, an established model in the study of locomotion control. They discuss the role of rhythmic properties of the endogenous local (segmental) CPGs vs inter-circuit coupling in the production of the functional, adaptable motor output during locomotion in the behaving animal. Yet another model insect, the cricket, is utilized by Naniwa and Aonuma (2021) in order to present the instrumental role of descending and ascending inputs into the thoracic motor control center (the CPGs controlling leg

movements) in maintaining the walking pattern. They demonstrate that descending signals from the head ganglia play an inhibitory role in initiating leg movements; and that both the descending and ascending signals from the abdominal nervous system are important in initiating and coordinating the walking gait patterns.

Inter-limb coordination is directly investigated by Niemeier et al. (2021) by way of controlled lesions of thoracic connectives in one of the leading models in the study of leg coordination - the stick insect. The importance of neural information transfer among the legs is nicely demonstrated. Furthermore, the findings show that spatial and temporal coordination of leg movements are obtained independently, with the former rather than the latter being affected by the experimental manipulations. Overall this offers yet another example of the importance of proprioceptive feedback in the generation of a coordinated gait.

Insects search for and find the source of a desired odor as a basic locomotion behavior, such as when searching for food or a mate. This behavior offers an interesting research topic in regard to motor-cognitive function: how is such successful locomotion achieved under conditions of turbulent odor plumes, utilizing the insects' small number of neurons. Hernandez-Reyes et al. (2021) measured the behavior of moths using a virtual reality system that presents accurate and reproducible odor stimuli by using blue light and optogenetic moths. Their results demonstrate that behavioral variations have a higher probability of obtaining more information than "programmed behaviors" (i.e., reactive, exploitative behaviors), suggesting that silk moths incorporate some stochasticity into their behavior in order to balance the exploration and exploitation of the acquired information.

Moving from invertebrate to vertebrate models, Donatelli et al. (2021) utilize the unique model of the bluespot salamander to

demonstrate the robustness of locomotion patterns. Animals adjust their gait to a changing environment. In addition to adjusting to heterogeneities in their environment, animals can adjust their locomotion to contend with damage to appendages (tail or legs). This is ubiquitous in salamanders, which have the potential to regenerate missing limbs, tails, and even parts of the spinal cord in some species. As the authors suggest, understanding the changes that take place in locomotion kinematics as a lost limb regrows, may provide important insights to assist roboticists working on terrestrial as well as amphibious locomotion.

As noted above, one level of control, allowing consistency and also adaptability in inter-limb coordination; is the muscular system. Camardella et al. (2021) visit the cutting edge technique of myo-control: a type of brain-machine interface in which recorded electromyographic (EMG) signals are utilized in a computed control signal that drives robots or machines (e.g., limb prostheses control). For such applications, there is much interest in characterizing the minimum muscle set, termed an optimal set, that preserves performance and demonstrates a high consistency of motor activity. Such an optimal set is described as considering the best trade-off in terms of myo-control performance and muscle set size.

3 ROBOTIC INTER-LIMB COORDINATION

To date, robotics research has made substantial progress in reproducing (adaptive) inter-limb coordination inspired by animal locomotion. The contributions to this special issue present various methods of control (including central and local (neural) control with sensory feedback) that have been investigated and developed, as well as validated on different animal-like robots (**Figure 1**, Right).

Starting with a snake-like robot, Inazawa et al. (2021) proposed a unified model-based method for designing the motion of a robot to deal with complicated pipe structures. The central control with a model considering slippage between robot and pipe coordinates the connected pitch-axis and yaw-axis joints of the robot body. It enables the robot to perform various maneuvers to deal with multiple pipe structures and obstacles such as junctions, bends, changes in pipe diameter, shears, and blockages.

Rather than employing system models for inter-limb coordination and locomotion generation, Owaki et al. (2021) proposed a model-free method for simulated bipedal robot locomotion. Their method is based on the Tegotae concept, which describes how well a perceived reaction based on sensory feedback matches the expectation (i.e., an intended motor command). The control method's implementation makes use of vertical and horizontal ground reaction forces (GRF), as well as decentralized local control circuits, to allow the robot to walk on both flat and uneven terrains while adapting to environmental changes.

In addition to the snake and biped robots, several studies in this special issue employ quadruped robots as their experimental platforms in order to investigate and develop control mechanisms

for adaptive inter-limb coordination. Sun et al. (2021) employed a simulated quadruped robot to investigate two classical adaptive inter-limb coordination mechanisms: continuous phase modulation (also known as Tegotae) and phase resetting. These mechanisms use decoupled neural central pattern generators (CPGs) or local neural control circuits with sensory feedback, such as GRFs, to generate self-organized robot locomotion. These authors compared the characteristics of the two mechanisms by observing the CPG phase convergence processes at different control parameter values. They also investigate the robustness of the mechanisms under various unexpected conditions, such as noisy feedback, leg motor damage, and carrying a load, in a simulated quadruped robot. From their findings, they suggest a strategy for the appropriate selection of adaptive inter-limb coordination mechanisms under different conditions and for the optimal setting of the control parameter values in order to enhance the control performance. Aoi et al. (2021) demonstrated the use of local CPG-based control with phase resetting as well as slow and fast adaptation mechanisms for quadrupedal locomotion on a split-belt treadmill. For the implementation, while the CPG control, modulated by phase resetting based on touch sensor signals (i.e., discrete GRFs) and desired (predicted) touchdown timing, forms adaptive inter-limb coordination, fast adaptation induces asymmetric inter-limb coordination following a change of the treadmill speed condition and slow adaptation slowly reduces or balances the asymmetry following fast adaptation. This leads to stable quadrupedal split-belt treadmill walking. Saputra et al. (2021) present central CPG-based control with multiple sensory feedback provided by exteroceptors (i.e., quad-composite time-of-flight and dual-laser range finder sensors), for detecting the surroundings and interoceptors (i.e., force and touch sensors and an inertial measurement unit (IMU)). Using this control approach, they are able to generate versatile locomotion and short-term adaptation for a cat-like quadruped robot. The robot can, consequently, walk on natural terrain, walk with a leg malfunction, avoid a sudden obstacle, and climb a vertical ladder.

Robust robot state estimation and sensory event mistiming detection are important issues for adaptive inter-limb coordination. Accordingly, Calandra et al. (2021) proposed a data-driven method using reservoir computing for translating local proprioceptive feedback, acquired at the leg joints of a simulated quadruped robot, into global exteroceptive information, which include both GRFs at the level of the different legs and information about the type of terrain traversed by the robot. This mechanism enables the robot to effectively estimate its walking state (i.e., estimating the GRFs from joint torques) and classify terrains for adaptive locomotion. Szadkowski et al. (2021) proposed a novel self-supervised method based on dynamic Hebbian-like rules for learning sensory event mistiming detection during robot walking. The sensory mistiming detector is integrated into central CPG-based control. Consequently, the CPG-based control engages with inter-limb coordination for gait generation while the detector engages with adaptive intra-limb coordination by triggering the elevator reflex, used to avoid an obstacle, and the search reflex,

used to grasp at a missed foothold. This control method enables a hexapod robot to negotiate an unstructured and slippery subterranean environment. As well demonstrated by the biological studies in **Section 1**, yet far from fully resolved, insects excel in highly variable limb coordination patterns. Fukuhara et al. (2022) address this gap by proposing a simple mathematical model for the mechanism of variable inter-limb coordination in insect locomotion. Their model, largely based on active load sensing, was tested in simulation experiments and shown to entitle a hexapod robot with a range of typical gait patterns and improved adaptability in different locomotion speeds.

The salamander constitutes a model animal for focusing on the following two issues, representing an evolutionary process of moving from water to land: 1) versatile behavior generation against a changing environment, based on CPGs coordinated by both descending signals and sensory feedback; and 2) body-limb coordination, i.e., coordination between undulatory movements of the body and leg movements based on the salamander's characteristic morphology. Using a robot, Knüsel et al. (2020) were able to reproduce the five motor behaviors observed in salamanders: swimming, struggling, forward underwater stepping, and forward and backward terrestrial stepping. A mathematical model is presented that allows the robot to switch between various motor patterns using a neural circuit with descending brain signals and proprioceptive feedback as input. The results suggest that a single flexible neural circuit contributes to the generation of various animal behaviors when modulated by descending drive and sensory feedback. When walking on level ground, the salamander coordinates not only its legs but also other body parts such as the trunk, head, and tail, i.e., body-limb coordination, to generate the standing and traveling waves of lateral bending depending on the walking speed and stride length. Suzuki et al. (2021) showed that a CPG-based controller with four feedback rules, limb-to-limb, limb-to-body, body-to-limb, and body-to-body, without assuming any inter-leg coupling is able to reproduce various walking patterns, suggesting that sensory feedback plays a crucial role in flexible body-limb coordination during sprawling quadruped locomotion.

Quadruped robots possess the minimum number of legs required for postural stability; hence, it is also a useful platform to discuss the effects of a lower level of control and of biomechanics, e.g., spinal reflexes or body softness, due to the high postural stability and relative simplicity of leg coordination control. Tanikawa et al. (2021) focused on spinal reflex, which is essential for quadruped walking, and experimentally verified the reflex mechanism using a robotic platform that mimics legs with high back-drivability and Hill-type muscle properties. Their findings suggest that the basic structure of the reflex circuit is that of the reciprocal coupling between extensor muscles via excitatory neural pathways, followed by the prolongation of the stance phase caused by the reciprocal excitatory reflex contributing greatly to the generation of a steady gait. Masuda et al. (2021) showed the feasibility of generating various quadruped gaits using only actuators and body dynamics. Although the developed robot has no sensors or

microprocessors, its motors were able to autonomously adjust the phase according to the leg dynamics and its locomotion eventually converges to a stable gait pattern. Furthermore, by increasing the input voltage to the motors, the robot is able to reproduce pacing, bounding, rotary galloping, and half-bound-like lateral galloping. Tanaka et al. (2021) developed a quadruped robot driven by McKibben pneumatic artificial muscles and verified its turning motion. In particular, the experiments demonstrate that the softness of legs leads to adaptive changes in inter-leg coordination and enables the robot to turn dynamically, merely by changing the phase difference between the left and right hind legs. Their results suggest that a soft body can simplify the design of the controller for leg coordination in locomotion even for complex tasks.

Hopping motion offers an effective test-bed for theoretical approaches and systematic verification of energy optimization. The simple mechanical structure and constrained one-dimensional vertical motion allows simulation and robotic platform to uncover the contributing mechanisms and control schemes. Zamboni et al. (2021) investigated optimal energy efficiency of Tegotae control based on proprioceptive feedback previously used in bipedal, quadrupedal, and hexapod robot locomotion in the context of embodiment. For this purpose, simple one- and two-legged mechanical hopping robot simulation were conducted. Their results suggested that the Tegotae-based approach combined with a reflex-like actuation generate optimal energy-efficient motion as well as environmental adaptability and gait transitions. Discrete impact with the ground is a major factor of instability during legged locomotion due to their unknown timing and impact magnitude. Ashtiani et al. (2021) examined the effect of the combination of passive and active compliance on leg control during the landing event. Simulation and experiment with a single leg robot, followed by simulation with a quadruped robot were conducted. Their results showed that hybrid passive/active control was robust against feedback delays, comparable to the sensory-motor delays of neuromuscular systems in animals.

4 CONCLUDING REMARKS

In this research topic, we have brought together studies that provide an overview of recent developments in biological and robotic inter-limb coordination. Since inter-limb coordination constitutes the fundamental basis of motion control, the studies covered range from high-level cognitive functions to CPGs and spinal reflexes, as well as biomechanics and interaction with the environment. In terms of animal species, the studies in biological inter-leg coordination incorporate insects, salamanders, and human muscle control. The robotic inter-leg coordination studies, center on quadrupedal robots that display posture stability and controllability, and include monopod, biped, salamander, hexapod, and even snake locomotion. A birds-eye-view of the overall research topic reveals that “modeling,” including abstract mathematical description and physical implementation, is a key approach for discussing and understanding inter-leg coordination mechanisms in a unified manner encompassing biology and engineering. In addition,

recent pioneering technologies, such as animal cyborgs that externally control the behavioral output of animals, and Virtual Reality (VR) or Augmented Reality (AR) systems that externally manipulate the sensory input to animals, are expected to lead to further understanding of the leg coordination mechanisms in animals. We hope that this research topic devoted to biological and robotic inter-limb coordination will help researchers to enter novel research areas related to leg coordination and that novel research results will ensue, based on the further integration of biology and robotics.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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FUNDING

PM acknowledges funding by the Human Frontier Science Program under grant agreement no. RGP0002/2017 and from Vidyasirimedhi Institute of Science and Technology (VISTEC)-research funding (Thailand) on Bio-inspired Robotics. DO acknowledges the support of JSPS KAKENHI (grant numbers JP18H03167, JP19K22855, and JP20H04260) and Grant-in-Aid for Scientific Research on Innovative Areas “Science of Soft Robot” project (JP21H00317).

ACKNOWLEDGMENTS

We thank all authors contributing with their work to this Research Topic.

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Reproducing Five Motor Behaviors in a Salamander Robot With Virtual Muscles and a Distributed CPG Controller Regulated by Drive Signals and Proprioceptive Feedback

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OPEN ACCESS

Edited by:

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Received: 09 September 2020

Accepted: 10 November 2020

Published: 23 December 2020

Citation:

Knüsel J, Crespi A, Cabelguen J-M, Ijspeert AJ and Ryczko D (2020) Reproducing Five Motor Behaviors in a Salamander Robot With Virtual Muscles and a Distributed CPG Controller Regulated by Drive Signals and Proprioceptive Feedback. *Front. Neurobot.* 14:604426. doi: 10.3389/fnbot.2020.604426

Diverse locomotor behaviors emerge from the interactions between the spinal central pattern generator (CPG), descending brain signals and sensory feedback. Salamander motor behaviors include swimming, struggling, forward underwater stepping, and forward and backward terrestrial stepping. Electromyographic and kinematic recordings of the trunk show that each of these five behaviors is characterized by specific patterns of muscle activation and body curvature. Electrophysiological recordings in isolated spinal cords show even more diverse patterns of activity. Using numerical modeling and robotics, we explored the mechanisms through which descending brain signals and proprioceptive feedback could take advantage of the flexibility of the spinal CPG to generate different motor patterns. Adapting a previous CPG model based on abstract oscillators, we propose a model that reproduces the features of spinal cord recordings: the diversity of motor patterns, the correlation between phase lags and cycle frequencies, and the spontaneous switches between slow and fast rhythms. The five salamander behaviors were reproduced by connecting the CPG model to a mechanical simulation of the salamander with virtual muscles and local proprioceptive feedback. The main results were validated on a robot. A distributed controller was used to obtain the fast control loops necessary for implementing the virtual muscles. The distributed control is demonstrated in an experiment where the robot splits into multiple functional parts. The five salamander behaviors were emulated by regulating the CPG with two descending drives. Reproducing the kinematics of backward stepping and struggling however required stronger muscle contractions. The passive oscillations observed in the salamander's tail during forward underwater stepping could be reproduced using a third descending drive of zero to the tail oscillators. This reduced the drag on the body in our hydrodynamic simulation. We explored the effect of local proprioceptive feedback

during swimming and forward terrestrial stepping. We found that feedback could replace or reduce the need for different drives in both cases. It also reduced the variability of intersegmental phase lags toward values appropriate for locomotion. Our work suggests that different motor behaviors do not require different CPG circuits: a single circuit can produce various behaviors when modulated by descending drive and sensory feedback.

Keywords: central pattern generator (CPG), proprioceptive sensory feedback, descending drive, distributed control, salamander, locomotion, numerical modeling, robotics

INTRODUCTION

Many motor behaviors in animals require coordinated rhythmic activation of multiple muscles. Neural networks capable of producing such activity patterns without rhythmic input from other networks or from sensory feedback are called central pattern generators (CPGs). It has been shown that CPGs in the spinal cord underlie locomotion in many vertebrate species (for review, Grillner and El Manira, 2020). Drive signals descending from brain neurons control locomotion initiation, speed and gait transitions (Brocard et al., 2010; Capelli et al., 2017; Caggiano et al., 2018; Josset et al., 2018) and steering movements (Fagerstedt et al., 2001; Ryczko et al., 2016b; Cregg et al., 2020). Sensory feedback plays an important role in modulating the CPG activity to adapt the locomotor pattern to the environment (e.g., Wyart et al., 2009; Akay et al., 2014; Hubbard et al., 2016; Knafo et al., 2017). These feedback signals depend on the interactions between the neural networks, the mechanical properties of the body and the environment, making it a challenge to fully understand the operation of the CPG even at a high level of abstraction. Numerical models of the complete system can be used to investigate the effect of sensory feedback on the CPG, but some aspects such as hydrodynamic and friction forces are difficult to simulate reliably. Robots are thus useful to validate simulation results in the real world, with real physics. Here, we used numerical simulations and robotics to investigate the generation of different behaviors in the salamander, an interesting animal model as it can move underwater and on ground (Ryczko et al., 2020). In particular, we addressed the following questions:

1. Can different motor behaviors be generated by a single spinal CPG circuit as opposed to requiring several dedicated CPG circuits?
2. What are the roles of descending drives in generating these different motor behaviors, and how many independent drives are necessary?
3. What is the potential role of sensory feedback in shaping the patterns and in reducing the variability of CPG activity observed in isolated spinal cords?

We used the *Salamandra robotica II* robot (Crespi et al., 2013) driven by a spinal CPG model and virtual muscles to reproduce the five salamander behaviors documented in Ryczko et al. (2015): forward swimming, forward and backward terrestrial stepping, forward underwater

stepping, and struggling. To match the biological data from that study, we focused on reproducing the patterns of muscle activation and body curvature along the body axis.

For the CPG, our starting point was the abstract oscillator model of Ijspeert et al. (2007), with modifications to allow for the flexible coordination of limb and axial network activities (Knüsel et al., 2013). This flexibility is required to reproduce the observations from Ryczko et al. (2015). Here, we extended the model to comprise 25 segments and introduced random parameters to account for the differences between individuals. The main hypotheses are the following: (1) limb oscillators project only to the axial oscillators close to the corresponding girdles; (2) couplings between axial oscillators are stronger in the head-to-tail direction; (3) limb oscillators saturate¹ at lower excitatory drives than axial oscillators; (4) hindlimb oscillators are intrinsically slower than forelimb oscillators. Hypotheses 1 and 2 make the model's intersegmental phase lag flexible and controllable (Knüsel et al., 2013). Hypotheses 3 and 4 allow the model to reproduce the distribution of phase lags of recordings *in vitro*.

We modeled the biomechanical properties of the body axis using virtual muscles that determine the torques of the axial joints based on the CPG activity and the current joint position and velocity (Ekeberg, 1993). The joint positions were also used for proprioceptive feedback, simulating stretch receptors that send phasic inputs to the local CPG segments. The virtual muscle model requires a small time step for stability and accuracy of the numerical integration, which is challenging to achieve with eight joints given the limited bandwidth and processing power of the robotic platform. We solved this difficulty by distributing the computation of the CPG and muscle models in the eight active modules, so that each module calculates the part of the model that controls its own joint. The modules use peer-to-peer communication, such that splitting the robot results in several functional pieces (unlike most robots).

The isolated CPG model was tuned to reproduce the diversity of coordination patterns observed in isolated spinal cords. To determine values for the proprioceptive feedback and virtual muscle parameters, we systematically explored the parameter space using a mechanical simulation of the robot: Using the same tonic drive for all oscillators, we identified parameter values

¹When the excitatory inputs to the spinal cord increase beyond a certain level, CPG units saturate: they cease to produce rhythmic output. In the model, this is implemented as a decrease of oscillation amplitude toward zero (see the left part of Figure 3 for an illustration).

that allowed feedback to have a positive effect on swimming speed while maintaining stable CPG rhythms. We then attempted to reproduce the five salamander behaviors without sensory feedback, by varying the tonic drive sent to different parts of the CPG, adapting other model parameters when necessary. Further simulations were made to investigate the effect of proprioceptive feedback during swimming and forward terrestrial stepping. Finally, we used the real robot to validate simulation results. Each behavior was reproduced on the robot using different “individuals” from the family of models used in modeling isolated spinal cords, to check the robustness of the control architecture to individual variations.

MOTOR CONTROL IN SALAMANDERS

The salamander spinal CPG produces the rhythmic movements of the limbs (Cheng et al., 1998; Lavrov and Cheng, 2004; Ijspeert et al., 2007), trunk (Delvolvé et al., 1999; Branchereau et al., 2000; Ryczko et al., 2010), and tail (Charrier and Cabelguen, 2013). This spinal circuitry is controlled by the brainstem in salamanders as in other vertebrates (for review, see Ryczko and Dubuc, 2013). Stimulation of the salamander mesencephalic locomotor region elicits stepping at low stimulation intensities, whereas swimming requires higher intensities (Cabelguen et al., 2003). These descending commands are carried to the spinal cord by reticulospinal neurons (Ryczko et al., 2016a, see also Ryczko et al., 2020 for a recent review).

The coordination of muscles along the body axis plays an important role in salamander locomotion, to generate thrust during swimming and to maximize the stride length during terrestrial stepping (Delvolvé et al., 1997). So far, at least five salamander motor behaviors have been characterized: forward swimming, forward and backward terrestrial stepping, forward underwater stepping, and struggling (Ryczko et al., 2015). Forward terrestrial stepping generally takes the form of a walking trot, but lateral sequence walks have also been observed (reviewed in Chevallier et al., 2008, see also Ashley-Ross et al., 2009). During forward underwater stepping, the salamander progresses at the bottom of water, with periods of suspension in water without ground contact. Struggling refers to the behavior of the salamander when it is firmly grasped at the pelvic girdle. Electromyographic (EMG) recordings of multiple segments in the salamander mid-trunk show that each of the five behaviors is characterized by a specific pattern of muscle activation, in terms of cycle frequencies and intersegmental phase lags: (1) rostrocaudal waves occur during forward swimming and, with lower cycle frequencies, during backward terrestrial stepping; (2) slow caudorostral waves occur during struggling; (3) standing waves are stable during forward terrestrial stepping but more variable during forward underwater stepping (Ryczko et al., 2015).

Kinematic recordings show similar patterns of trunk curvature. However, kinematic intersegmental phase lags are significantly larger during forward terrestrial stepping and swimming (Frolich and Biewener, 1992; Ryczko et al., 2015). In other words, the delay between muscle activation and body

bending gets larger toward the tail. This suggests that the mechanical properties of body tissues play an important role during these behaviors, as suggested by a lamprey modeling study (Tytell et al., 2010).

The increasing EMG-mechanical delay toward the tail also suggests that proprioceptive feedback might have a different effect at various points along the body axis. Salamanders are known to have sensory cells that generate proprioceptive information relative to axial movements: The skin contains mechano-sensitive Merkel cells (Scott et al., 1981; Diamond et al., 1986), and some cells in the spinal cord are morphologically similar to the mechano-sensitive “edge cells” (Schroeder and Egar, 1990) that encode body bending in lampreys (Grillner et al., 1982, 1984). They also have cerebrospinal fluid contacting neurons (Kolmer-Agduhr cells, Harper and Roberts, 1993), which are active during body bending in zebrafish (Böhm et al., 2016) and provide mechanosensory input to the swimming CPG (Wyart et al., 2009; Hubbard et al., 2016; Orts-Del’Immagine et al., 2020, see also Jalalvand et al., 2016 in lampreys). The limbs are another source of proprioceptive feedback, as they contain fibers that respond to stretch similarly to muscle spindles in other species (Bone et al., 1976).

According to *in vitro* recordings of the salamander spinal cord, the isolated CPG can generate stable patterns for the three types of axial waves (caudorostral, standing and rostrocaudal waves), with occasional switches between two wave types (Ryczko et al., 2015). The intersegmental phase lags generated by the isolated CPG cover a greater range than those observed in EMG recording (-12.6 to $+12.4\%$ of a cycle duration for recordings *in vitro*, and -4.8 to $+6.4\%$ for EMG recordings), with a distribution showing three peaks centered on -9.6 , -1.0 , and $+6.6\%$. The salamander CPG thus provides a flexible ground onto which sensory feedback and descending drives could act to influence the spinal motor output.

RELATED MODELING WORK

Previous studies have modeled the CPG components using abstract oscillators (Ijspeert et al., 2005, 2007; Knüsel et al., 2013; Yin et al., 2016), single bursting neurons (Liu et al., 2018, 2020), integrate-and-fire neurons (Ijspeert, 2001; Bem et al., 2003; Harischandra et al., 2011; Knüsel et al., 2013) and detailed networks of three compartment Hodgkin-Huxley neurons (Bicanski et al., 2013).

The mechanical body of the salamander has been modeled with varying accuracy. Many models include four joints between the girdles and a single degree of freedom (DOF) per limb (Ijspeert, 2001; Ijspeert et al., 2005, 2007; Suzuki et al., 2019a) or three DOFs per limb (Harischandra et al., 2010, 2011; Liu et al., 2018, 2020). The simplest model has one of each (Yin et al., 2016), while other models have one joint between the girdles and two DOFs per limb (Zhong et al., 2018; Suzuki et al., 2019b). Bem et al. (2003) have modeled the swimming salamander as a chain of ten links, corresponding roughly to three trunk joints and no limbs. The most accurate model has five joints between the girdles and four DOFs in each limb (Karakasiliotis et al., 2016; Horvat

and Ijspeert, 2017; Horvat et al., 2017). Mechanical properties (damping and elasticity) of the body tissues were included in the muscle models used by Ijspeert (2001; 2005) Bem et al. (2003), Harischandra et al. (2010, 2011), and Liu et al. (2018, 2020), and in the controller of Suzuki et al. (2019b).

The effect of sensory feedback on the activity of the salamander CPG has only been investigated in simulation (Bem et al., 2003; Ijspeert et al., 2005; Harischandra et al., 2011; Liu et al., 2020). The role of sensory feedback in body-limb coordination has also been investigated using controllers without CPG, both in simulations (Horvat and Ijspeert, 2017) and with a robot (Suzuki et al., 2019a).

Most studies have focused on the reproduction of forward terrestrial stepping (with a walking and/or trotting gait), swimming, transitions between these behaviors, and turning. The exceptions are the works of Karakasiliotis et al. (2016) which reproduced underwater stepping in addition to swimming and forward terrestrial stepping (though using predefined joint trajectories rather than a CPG) and Liu et al. (2018) which reproduced backward terrestrial stepping in addition to forward terrestrial stepping (using dedicated networks for each gait).

Table 1 summarizes the particularities of past studies and how they compare to the present one. To our knowledge, the present

TABLE 1 | Related studies.

	CPG	Trunk joints	Limb DOFs	Robot	Biomech	Proprio. feedback		Force feedback		Behaviors					Turning	Transition
						Trunk	Limbs	Trunk	Limbs	Swim	Walk	Trot	Back step	U.w. step		
Bem et al. (2003)	IF	•••														
Bicanski et al. (2013)	HH															
Knüsel et al. (2013)	AO+IF															
Ijspeert (2001)	IF	•••••	•													
Ijspeert et al. (2005)	AO	•••••	•													
Ijspeert et al. (2007)	AO	•••••	•													
Harischandra et al. (2010)		•••••	••••													
Harischandra IF et al. (2011)		•••••	••••													
Yin et al. (2016)	AO	•	•													
Karakasiliotis et al. (2016)		••••••	•••••													
Horvat et al. (2017)		••••••	•••••													
Horvat and Ijspeert (2017)		••••••	•••••													
Liu et al. (2018)	BN	•••••	••••													
Zhong et al. (2018)		•	••													
Suzuki et al. (2019a)		•••••	•													
Suzuki et al. (2019b)	AO	•	••													
Liu et al. (2020)	BN	•••••	••••													
This study	AO	•••••	•													

CPG: IF, Integrate and fire; HH, Hodgkin-Huxley; AO, Abstract oscillators; BN, Bursting neurons. Trunk joints: counting joints between girdles (a joint on the girdle counts as a half). DOFs: degrees of freedom. The number of black dots represents the number of trunk joints and limb degrees of freedom respectively. Biomech: mechanical properties from body tissues such as muscles. Walk: forward terrestrial stepping with lateral sequence walking. Trot: forward terrestrial stepping with walking trot. Colors indicate different groups of model features: mechanical model (green), sensory feedback modalities (orange), behaviors (gray).

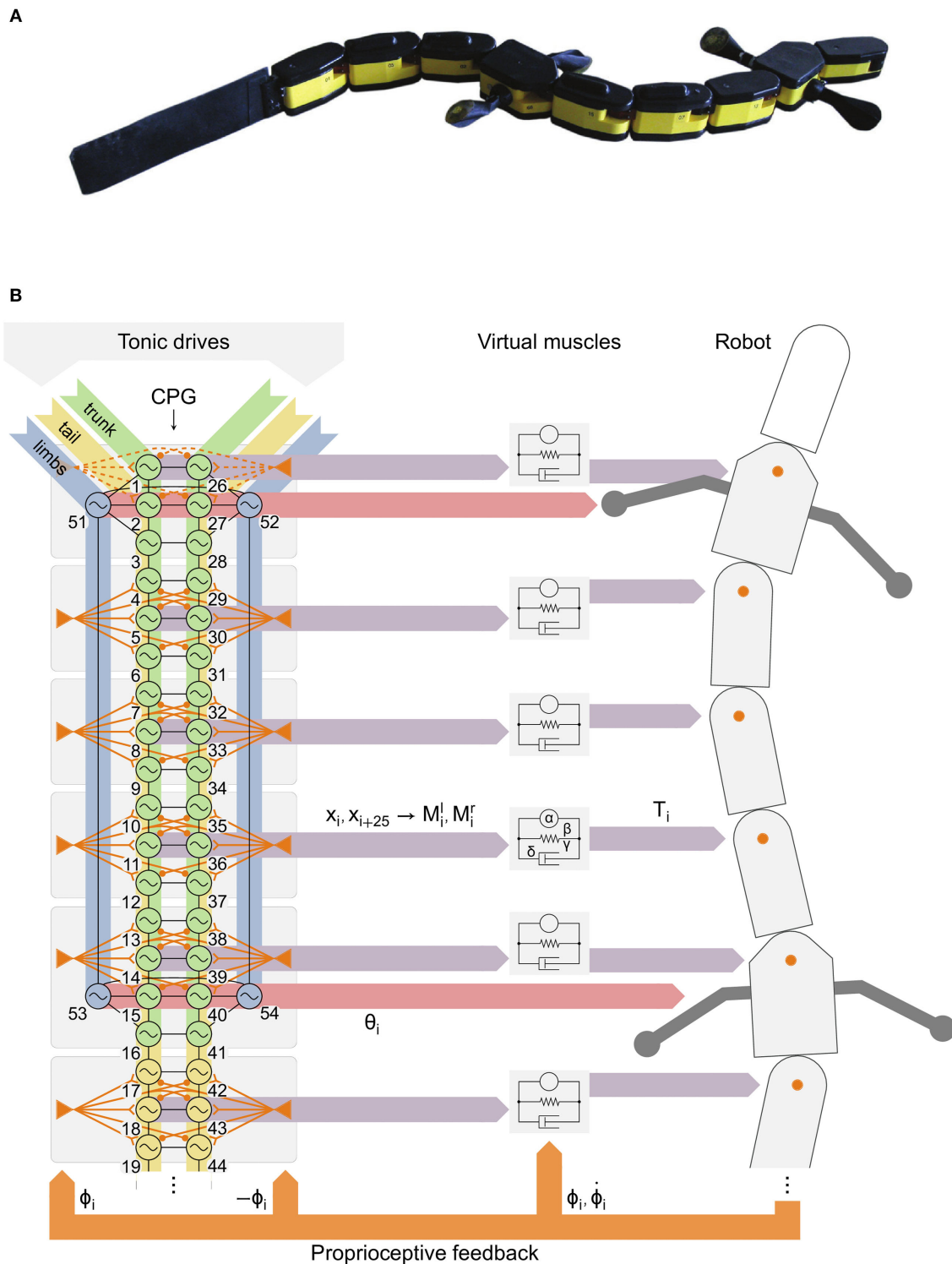


FIGURE 1 | Robot with distributed controller with the spinal central pattern generator (CPG) model, axial proprioceptive feedback, descending drives and virtual muscles. **(A)** The robot *Salamandra robotica II*. **(B)** The axial CPG was divided in 8 groups (gray rectangles) to distribute the computations in the 8 robot modules with active joints. *Left*: tonic descending drives are applied to limb (blue), trunk (green) and tail (yellow) oscillators. Virtual stretch receptors (orange triangles) project to the 3 nearest segments with opposite ipsilateral (excitatory) and contralateral (inhibitory) weights. Feedback from the neck joint (dashed orange) was disabled for robot experiments (see Results). Black lines indicate bidirectional couplings between oscillators (see **Figure 2A**). *Middle*: 2 outputs x_i, x_{i+25} of each group (purple horizontal arrows) govern left (l) and right (r) muscle activities M_i^l, M_i^r from which the muscle model calculates an output torque T_i . *Right*: the torque T_i is applied at each axial joint (orange circles). The joint position ϕ_i and velocity $\dot{\phi}_i$ are fed back (orange arrows) to the muscles. Virtual stretch receptors only receive ϕ_i . The phases θ_i of limb oscillators (red horizontal arrows) determine the limb positions.

work is the first to incorporate biomechanical properties and proprioceptive sensory feedback in a real salamander robot.

MATERIALS AND METHODS

CPG Model

The model was developed using the Codyn framework and exported to C code to run on the robot microcontrollers. Only the 25 most rostral axial segments (each comprising 1 left and 1 right hemisegments) are modeled out of the 40 segments that salamanders typically have (for review see, Chevallier et al., 2008). Four additional oscillators control the limbs. The 25 axial segments control the active part of the robot. The caudal half of the robot tail is a passive, flexible caudal fin (**Figure 1A**). Each axial hemisegmental oscillator and each limb oscillator is modeled as a phase oscillator with controllable amplitude, and the connections between oscillators are functions of the phase difference between sender and receiver:

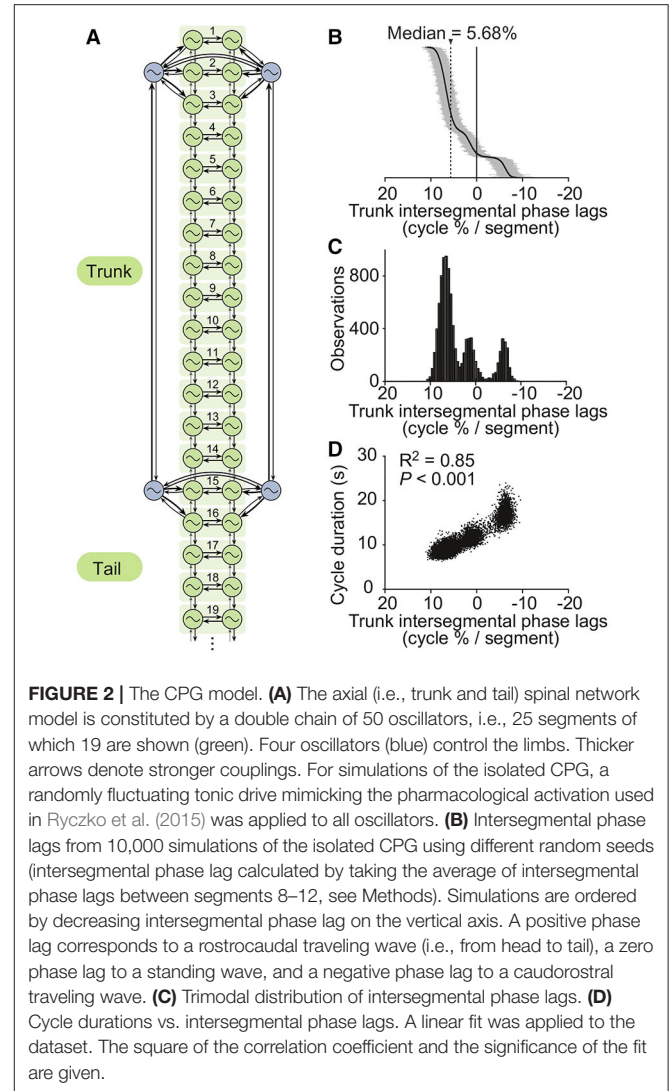
$$\begin{aligned}\dot{\theta}_i &= 2\pi v_i + \sum_j r_j w_{ij} \sin(\theta_j - \theta_i - \varphi_{ij}) - \frac{s_i}{r_i} \sin \theta_i \\ \dot{r}_i &= a(R_i - r_i) + s_i \cos \theta_i \\ x_i &= r_i(1 + \cos \theta_i) \\ v_i &= d_i e_i \\ R_i &= d_i P(d_i, d_i^{th})\end{aligned}$$

A positive output x_i (which determines the muscle activation) is calculated from the instantaneous phase θ_i and amplitude r_i . The intrinsic frequency v_i is proportional to the oscillator excitability e_i and to a drive d_i that represents the excitation from descending drives. The intrinsic amplitude R_i increases with increasing drive until it approaches a saturation threshold d_i^{th} after which it decreases progressively to zero due to the sigmoid function $P(d, d^{th}) = \frac{1}{1 + e^{b(d - d^{th})}}$ with b the saturation rate. The excitability e_i determines the intrinsic frequency of a particular oscillator as a function of the external drive. The excitability of each oscillator is drawn from a Gaussian distribution with different means for forelimb, hindlimb and axial oscillators. The saturation thresholds of the forelimbs, hindlimbs and axial network are also drawn from a Gaussian distribution with different means for the axial and limb networks. The coupling from oscillator j to oscillator i is characterized by a strength w_{ij} and phase bias φ_{ij} . The gain a determines the speed of convergence for the amplitude. The symbol s_i represents the feedback signal from simulated stretch receptors (see below). The terms $-\frac{s_i}{r_i} \sin \theta_i$ and $s_i \cos \theta_i$ are the polar coordinate equivalent of adding s_i to the derivative $\dot{x}$ of an oscillator in Cartesian coordinates (see Supplementary Materials for the derivation).

The network connectivity is described in **Figure 2A** and **Table 2**. Other parameter values are provided in **Tables 3, 4**.

Simulations of the Isolated CPG

For simulations of *in vitro* electrophysiological recordings of the isolated salamander spinal cord reported in Ryczko et al. (2015), the same drive $d_i = d$ was used for all oscillators



to represent a tonic pharmacological stimulation, with small fluctuations over time added in the form of a mean reverting random walk: $\dot{d} = c(d_0 - d) \pm \sigma$ with d_0 the drive picked from a Gaussian distribution, c a convergence factor, and $\pm \sigma$ a random process yielding positive and negative steps with equal probability. Multiple simulations were performed with different random seeds to reflect the diversity of coordination patterns observed in individual spinal cord preparations.

Muscle Model

A linear spring-damper model with variable stiffness (Ekeberg, 1993) was used to model a pair of antagonist muscles and calculate the resulting torque at each axial joint (**Figure 1B**):

$$T_i = \alpha (M_i^l - M_i^r) - \beta (M_i^l + M_i^r + \gamma) \phi_i - \delta \dot{\phi}_i$$

An active term is calculated from the difference of the left and right muscle activations M_i^l and M_i^r multiplied by a gain α . A stiffness term is calculated from the muscle activities, the tonic

TABLE 2 | CPG coupling parameters.

Coupling type	Strength w_{ij}	Phase bias φ_{ij} (rad.)
Intersegmental, rostrocaudal	5	$0.066 \cdot 2\pi$
Intersegmental, caudorostral	1	$-0.066 \cdot 2\pi$
Intrasegmental, lateral	10	π
Interlimb, rostrocaudal	3	π
Interlimb, caudorostral	30	π
Interlimb, lateral	10	π
Limb to axial oscillators	30	4 (BTS: 5.5°)
Axial to limb oscillators	2.5	-4 (BTS: -5.5°)

*BTS, backward terrestrial stepping.

TABLE 3 | Other CPG parameters.

Name	Symbol	Value (mean $\pm$ SD)
Amplitude convergence factor	a	5
Saturation rate	b	500
Drive random walk convergence factor	c	0.001 (<i>in vitro</i>) 0 (<i>in vivo</i>)
Drive random walk step size	σ	0.03 (<i>in vitro</i>) 0 (<i>in vivo</i>)
Drive	d_i	See Table 4
Saturation threshold	d_i^{th}	0.3 (axis, <i>in vitro</i>) 3 (axis, <i>in vivo</i>) 0.09 $\pm$ 0.02 (limbs, <i>in vitro</i>) 1.27 $\pm$ 0.02 (limbs, <i>in vivo</i>)
Excitability	e_i	1.1 $\pm$ 0.07 (axis) 0.8 $\pm$ 0.05 (forelimbs) 0.5 $\pm$ 0.03 (hindlimbs)
Axial proprioceptive feedback, ipsilateral	w^{ipsi}	See Table 4
Axial proprioceptive feedback, contralateral	w^{contra}	$-w^{ipsi}$

stiffness γ , a stiffness gain β and the joint angle ϕ_i . A damping term is calculated from a damping constant δ and the joint angular velocity $\dot{\phi}_i$. Parameter values are given in **Table 5**.

In simulations, a delay of 10 ms was introduced between the CPG outputs x_i, x_{i+25} and the corresponding muscle activations M_i^l, M_i^r , respectively, as a minimum to account for the muscle activation dynamics. This delay was not necessary in robot experiments since the motor torque controller already introduces a larger delay of the order of 50 ms, which is consistent with the reported range (50 ms to 1 s) of the low-pass filter properties of muscle contraction (Partridge, 1965).

Limb Joints

For the limbs, the oscillator phase θ_i is used directly as a representation of the desired position, with a piece-wise linear transfer function that modulates the swing and stance rotation speeds such as to obtain a duty factor of 77% (Ashley-Ross and Lauder, 1997; Ashley-Ross et al., 2009). For backward terrestrial

stepping the direction of limb rotation was inverted by using $-\theta_i$ instead of θ_i .

Sensory Feedback

Proprioceptive feedback signals s_i are derived from the joint angles ϕ_i by simulating the activity of stretch receptors: $s_i = w^{ipsi}s_i^{ipsi} + w^{contra}s_i^{contra}$, with s_i^{ipsi} and s_i^{contra} the positive part of ϕ_i and $-\phi_i$, respectively, for the left side ($-\phi_i$ and ϕ_i for the right side), and w^{ipsi} and w^{contra} the feedback weights. Since the axial part of the CPG model has 25 segments (each containing 2 hemisegmental oscillators) and the robot only 8 active axial joints (**Figure 1B**), some mapping is necessary. The signal from each joint is sent to the 3 neighboring segments, while only the middle segment is used to drive the joint muscles (**Figure 1B**). This leaves segments 3 and 16 without feedback, which is reasonable since the amplitude of the body curvature is smallest at these positions in the animal (Karakasiliotis et al., 2013).

In some simulations, an additional term was added to the $\dot{\theta}_i$ equation for limb oscillators to represent excitatory proprioceptive feedback from the limbs, as used in a previous study (Harischandra et al., 2011). Here a simplified form was used:

$$\dot{\theta}_i = 2\pi v_i + \sum_j r_j w_{ij} \sin(\theta_j - \theta_i - \varphi_{ij}) + w^{limb} \max\left(0, 1 - \frac{|\phi_i - \phi_i^0|}{\frac{\pi}{2}}\right)$$

Here w^{limb} is the feedback weight, ϕ_i the joint angle of the robot rotational limb and ϕ_i^0 the angle at the transition from stance to swing. The feedback is maximal at the end of the stance and decreases linearly on either side until it reaches zero. The rate of decrease is such that the feedback is non-zero for half of the leg rotation. The value is always positive or zero, so this feedback term can only have an accelerating effect.

Mechanical Simulation

3D simulations of the robot were performed using the Webots 6 software (Cyberbotics, Switzerland), which is based on the Open Dynamics Engine (ODE, www.ode.org). The physics engine was extended with a hydrodynamics model that includes reactive and resistive forces (Porez et al., 2014). The passive tail fin was modeled as a chain of 10 small segments with passive stiffness. The physics was simulated with a time step of 0.5 ms. The robot controller used a time step of 1 ms, the minimum value supported by Webots. This was just too high for a stable simulation of the muscles, so the physics plugin was used to implement the muscle model and set the joint torques.

Robot Hardware

The robot *Salamandra robotica II* (Crespi et al., 2013) is made of a head module (9.6 cm long), 8 active modules (9.6 cm long each) and a 24.6 cm long, passive, flexible caudal fin (**Figure 1A**). This allowed the robot to approximately reach the tail length/total body length ratio of the real animal (around 0.5–0.6, see Ryczko et al., 2015). Each module actuates an axial joint with motion

TABLE 4 | Parameters regulating the CPG activity.

	Drives d_i			Feedback weights	
	Seg. 1–3	Seg. 4–25	Limbs	w_{psi}	w_{limb}
Robot experiments with 5 individuals (Figure 5)					
Swimming		1		10	0
Forward terrestrial stepping	0.60 ± 0.02		1.00 ± 0.04	0	0
Forward underwater stepping	0.42 ± 0.01		0.71 ± 0.03	0	0
Backward terrestrial stepping	0.23 ± 0.01		0.46 ± 0.02	0	0
Struggling	0.27 ± 0.01		0.38 ± 0.01	0	0
Other robot experiments					
Swimming without regulation (Supplementary Movie 1)		1		0	0
Swimming with differential drive (Supplementary Movie 2)	0.9		1	0	0
Forward terrestrial stepping with feedback (Figure 6E)		0.61	0.98	from –10 to 6	0
Simulations					
Isolated CPG (simulation of <i>in vitro</i> experiments) (Figures 2, 3)		0.1 ± 0.01		0	0
Swimming without regulation (Supplementary Figure 4A)		1.34		0	0
Swimming with differential drive (Supplementary Figure 4B)	1.03		1.34	0	0
Swimming with axial feedback (Supplementary Figures 4C,D)		1.34		21	0
Forward terrestrial stepping without regulation (Figure 6A)		0.98		0	0
Forward terrestrial stepping with differential drive (Figure 6B)		0.63	0.98	0	0
Forward terrestrial stepping with axial feedback (Figure 6C)		0.98		–0.65	0
Forward terrestrial stepping with limb feedback (Figure 6D)		0.98		0	3.7

Robot experiments used lower drives for swimming to stay in the robot operating range (see Results). Standard deviations for the drive reflect variations between the simulated individuals. Drive values are shown centered across two or three columns in cases where the same value was applied to the corresponding groups of oscillators.

TABLE 5 | Muscle parameters.

Name	Symbol	Value
Muscle active gain (N·m)	α	0.4 (BTS, ST: 4*) (simulation)
		0.5 (BTS, ST: 5*) (robot)
Muscle stiffness gain (N·m/rad)	β	1.2 (BTS, ST: 12*)
Muscle tonic stiffness (no unit)	γ	0.2
Muscle damping (N·m·s/rad)	δ	0.1

*BTS, backward terrestrial stepping; ST, struggling.

restricted to the horizontal plane; the two girdle modules also include rotational joints for the limbs. The entire robot measures 111 cm and weighs 2.48 kg. The robot modules have LEDs on the covers which were used to track the robot's motion with two Basler A622F video cameras (15 frames/s) to cover the whole track length (6 m) with an accuracy of ± 1 cm. The Supplemental Movies of the robot were captured with another camera at 15 or 30 frames/s. Two adaptations were made to the robot to reproduce the different behaviors. During forward underwater stepping, the buoyancy was adjusted by adding 72 g of lead in the head. This corresponds to +2.9% of the total robot weight, or + 41.8% of the normal weight of the head module (172 g). During struggling, tape was added under the feet to increase slipping, mirroring the conditions of the animal experiments (Ryczko et al., 2015).

Distributed Electronics and Control Software

The robot controller is distributed: each module reads the position and velocity of the local joint and computes the control loop for the corresponding part of the CPG and the joint's virtual muscles, with a time step of 10 ms. The numerical integration of CPG segments with floating-point operations required a modification to the hardware described by Crespi et al. (2013): the modules were upgraded to include an LPC2129 ARM7TDMI microcontroller running at 60 MHz, as already present in the head. Communications between modules are restricted to drive signals from the head and CPG couplings between adjacent modules, sent over the CAN bus running at 1 Mbps. The leg positions are set by PD controllers using the motor encoders. The axial torques are set by PI controllers using current sensing. The CPG state from each module was recorded by logging coupling and debug messages sent over the CAN bus. This logging was done on an external computer, by spying on the bus using long, thin wires attached to the caudal end of the robot. Two modifications were made to the distributed controller between the initial tests and the final version (see Results): (1) The numerical integration of the CPG was changed to estimate the phases θ_j and amplitudes r_j of coupling sources at the time of integration using a linear extrapolation of the values from the two latest CAN messages and their times of arrival (coupling terms are dropped entirely from the integration if the two previous CAN messages are older than 200 or 400 ms, respectively); (2) The phases and amplitudes were encoded in

CAN messages as 16-bit half-floats rather than 32-bit floats, such that coupling signals from a module to a particular neighbor would fit in a single message.

Selection of Parameter Values

The CPG parameters were hand-tuned to reproduce the distribution of intersegmental phase lags and cycle durations from *in vitro* recordings of isolated spinal cords (Ryczko et al., 2015). To emulate the motor behaviors displayed by the animal *in vivo*, the CPG model was subjected to higher excitatory drives which were tuned to reproduce typical electromyographic patterns for each of the five motor behaviors, in terms of cycle frequency and intersegmental phase lags (Ryczko et al., 2015). However, the cycle frequencies targeted with the model were set to half that of the *in vivo* recordings. This was chosen to reflect the scaling of locomotion frequency with body mass observed in animals (Bejan and Marden, 2006). For robot experiments, the target frequency for swimming was further lowered to 1.1 Hz due to the limits of operation of the robot (in particular torque limits). Other than the drive levels and sensory feedback, the only changes from *in vitro* to *in vivo* CPG conditions were in the average saturation thresholds which had to be increased to match the higher drives used *in vivo*.

The parameter space for the virtual muscles and proprioceptive feedback was explored systematically using the 3D mechanical simulation of the robot during swimming. An “average individual” was used by setting the standard deviations of the CPG excitabilities to zero, to increase reproducibility (this restriction was relaxed for robot experiments). We used uniform muscle parameter values for trunk joints, and progressively smaller values in the tail to emulate body taper: the values of α and β in modules 6, 7, and 8 were multiplied by a factor 0.7, 0.5, and 0.2, respectively. The same feedback parameter values were used for all joints, and the same feedback weights (with opposite signs) were used for ipsilateral and contralateral projections. Initial tests were made with a tonic muscle stiffness $\gamma = 0$: this parameter is mostly redundant with the stiffness gain β for a given (non-zero) amplitude of CPG oscillations. A uniform excitatory drive was used for all oscillators, which in absence of feedback results in high intersegmental phase lags inappropriate for swimming. The drive was set to 1.34, corresponding to a swimming frequency of 1.47 Hz (in absence of sensory feedback), which is close to our target of half the frequency observed in the animal (2.78 Hz and 3.12 Hz during EMG and kinematic recordings, respectively, Ryczko et al., 2015). We selected muscle and feedback parameter values that showed a significant increase in swimming speed and high stability of the CPG and kinematic patterns, while keeping the joint torques close to the robot's limit of 0.7 Nm (**Supplementary Figures 1–3**).

The five salamander behaviors were first reproduced in simulation without sensory feedback, by tuning the CPG drive levels and optimizing the limb-body phase bias for speed of locomotion. Additional simulations were done with varying strengths of axial proprioceptive feedback during forward terrestrial stepping and swimming. Further simulations were made with proprioceptive limb feedback during forward terrestrial stepping.

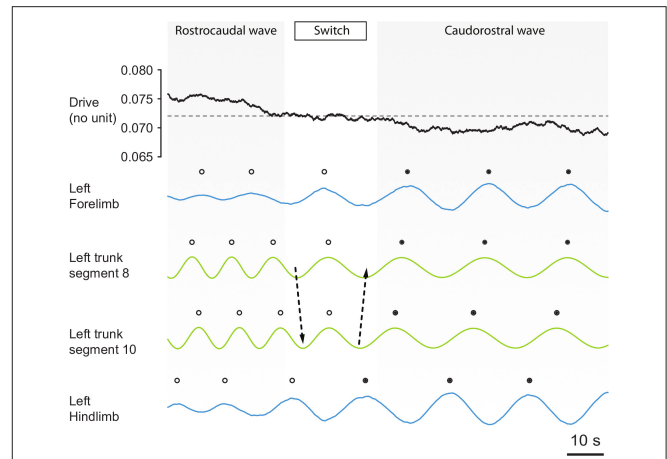


FIGURE 3 | The CPG spontaneously switches between axial motor patterns as a function of a fluctuating background drive strength. The strength of the simulated pharmacological drive applied to the CPG is shown together with the outputs of the oscillators of the left forelimb, left trunk segments 8 and 10, and the left hindlimb. Before the switch, limb oscillators (blue lines) are saturated by the drive strength. Therefore, they show low amplitude oscillations and are entrained to the higher frequency of the trunk oscillators, and the motor pattern in the trunk segments (green) is a rostrocaudal wave (white dots). Then, a progressive decrease in drive strength occurs through random fluctuations, and this progressively de-saturates the limb oscillators. The de-saturation allows limb circuits to oscillate at higher amplitude, causing a switch (arrows) from a fast rostrocaudal wave to a slower caudorostral wave (black dots). After the switch, the de-saturated limbs show high amplitude oscillations and therefore entrain to their slower frequency the trunk oscillators, because effective connection strength in the model is proportional to the amplitude of oscillations from the sender (see Methods). The same switches have been observed in the isolated spinal cord [Figures 5A,B of Ryczko et al. (2015)].

The limb-body phase bias was optimized again on the robot, due to the different zero-point reference and the backlash in the gears. The main simulation results were then reproduced on the robot with five different “individuals,” which were modeled by initializing the CPG parameters using different random seeds. The descending drives were adjusted for each “individual” and each motor behavior. Other parameters were sometimes adjusted between behaviors but always using the same values for all individuals (see Results). The movies shown in the Supplemental Materials were prepared using an average individual.

Data Processing

The joint angles from simulations and robot experiments were calculated in Matlab by fitting the kinematic chain of the robot to the positions of the LEDs. The CPG and kinematic intersegmental phase lags were calculated in Matlab from the CPG output and joint angle oscillations using the same algorithm: The timing of each cycle was defined as the centroid of the positive part of each oscillation (Knüsel et al., 2013). These timings were used to calculate a median phase lag (over time) for each pair of consecutive segments (CPG lag) or consecutive joints (kinematic lag). The CPG intersegmental phase lag was calculated using the average of the median phase lags between segments 8 to

12. For simulations, the kinematic intersegmental phase lag was calculated using the average of the median phase lags between joints 3 to 5. For robot experiments, joint 5 was often an outlier due to the robot torque limits, so joints 2 to 4 were used instead.

Statistics

Data are given as means $\pm$ standard deviation (SD) unless specified otherwise. Correlations between variables were evaluated in SigmaPlot 11.0 using the Pearson Product Moment Correlation test.

RESULTS

The Isolated CPG Model Reproduces the Main Features of Recordings From Isolated Spinal Cords

We found that asymmetric intersegmental couplings, together with different excitabilities and saturation thresholds between forelimb, hindlimb and axial oscillators, enabled the spinal cord model to reproduce the trimodal distribution of phase lags observed *in vitro* during fictive locomotion (Ryczko et al., 2015). The values shown in **Tables 2, 3** were found to produce a range of phase lags similar to the biological data, with peaks centered on 6.7 ± 1.3 , 1.3 ± 1.3 , and $-6.1 \pm 1.0\%$ (**Figures 2B,C**). The positive correlation between phase lag and cycle duration (Ryczko et al., 2015) was also reproduced (**Figure 2D**). Furthermore, the small fluctuations in the excitatory drive over time allowed the model to reproduce the spontaneous switches between slow caudorostral waves and fast rostrocaudal waves of axial activity reported in the isolated spinal cord (Delvolvé et al., 1999; Ryczko et al., 2015). **Figure 3** shows an example of the model producing such a switch.

Improving Swimming With Proprioceptive Feedback Requires Specific Muscle Stiffness and Damping Properties

Using a uniform drive yielded an intersegmental phase lag of 6.6% in an average individual (leftmost peak of the distribution). This resulted in inefficient swimming, with too many nodes in the traveling wave (**Supplementary Movie 1**). We looked for muscle parameters that would allow proprioceptive feedback to improve swimming by decreasing the phase lag toward more physiological values. For the active gain α , a value of 0.4 proved optimal, as higher values (together with higher stiffness β or γ) would have given higher swimming speeds but would have required torques beyond our robot's limits. Systematic tests in the β, δ, w^{ipsi} space showed a single region where feedback increased the swimming speed thanks to a decrease of the phase lag, while keeping the CPG rhythm stable. This stable region corresponds to a stiffness gain β between 1.6 and 2.3, a damping δ between 0.05 and 0.15 and feedback weights $w^{ipsi} = -w^{contra}$ between 17 and 22 (**Supplementary Figures 1–3**). Further tests in the β, γ, w^{ipsi} space showed that we could trade some fitness gain β for tonic stiffness γ . We settled on $\beta = 1.2$, $\gamma = 0.2$, which give qualitatively reasonable passive mechanical properties (**Table 5**).

Simulation Results Transferred to the Robot Following Some Adaptations

The simulation results could be reproduced on the robot, with the following changes made based on qualitative judgements: the muscle active gain α had to be increased from 0.4 to 0.5 to obtain reasonable amplitudes of oscillation during swimming. Uniform muscle parameter values were used in all robot joints: the tapering of the active and stiffness gains was removed to obtain reasonable amplitudes of oscillations in the tail and good swimming speeds. Due to the limits of operation of the robot, the target frequency for swimming had to be lowered down to 1.1 Hz². The feedback weights were reduced to 10. Sensory feedback from the neck joint was removed as it was destabilizing, leading to aperiodic rhythms. Finally, in simulation we found that a common limb-body phase bias gave near-optimal speed for all stepping behaviors. This was not the case with the robot: a specific limb-body phase bias was required for backward stepping (**Table 2**) to obtain the optimal speed for that behavior.

Two Drive Signals Suffice to Reproduce the Five Motor Behaviors, but Backward Terrestrial Stepping and Struggling Require Stronger Muscle Contractions

We found that tonic drives with only two different values applied to different parts of the CPG were sufficient to reproduce qualitatively the five motor behaviors with the robot, as shown by movies (**Supplementary Movies 2–6**), frame sequences (**Figure 4**) and robot kinematics (**Figure 5, Supplementary Figure 4B**). In particular, the differences in CPG and kinematic intersegmental phase lags between the five behaviors were reproduced (**Figures 5F,G**), as well as the differences in cycle durations (**Figure 5H**). **Figures 5A–E** show the CPG outputs and joint oscillations for a single individual. The rostrocaudally increasing lag between CPG and kinematic waves is reproduced (increasing gap between the thick red and thick black lines).

Swimming could be obtained by sending a strong drive (i.e., saturating limb oscillators, Hypothesis 3) to the whole CPG, with a slightly lower drive to the most rostral oscillators (segments 1–3 in **Figure 2**) to adjust the phase lag as proposed in numerical simulation of the lamprey locomotor CPG (Kozlov et al., 2009). The other behaviors were obtained by adjusting the drive to the limb oscillators independently from the drive to the axial oscillators (**Figure 5H, Supplementary Movies 3–6**). Higher axial phase lags required a greater relative difference between the two drives, and higher frequencies required higher values of both drives.

While two drives were sufficient to generate the CPG activity patterns for all behaviors, we found that stronger forces from the virtual muscles were required to reproduce the

²This meant producing a swimming gait in the frequency range of forward terrestrial stepping, i.e. with drives under the limb saturation threshold, so limb oscillators had to be silenced artificially.

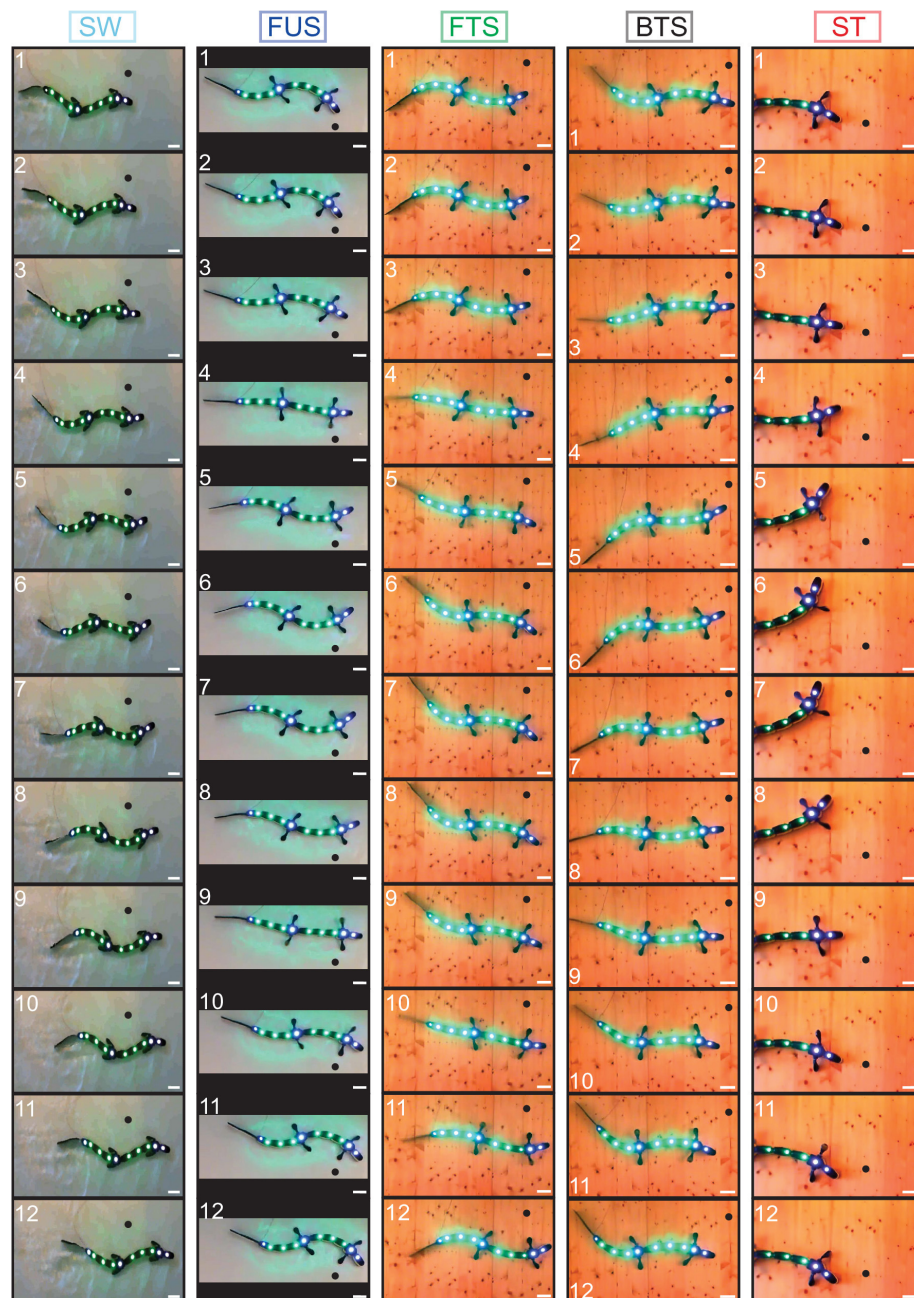


FIGURE 4 | Frame sequences showing from top to bottom one complete stride for the five motor behaviors. Light-emitting diodes were tracked on each module for kinematic analysis. A black dot was added on each frame to illustrate robot progression. Inter-frame time intervals in ms are, respectively: 200 (swimming, SW); 133.3 (forward underwater stepping, FUS); 166.7 (forward terrestrial stepping, FTS); 400 (backward terrestrial stepping, BTS); 466.7 (struggling, ST). Scale bar (white), 10 cm. The different background colors are due to the different environments: water tank for SW and FUS, wooden board for the other behaviors. The behaviors are close to those observed in the real animal [Figure 1 of Ryczko et al. (2015)].

kinematics of backward terrestrial stepping and struggling. To avoid introducing additional parameters, this was implemented by increasing the muscle gains α and β . A 10-fold increase was found appropriate to avoid large deviations between the CPG activity and the kinematics (Table 5, Figures 5A,E).

Proprioceptive Feedback Can Regulate the Phase Lag During Swimming and Forward Terrestrial Stepping, and Reduces Variability

With axial proprioceptive feedback, swimming could be reproduced with a single drive to the whole CPG (Figures 5B,I,

Supplementary Movie 8). In absence of feedback, the axial network of the five robot “individuals” produces intersegmental phase lags of $6.1 \pm 1.4\%$ (**Supplementary Figure 4A**, **Supplementary Movie 1**). With feedback, this could be reduced to $1.9 \pm 1.1\%$, which matches the values observed in the animal ($1.89 \pm 0.25\%$, Ryczko et al., 2015). Feedback also reduced the variability between individuals: Without feedback, the individual corresponding to the leftmost curve in **Figure 5I** (dashed lines) was an outlier. Using feedback with identical weights in all individuals (solid lines), the outlier showed phase lags similar to the other individuals.

Axial proprioceptive feedback could also replace differential drives (i.e., different drive values for different parts of the CPG) as a means of obtaining axial phase lags close to zero in simulations of forward terrestrial stepping. However, this required feedback weights of opposite signs compared to swimming. Using uniform drives and no feedback, the CPG generated negative phase lags (**Figure 6A**). With uniform drives, positive values of w^{ipsi} (as used in swimming) had a destabilizing effect on the CPG, with oscillators failing to lock in frequency. With differential drives as in **Figure 6B**, we found that positive values of w^{ipsi} were counterproductive, decreasing again the CPG phase lag to negative values. However, negative values of w^{ipsi} produced higher phase lags as desired and could be used to reproduce forward terrestrial stepping with uniform drives (**Figure 6C**). This effect of an increasing intersegmental phase lag with decreasing feedback weights during forward terrestrial stepping was reproduced in robot experiments (**Figure 6E**).

Instead of axial feedback, the differential drive could also be replaced with limb proprioceptive signals fed back to the limb oscillators. This was only tested in simulation (**Figure 6D**). The effect of feedback here was again to increase the negative CPG phase lags toward slightly positive values, close to zero.

A Passive Tail Decreases the Drag During Underwater Stepping

During forward underwater stepping, the locomotor performance could be improved by using “passive” tail segments (**Supplementary Movie 7**), similar to the animal which shows passive tail undulations during this locomotor behavior (see Cabelguen et al., 2014). This was implemented using a third drive level of zero to the tail segments. The tail CPG was then inactive, but the robot modules continued to generate torques corresponding to the passive parts of the muscle model (the terms that remain when M_i^l and M_i^r are 0). Measurements of the hydrodynamic forces in the 3D mechanical simulation suggest that for this particular gait, the undulations of passive tail segments allow the caudal fin to generate more thrust than in the case of active tail segments (**Figure 7**). The drag at the head and girdles is also reduced in the passive case. The net drag on the body axis is thus reduced from -0.0422 ± 0.0003 N to -0.0295 ± 0.0004 N (standard errors).

Coupling Delays Introduce Systematic Phase Biases in the Distributed Robot Controller

Initial tests on the robot with the distributed controller gave non-uniform phase lags along the body, unlike what was seen in simulation. We investigated the issue using a chain of 7 simple modules (no girdles) and a CPG model with symmetrical ascending and descending coupling weights and phase biases of 5%. We found increased phase lags between the first modules and decreased phase lags between the more caudal ones (**Figure 8A**). An analysis of the coupling terms used in the numerical integration of the CPG showed that rostral modules were significantly slowed down by caudal ones (**Figure 8B**). This suggested that the θ_j values (the phases of the couplings’ source oscillators) used in the numerical integration of the target oscillators were out of date. We modified the numerical integration to estimate the state of the source oscillator at the time of integration using a linear extrapolation of the two previous coupling messages and their times of arrival (see Methods). This considerably reduced the slow-down effect and yielded almost uniform phase lags (**Figures 8C,D**). Further improvements (not shown) were obtained by encoding the coupling phases and amplitudes as 16-bit half-floats. This halved the number of messages sent over the CAN bus and helped decrease the rate of transmission errors.

The Distributed Controller Allows for Autonomously Moving Robot Parts

We found that the distributed implementations of the CPG and muscle models have the side effect of making the robot modular at runtime. We conducted forward terrestrial stepping experiments with screws between some modules removed, causing the robot to break into parts (no other changes were made to the hardware or software). Each part kept functioning, still coordinated by its own section of the CPG model. This is demonstrated in **Supplementary Movie 9**, **Figure 9**.

DISCUSSION

A Modulable CPG Architecture

Our results suggest that the answer to question 1 is yes: a modulable CPG provides a robust framework for generating multiple motor patterns, such that different motor behaviors do not necessarily require dedicated CPGs. This concept was proposed by Grillner (1981) as the “unit burst generator” theory, which states that independent rhythmogenic circuits can be flexibly coupled from one behavior to another. Such circuits have been identified in many animals. In the salamander, specific spinal hemisegments have been shown to control muscles of the trunk (Ryczko et al., 2010), tail (Charrier and Cabelguen, 2013) and limbs (Cheng et al., 1998; Lavrov and Cheng, 2004; Ijspeert et al., 2007). Other examples include the spinal hemisegments in the lamprey (Cangiano and Grillner, 2003, 2005; Cangiano et al., 2012), the flexor

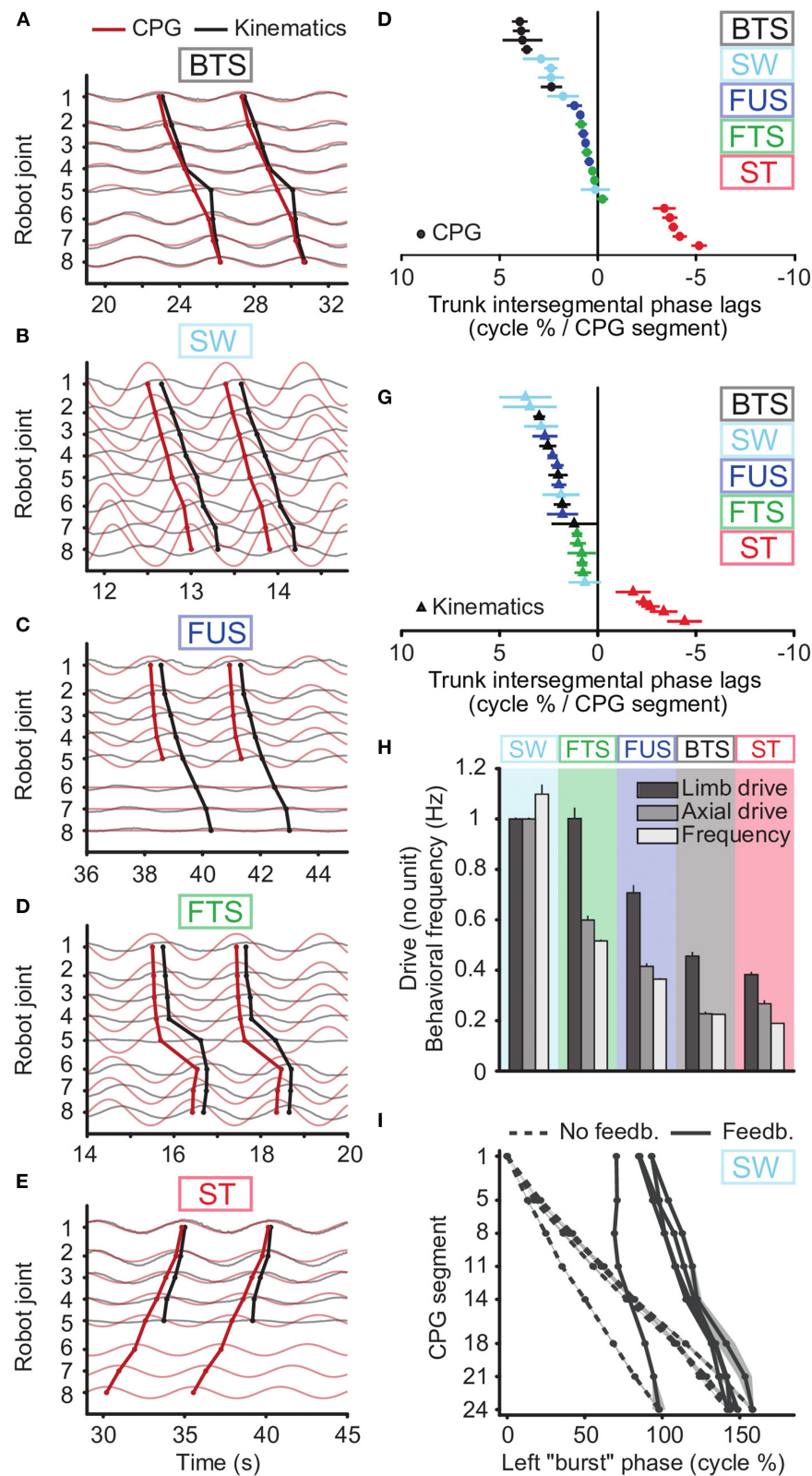


FIGURE 5 | CPG output and joint kinematics during the five motor behaviors reproduced with the robot. Results obtained using a single drive level and proprioceptive feedback for swimming, two drive levels (to limb and axial oscillators) and no feedback for the other behaviors, with a third drive of zero for the tail during underwater stepping. **(A–E)** and **(F,G)** emulate the biological data illustrated in Figures 2, 3 of Ryczko et al. (2015), respectively. **(A–E)** Kinematic angular oscillations (thin black

(Continued)

FIGURE 5 | lines) and CPG outputs x_i (thin red lines) are shown for each joint, with circular markers indicating the centroid of the positive half of each cycle. Rostrocaudal (A-C, line descending to the right), standing (D, almost vertical line) and caudorostral (E, line descending leftward) kinematic waves (thick black lines) followed the CPG activity (thick red lines) with variable delays during the 5 motor behaviors: backward terrestrial stepping (BTS), forward swimming (SW), forward underwater stepping (FUS), forward terrestrial stepping (FTS) and struggling (ST). All figures are from the same simulated individual. **(F,G)** Intersegmental phase lag distributions for CPG waves **(F)** and for kinematic waves **(G)** in the robot trunk. Each marker represents a single recording. **(H)** Comparison of the tonic drive signals applied to the CPG and resulting oscillation frequencies (Hz) for each motor behavior. Data represent mean $\pm$ SD over the 5 simulated individuals. The overlap in limb drive values between SW and FTS is due to reduced drive and limb saturation thresholds during SW to accommodate for the robot's torque limitations (See Methods). Without these limitations, the limb and axial drives for SW would be 1.34 as in simulation. **(I)** Rostrocaudal axial waves generated during SW by the CPG without sensory feedback (dashed lines) and with sensory feedback (solid lines), with uniform drive $d_i = 1$, in the 5 simulated individuals. For each individual, the wave with feedback is horizontally positioned in the figure to connect to the wave without feedback. The experiments with sensory feedback correspond to the SW data in **(F-H)**.

and extensor networks in the left and right side of the mouse spinal cord (Häggglund et al., 2013), the crayfish swimmeret system (Mulloney and Smarandache-Wellmann, 2012) and the networks controlling individual leg joints in the stick insect (Büschges et al., 1995). A modeling study of insect locomotion suggests that the recruitment of a single neural structure for various behaviors also applies to situations where locomotion is largely driven by sensory feedback (Schilling and Cruse, 2020).

Oscillator Couplings

Biological data indicate that in salamanders, limb activity can occur together with traveling waves *in vivo* and *in vitro* (Ryczko et al., 2015). In our previous robotic study (Ijspeert et al., 2007), limbs projected to all axial oscillators (forelimb oscillators to trunk oscillators, and hindlimb oscillators to tail oscillators). Two axial outputs were therefore possible: either a standing wave when limb oscillators were active (during stepping), or a rostrocaudal wave when limbs were saturated (during swimming). Here we made the limb oscillators project only to neighboring axial oscillators (Hypothesis 1), which gives more flexibility for the coordination of axial oscillators when limbs are rhythmically active (Ijspeert et al., 2005; Knüsel et al., 2013). In the animal, a unidirectional connection from excitatory interneurons generating the limb rhythm to those generating the axial rhythm would be sufficient to impose the slow limb oscillations to the axial segment, according to a detailed model of salamander spinal networks based on Hodgkin-Huxley neurons (Bicanski et al., 2013).

In our model, the asymmetry between ascending and descending coupling weights w_{ij} is required to reproduce a wide diversity of axial phase lags with consistent values along the axis as observed *in vitro* and *in vivo* (Ryczko et al., 2015). Symmetric weights as used in Ijspeert et al. (2007) produce non-uniform phase lags along the axis when the oscillators have different intrinsic frequencies. Future studies should determine whether such a coupling is present in salamanders and how it is implemented. Possibilities include an asymmetry at the neuroanatomical level (dominance of descending projections, see Buchanan et al., 1989; Buchanan, 2001 in lamprey) or in electrophysiological terms (stronger synaptic strengths toward caudal segments, see Smarandache et al., 2009 in crayfish; more spikes per locomotor cycle in neurons projecting caudally, see Mulloney et al., 2006 in crayfish).

Oscillator Frequencies and Saturation

For our CPG model to be able to generate the three types of axial waves recorded *in vitro* and *in vivo* in salamanders, and the positive correlation between cycle duration and phase lag (Ryczko et al., 2015), we had to modify the intrinsic frequency of limb networks compared to our previous study (Ijspeert et al., 2007). Forelimb and hindlimb oscillators still have an intrinsic frequency slower than axial oscillators, but here forelimb oscillators are faster than hindlimb ones (Hypothesis 4). Data in mammals suggest that forelimbs deprived of normal interactions with the hindlimb networks tend to accelerate *in vivo*. Indeed, in adult cats where the spinal cord is partially lesioned, forelimb and hindlimb rhythms often dissociate, and forelimbs adopt a faster rhythm, yielding a 2:1 forelimb-hindlimb coupling (for review, see Frigon, 2017). At the cellular level, modification of a single conductance controlling burst termination should be sufficient to make limb segments generate slower oscillations, as suggested by a detailed Hodgkin-Huxley model of a salamander spinal segment (Bicanski et al., 2013).

A hypothesis that we kept from our previous work (Ijspeert et al., 2007) is that with a strong descending drive, limb networks “saturate” whereas axial oscillators do not (Hypothesis 3). Future studies should examine whether and how such a function is implemented in the animal. It could be a differential recruitment of specialized interneuron populations as a function of drive strength, as documented as a function of speed in zebrafish (McLean et al., 2007, 2008; Gabriel et al., 2011; Ampatzis et al., 2014, for review see Berg et al., 2018) and mice (Talpalar et al., 2013, for review see Kiehn, 2016). It could also involve a shift in the active set of reticulospinal neurons as a function of speed/gait. Some reticular neurons increase their firing specifically during swimming in salamanders (Lowry et al., 1996). Different reticulospinal neurons are activated as a function of speed in zebrafish (Kinkhabwala et al., 2011).

Regulation Through Descending Drives

In answer to question 2, our results (Figure 5, Supplementary Figure 4B, Supplementary Movies 2–6) suggest that independent drive levels to a few parts of a CPG network (here two, or three to reproduce passive tail undulations) are sufficient to emulate a diversity of motor behaviors. In the model, the regulation of CPG activity by descending drives can be understood intuitively. The drive signals control the intrinsic (uncoupled) frequencies of the oscillators. Because rostrocaudal couplings are stronger than caudorostral couplings,

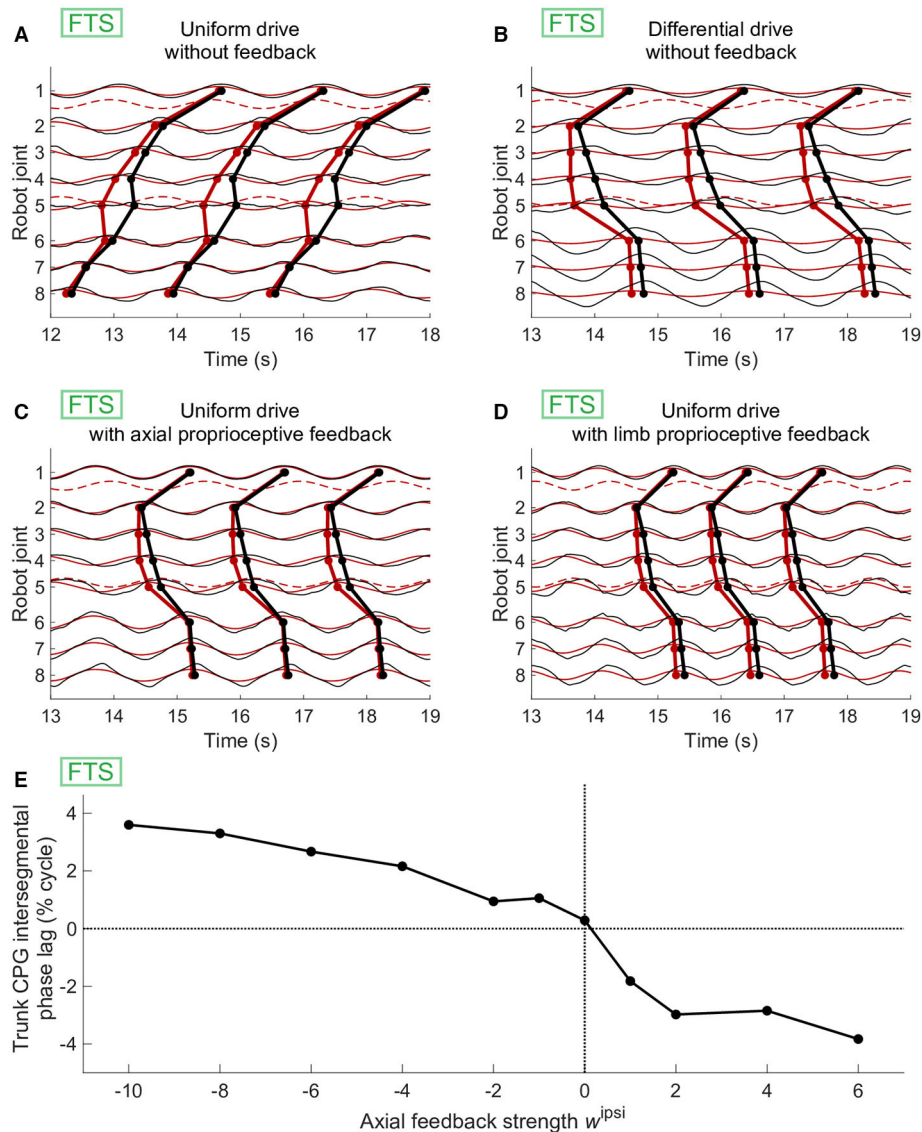


FIGURE 6 | Effect of axial or limb proprioceptive feedback on CPG activity and kinematics during forward terrestrial stepping (FTS). **(A–D)** Joint kinematics (black) and CPG activity (red, dashed for limb oscillators) in simulation. Circular markers indicate the centroid of the positive half of each cycle. The limb-body phase bias φ_{ij} was adapted in each case for optimal speed of locomotion. **(A)** With uniform drive ($d_i = 0.98$) and no feedback, the CPG with active (non-saturated) limb oscillators produces caudorostral waves of activity. **(B)** Standing waves of CPG activity can be obtained by using a different drive of 0.63 for the limb oscillators. **(C)** Standing CPG waves can also be obtained using uniform drives and axial proprioceptive feedback, with $w^{\text{ipsi}} = -w^{\text{contra}} = -0.65$. **(D)** Standing waves of CPG activity could also be obtained with uniform drives using proprioceptive limb feedback, with $w^{\text{limb}} = 3.7$. **(E)** Effect of the axial feedback weight on CPG axial intersegmental phase lag in robot experiments. Before introducing feedback, differential drives to the limb ($d_i = 0.98$) and axial ($d_i = 0.61$) oscillators were used to increase the phase lag toward zero. Positive ipsilateral feedback weights (as those used during swimming with sensory feedback, **Figure 5I**) decreased the phase lag, whereas negative ipsilateral weights increased it.

a segment will entrain a slower or faster caudal neighbor, and the resulting common frequency will be close to the frequency of the rostral segment. However, the faster segment will lead the slower one with a delay that increases with the difference in uncoupled frequencies (this delay being in addition to the coupling's natural phase bias). This effect will propagate down the chain of segments, such that the resulting frequency and phase lag of the whole chain can be controlled by adjusting two

values: the uncoupled frequency of the first segment, and that of the other segments.

This mechanism of regulation is close to the “trailing oscillator hypothesis,” which states that the oscillator of higher excitability becomes the leader of the chain. This hypothesis is based on lamprey experimental data showing that increasing the excitability in caudal segments causes a switch from a rostrocaudal to a caudorostral wave in isolated spinal cords

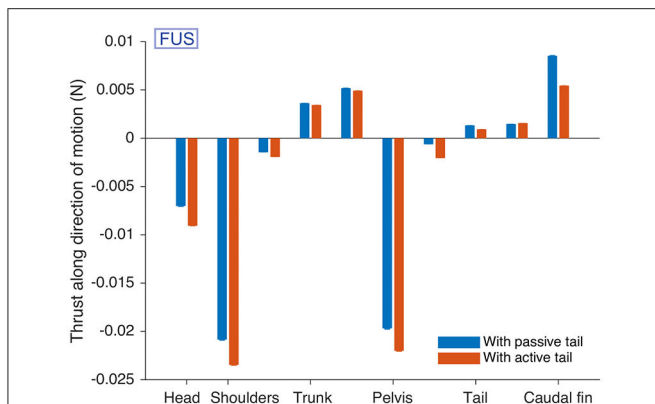


FIGURE 7 | Passive tail CPG segments reduce drag during forward underwater stepping (FUS) in simulation. The hydrodynamic forces acting on different parts of the robot modules along the direction of motion are given. The caudal fin provides more thrust when the tail is passive. Forces on each module were measured for an “average individual” during 15 s after a warm-up period of 15 s, and averaged over the 30,000 time steps. The procedure was repeated 100 times with different starting conditions. The bars show the means over the 100 repetitions. Error bars for the standard error are shown, but barely visible (all standard errors are < 0.00013).

(Matsushima and Grillner, 1990, 1992). However, this lamprey model assumed symmetrical rostrocaudal and caudorostral couplings, while we found that the coupling asymmetry is important to maintain a uniform phase lag along the chain of oscillators. A later lamprey modeling study with a detailed neural network of Hodgkin–Huxley neurons showed that dominant descending couplings allow for flexible control of forward and backward swimming with constant phase lag along the spinal cord at different speeds: the frequency and intersegmental phase lag can be controlled by adjusting the excitatory drive of the first segments compared to the remaining ones (Kozlov et al., 2009).

In our salamander model, the differential excitation of the first segments can be realized through the strong connections from the forelimb oscillators (when they are active). The regulation of the axial CPG pattern is then achieved by adjusting the excitation of the limb oscillators compared to the axis, instead of the first axial segments compared to the others as in the swimming case. This mechanism of regulation has been investigated with abstract oscillators and validated with a more detailed integrate-and-fire model (Knüsel et al., 2013).

The coordination of limb muscles was beyond the scope of this study: the limbs of our robot have a single rotational degree of freedom, and the direction of rotation was artificially inverted for backward stepping. We expect that more drives would be required in a model with more realistic limbs. Turning was also not investigated here but can in principle be obtained during swimming and stepping using different drives for axial oscillators on the left and right sides (Ijspeert et al., 2007).

The Regulation Mechanism in the Isolated CPG

The mechanism of regulation described above, together with the differences in excitability and saturation thresholds between

forelimb, hindlimb and axial oscillators (Table 3), enable the isolated CPG model to reproduce the trimodal distribution of phase lags observed *in vitro*: In the model, hindlimb oscillators are intrinsically slower than forelimb oscillators. Given the random nature of the saturation thresholds, forelimbs or hindlimbs can selectively saturate due to slightly different threshold values. When all oscillators are active, the hindlimb oscillators slow down the forelimbs, and the strong local connections from limb to axial oscillators slow down the girdle segments, leading to a highly negative phase lag in the trunk and tail axial networks. This corresponds to the rightmost peak of the distribution (i.e., negative lags, Figures 2B–D). When the hindlimb oscillators saturate, the forelimb oscillators accelerate a bit but continue to slow down the first segments, yielding the phase lags that make up the middle peak of the distribution (i.e., near zero lags, Figures 2B–D). When all limb oscillators saturate, the axial network is no longer influenced by limb network activity and generates the higher, positive phase lags found in the leftmost peak (i.e., positive lags, Figures 2B–D).

This mechanism also explains the spontaneous switches between slow caudorostral waves and fast rostrocaudal waves of axial activity: In the isolated CPG model, the transitions between the active and saturated states are triggered by small fluctuations in the excitatory drive (Figure 3), which represents tonic pharmacological excitation as in Ryczko et al. (2010, 2015) or Delvolvé et al. (1999). The progressive saturation of the limb oscillators causes their oscillation amplitude to diminish as the cycle frequency increases. The model thus suggests that limb burst amplitude *in vitro* should be higher during slow caudorostral wave of activity than during a rostrocaudal wave (Figure 3).

Regulation Through Proprioceptive Feedback

Recordings from isolated spinal cords show much more variability among salamander individuals than EMG recordings of intact animals (Ryczko et al., 2015). In response to question 3, our results from robot experiments with five swimming “individuals” suggest that local sensory feedback could explain this reduction of variability from the *in vitro* to the *in vivo* condition (Figure 5I): sensory feedback made it unnecessary to tune the drive levels in each individual (compare the standard deviation of the drives in Figure 5H for swimming vs. the other behaviors). Results from robot experiments and simulations also suggest that local sensory feedback can replace differential drive as a modulator of the CPG activity to produce forward terrestrial stepping (Figure 6) and swimming (Figures 5B,I, Supplementary Figures 4A,C, Supplementary Movies 1, 8), which answers the other part of question 3.

The regulation of our CPG model by proprioceptive feedback can be explained with the same mechanism as regulation by different drive signals. Sensory feedback has been previously reported to increase the locomotion cycle frequency through an excitatory effect on the lamprey CPG activity (e.g., Kiemel and Cohen, 2001). In our model, the addition of proprioceptive

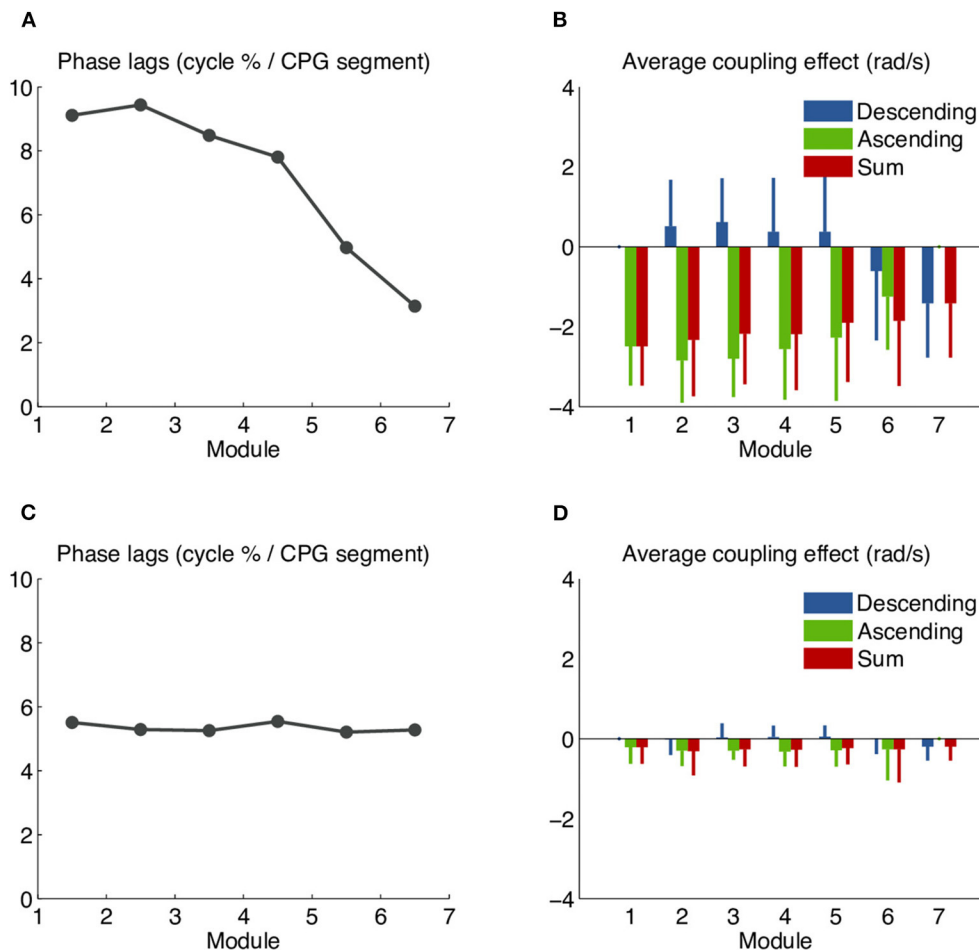


FIGURE 8 | Systematic phase biases due to the slow-down effect of coupling delays in the robot's distributed controller. Undesired phase lags in the distributed controller were analyzed using a chain of 7 simple (non-girdle) robot modules and a CPG model with symmetrical ascending and descending coupling weights and a uniform intersegmental phase bias of 5%. **(A)** CPG intersegmental phase lags calculated from the middle segment of each module, as percentage of the cycle duration. The observed values are higher than the target of 5% in the rostral modules and lower than the target in the caudal ones. **(B)** Average effect of the ascending and descending couplings on the left oscillator of the middle segment in each module. Values shown correspond to the coupling terms $r_i w_{ij} \sin(\theta_i - \theta_j - \varphi_{ij})$, averaged over the whole recording. The negative red bars show that the net effect of both coupling types is to slow down the oscillation. The effect is stronger in more rostral modules. **(C)** Phase lags observed after the implementation of coupling message extrapolation. The observed values are almost uniform and close to the target of 5%. **(D)** With coupling message extrapolation, the slow-down effect has almost vanished.

feedback in the axis increases the uncoupled frequency of the segments in the axial network. If the first segment receives no feedback, as is the case in robot experiments, its uncoupled frequency is comparatively reduced. This leads as expected to a decrease in phase lags during swimming (Figure 5I).

Interestingly, simulations showed that feedback can also regulate swimming when neck feedback is included (Supplementary Figures 1–3, 4C). This suggests that feedback has a weaker accelerating effect in the first segment than in the others, even though the feedback amplitude is comparable (see Supplementary Figure 4C). This can be explained by looking at the model equations: axial feedback adds the term $-\frac{s_i}{r_i} \sin \theta_i$ to the instantaneous frequency $\dot{\theta}_i$ of the oscillator. The average value of this term is highly dependent on the

phase relationship between θ_i and the phase of the feedback signal s_i . In particular, if the kinematics follow closely the CPG output, and if we approximate s_i with a sine wave, then s_i will be proportional to $\cos \theta_i$. Assuming a constant amplitude r_i , the effect of feedback on $\dot{\theta}_i$ can be written $k \cos \theta_i \sin \theta_i$, which averages to zero over a 2π interval for θ_i . We conclude that if θ_i increases approximately linearly with time, the effect of feedback on the frequency will approach zero when the CPG-mechanical phase lag approaches zero. And this lag (the distance between the red and black dots) is indeed very small for the neck joint in Supplementary Figure 4C.

We can also explain the need for reversed axial feedback weights during forward terrestrial stepping: Excitatory axial feedback (as in swimming) accelerates the mid-trunk oscillators, which tends to decrease the intersegmental phase lag. This is



FIGURE 9 | Frame sequences showing the behavior of the robot when split into several parts. **(A)** After losing its tail, the robot keeps moving (although with a malfunction in the pelvic girdle module). The tail modules continue to oscillate. The tail CPG maintains the coordination in the form of a rostrocaudal traveling wave. **(B)** The robot splits behind both girdles. The three robot parts keep moving independently.

counter-productive since the unregulated intersegmental phase lag is already too low (**Figure 6A**). With inverted weights, axial feedback slows down the mid-trunk and increases the phase lag as desired. The inclusion of neck feedback has little importance in this case: when the limbs are active, the activity of segment 3 is largely determined by the strong connections from the forelimb oscillators, irrespective of the activity in the first and second segments. This also means that we would expect similar results with a model that includes head stabilization as observed in the animal during forward terrestrial stepping (Ryczko et al., 2015). Our results with inverted weights are reminiscent of the reversal of the effects of sense organs that signal forces on a leg when switching from forward to backward stepping in the stick insect (Akay et al., 2007, for review see Mantziaris et al., 2020). The mechanism underlying such a switch in sensory encoding could involve an interplay between the descending drive to the CPG and sensory feedback. In line with this possibility, brainstem stimulation changes how lamprey motoneurons respond to rhythmic movements imposed to the spinal cord (Hsu et al., 2013).

The regulation mechanism also explains the effect of limb feedback: the excitatory signal increases the frequency of the

limb oscillators. These in turn increase the frequency of the first segments, and thus the intersegmental phase lag. Such limb feedback has been proposed in a simulation study as a way of facilitating the transition from walking to trotting in the salamander (Harischandra et al., 2011).

The cells underlying proprioceptive axial feedback remain to be identified in salamanders (see section Motor control in salamanders). The limb sensory feedback introduced in simulation could be provided by cutaneous receptors during foot contact since mechano-sensitive Merkel cells are present on the skin of salamanders (Scott et al., 1981, Diamond et al., 1986), and/or stretch receptors of limb muscles that are sensitive to joint angle, since fibers behaving as muscle spindles have been identified in salamanders (Bone et al., 1976). In mammals, it is well-established that limb feedback plays a key role in establishing the locomotor patterns (e.g., Musienko et al., 2012; Akay et al., 2014; Takeoka et al., 2014; for review see Frigon, 2017).

Muscles and Passive Biomechanical Properties

We found that higher muscle torques were required to emulate struggling and backward stepping (**Table 5**). Behavior-dependent changes in limb electromyographic activity have been reported in salamanders when comparing forward and backward terrestrial stepping. The electromyographic bursts increase during backward stepping in the extensor iliobtibialis pars posterior (the homolog of the rectus femoris in mammals, which elevates the femur and extends the knee), mostly during the swing phase, whereas the bursts decrease in the other limb muscles (Ashley-Ross and Lauder, 1997). Future studies should determine whether an increase in electromyographic activity occurs in axial muscles during backward terrestrial stepping. A differential ratio of activation of epaxial vs. hypaxial muscles in the animal could also occur, as observed when comparing forward underwater stepping and forward terrestrial stepping in salamanders (Deban and Schilling, 2009). The same comparative electromyographic measurements should be done for struggling in salamanders. Caudorostral waves of axial activity are also used during struggling in *Xenopus* and during backward swimming in eels and lampreys. Lateral body undulations are much larger during struggling and backward swimming than during forward swimming in *Xenopus* (Kahn and Roberts, 1982), in eel (D'Aout and Aerts, 1999) and in lamprey despite a similar duty cycle of the electromyographic burst (Islam et al., 2006), suggesting that an increase in muscle strength occurs during caudorostral waves.

Passive tail segments reduced the drag during forward underwater stepping in simulation (**Figure 7**). In line with this, tail muscles show weak or no activation despite large tail undulations during forward underwater stepping in salamanders, suggesting that the body generates thrust by transmitting trunk movements passively to the tail (Cabelguen et al., 2014). At the low frequencies of underwater stepping, the passive biomechanical properties of the tail could be sufficient to propagate the body undulation, while higher frequencies might require a higher stiffness and thus active muscles (Blight, 1976, 1977) as observed in the salamander during swimming (Delvolvé et al., 1997). In salamanders, whether tail deactivation during forward underwater stepping is due to reduced activity of

e.g., some reticulospinal neurons remains to be determined. Biological observations and robotic experiments suggest that salamanders can use their tail as a “fifth limb” to provide thrust in slippery conditions (Karakasiliotis and Ijspeert, 2009). This suggests the existence of reticulospinal neurons that can both decrease and increase the activity of the tail independently from the trunk.

Robotic Platform and Distributed Control

Some of the adaptations required to reproduce the simulation results on the robot can be explained by mechanical differences: The need for stronger muscle forces (no tapering) in the robot’s tail might be due to the passive fin exerting more resistance than in the simulation. The different optimal limb-body phase bias for backward stepping could be due to the backlash in the leg gears.

Our initial implementation of the controller was centralized in the head module. This required retrieving the position and velocity of all joints and sending back the torque setpoints at each time step over the CAN bus. These are slow operations since the module has to forward the requests over a local I²C bus. The resulting control loop was too slow, making the muscle model unstable. The distributed controller solved this problem by keeping the communication of joint positions, velocities and torque setpoints local to each module. This solution shows interesting similarities with the vertebrate nervous system, which distributes the processing of sensory signals and the generation of locomotor patterns along the spinal cord, close to the target muscles.

Watanabe et al. (2009) have shown that a distributed controller with proprioceptive feedback can have interesting fault-tolerance properties, such as robustness to lesions in the communication pathways. It would be interesting to experiment with such lesions in our CPG model. The distributed controller would probably accommodate such experiments: the **Supplementary Movie 9** shows that the different sections of the CPG continue to function after the robot has been split in several parts. This is an interesting feature that few robots have. It is made possible by the distributed computation of the CPG and muscle model, the multi-master nature of the CAN bus and the nearest-neighbor couplings of the CPG model.

The distributed controller also introduces a difficulty in the form of coupling delays, which can be hard to predict when many modules share the same communication bus. As illustrated in **Figure 8A**, these delays can have a significant impact on the coordination between modules: the phase lags between rostral modules are markedly increased, while those between caudal modules are decreased. The asymmetry is probably related to the priority of messages on the CAN bus: the last modules have higher CAN identifiers so lower priorities when several modules attempt to talk at the same time. This means that ascending couplings will be on average more delayed than descending couplings, inducing larger lags in the rostral modules (**Figure 8B**). The problem was mostly solved by extrapolating in the receiver module the state of the oscillators at the origin of the couplings (see Results). Extrapolating these states is easily done in our CPG model, where the state variables are the phase and amplitude of the oscillators: during steady state locomotion, these variables, respectively, grow at an almost constant rate or

stay almost constant. It would be more difficult to extrapolate the state in a model without explicit phase variables. In conclusion, the CAN bus, being shared by all modules, limits the benefits of the distributed controller. A future revision of the robot should include direct communication between adjacent modules, in addition to the shared bus, to fully realize the benefits of distributed control.

CONCLUSION

Following the analogy proposed by Loeb (2001), our study suggests that the spinal cord is as a puppet on strings, and that a complex motor repertoire can be generated by pulling a limited set of “sensory” or “descending” strings, which in turn take advantage of a flexible spinal motor circuit.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

DR, JK, AI, and J-MC designed the study. JK and AC performed numerical modeling, simulations, and robotic experiments. JK, J-MC, AI, and DR analyzed data. JK, AI, and DR wrote the paper. All authors contributed to the article and approved the submitted version.

FUNDING

The support from the European Community (LAMPETRA grant: FP7-ICT-2007-1-216100) and the *Fondation pour la Recherche Médicale* (FRM, DBC 20101021008) are acknowledged. DR receives support from the Canadian Institutes of Health Research (407083); the Fonds de la Recherche - Québec (FRQS Junior 1 awards 34920 and 36772); the Natural Sciences and Engineering Research Council of Canada (RGPIN-2017-05522 and RTI-2019-00628); the Centre de Recherche du Centre Hospitalier Universitaire de Sherbrooke (CHUS); the fonds Jean-Luc Mongrain de la fondation du CHUS, the Faculté de médecine et des sciences de la santé; the Centre d'excellence en Neurosciences de l'Université de Sherbrooke. AI receives support from Swiss National Science Foundation (Project CR23I2_140714).

ACKNOWLEDGMENTS

The authors would like to thank Örjan Ekeberg for his valuable comments on a previous version of the manuscript, and Konstantinos Karakasiliotis for his help in preparing a movie of the robot. Part of this work was previously published as a thesis (Knüsel, 2013).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fnbot.2020.604426/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer CL declared a past co-authorship with one of the authors AI to the handling editor.

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Identification of Exploration and Exploitation Balance in the Silkmoth Olfactory Search Behavior by Information-Theoretic Modeling

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OPEN ACCESS

Edited by:

Dai Owaki,
Tohoku University, Japan

Reviewed by:

Hitoshi Aonuma,
Hokkaido University, Japan
Dominique Martinez,
UMR7503 Laboratoire Lorrain de
Recherche en Informatique et ses
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Received: 14 November 2020

Accepted: 08 January 2021

Published: 01 February 2021

Citation:

Hernandez-Reyes CA, Fukushima S,
Shigaki S, Kurabayashi D, Sakurai T,
Kanzaki R and Sezutsu H (2021)
Identification of Exploration and
Exploitation Balance in the Silkmoth
Olfactory Search Behavior by
Information-Theoretic Modeling.
Front. Comput. Neurosci. 15:629380.
doi: 10.3389/fncom.2021.629380

Insects search for and find odor sources as their basic behaviors, such as when looking for food or a mate. This has motivated research to describe how they achieve such behavior under turbulent odor plumes with a small number of neurons. Among different insects, the silk moth has been studied owing to its clear motor response to olfactory input. In past studies, the “programmed behavior” of the silk moth has been modeled as the average duration of a sequence of maneuvers based on the duration of periods without odor hits. However, this model does not fully represent the fine variations in their behavior. In this study, we used silk moth olfactory search trajectories from an experimental virtual reality device. We achieved an accurate input by using optogenetic silk moths that react to blue light. We then modeled such trajectories as a probabilistic learning agent with a belief of possible source locations. We found that maneuvers mismatching the programmed behavior are related to larger entropy decrease, that is, they are more likely to increase the certainty of the belief. This implies that silkmoths include some stochasticity in their search policy to balance the exploration and exploitation of olfactory information by matching or mismatching the programmed behavior model. We believe that this information-theoretic representation of insect behavior is important for the future implementation of olfactory searches in artificial agents such as robots.

Keywords: *Bombyx mori*, infotaxis, olfaction, ethology, adaptive-behavior, exploration-exploitation

1. INTRODUCTION

Odor source localization is a search problem that requires fast decision-making based on sporadic and stochastic detection of chemical particles. Despite the challenge of turbulent and dilute plumes that often have a complex spatio-temporal structure (Mafra-Neto and Cardé, 1994; Celani et al., 2014), insects such as the fruit fly (van Breugel and Dickinson, 2014) and various species of moths (Vickers, 2005) rely on olfactory searches to conduct essential behaviors such as searching for food or potential mates. The high performance that insects show on such a complex search problem

despite their simple brain motivates researchers to further analyze and understand the decision processes that these insects execute when conducting olfactory searches (Baker et al., 2018).

With this motivation, our research group has analyzed the olfactory behavior of the male silk moth *Bombyx mori* (Lepidoptera: Bombycidae). Despite having wings, this insect is unable to fly, and has a body that is on average 30 mm long and 10 mm wide. It has two antennae of approximately 6 mm in length on its head. This insect has been widely employed to analyze olfactory behavior because it exhibits only one action: It walks only when it detects a pheromone (*Bombykol*) released by its female counterpart (Obara, 1979). Such behavior consists of a series of maneuvers called a “surge,” “zigzag,” and “loop.” This sequence of maneuvers has been approximated to a mean-response model denoted as “programmed behavior” (Kanzaki et al., 1992).

Based on the mean durations of the surge, zigzag, and loop maneuvers, the programmed behavior has been algorithmically defined as follows: first, immediately after a pheromone stimulus, the moth advances in a straightforward manner through a *surge* motion. Then, if there is an absence of pheromone detections, the moth moves on a *zig-zag* pattern, trying to detect pheromones again. Finally, if the pheromone remains undetected, the moth transitions into a *loop* motion until the next detection. A diagram of the programmed behavior is shown in **Figure 1**. Because the silk moth is motionless by default and only elicits its programmed behavior after the first pheromone hit, this search strategy has been labeled as “reactive” by Voges et al. (2014). Despite the simplicity of this sequential pattern, the male silk moth can effectively locate females with remarkable efficiency.

However, this model does not reflect how the motions of the moth vary in response to fine spatio-temporal fluctuations of the odor plume and individual differences among specimens. In previous studies, such variability was investigated by identifying maneuver transitions with machine learning (Shigaki et al., 2018b) and fuzzy logic (Shigaki et al., 2019b). Although these studies succeeded in identifying deviations from the programmed behavior, they relied on data from electrophysiological signals obtained from implanting electrodes in the wing muscles or brain of the silk moth; however, electrode implantation is technically challenging and risks degrading the tissues of the moth. Therefore, an analysis method that allows modeling adaptive olfactory behavior from non-intrusive experimental measurements is necessary.

To identify adaptive olfactory behavior, recent studies have used the information-theoretic framework of infotaxis, which was first proposed by Vergassola et al. (2007). A recent study by Pang et al. (2018) investigated the features of odor encounters that modulate the intensity of upwind turns in the fruit fly *Drosophila melanogaster* and the mosquito *Aedes aegypti*. The authors found through simulations that, compared to a *centerline inferring* odor source search algorithm, infotaxis produced trajectories that were more similar to those of the actual animals, in the sense that they exhibit weaker upwind turns later in a sequence of odor encounters. Similarly, Calhoun et al. (2014) recently demonstrated the possibility of using infotaxis to model the multi-stage foraging behavior of the nematode

Caenorhabditis elegans. In their paper, the authors showed that infotaxis-like search strategies, which minimize the entropy of the probability distribution of odor source locations, reflects both the “local” and “global” stages of the *C. elegans* foraging behavior.

In this paper, we investigate the potential causes of variability in the behavioral maneuvers of the silk moth *B. mori* by using a non-invasive experimental method and an infotaxis-based model similar to those described in recent studies. We measured the silk moth trajectories and input stimuli data with a tether, a two-dimensional treadmill, and a virtual odor plume. To ensure accurate and reproducible stimuli, we used optogenetic silk moths that react to the impulses of blue light in the same way as with pheromone particles. We modeled the trajectories and stimuli measurements as infotaxis agents and found that; maneuvers that mismatch the *programmed behavior* model correspond to higher expected information rewards regarding the location of the source. In summary, we believe that this paper demonstrates the possibility of using non-invasive experimental measurements and infotaxis-based modeling to identify variability in the olfactory behaviors of the male silk moths.

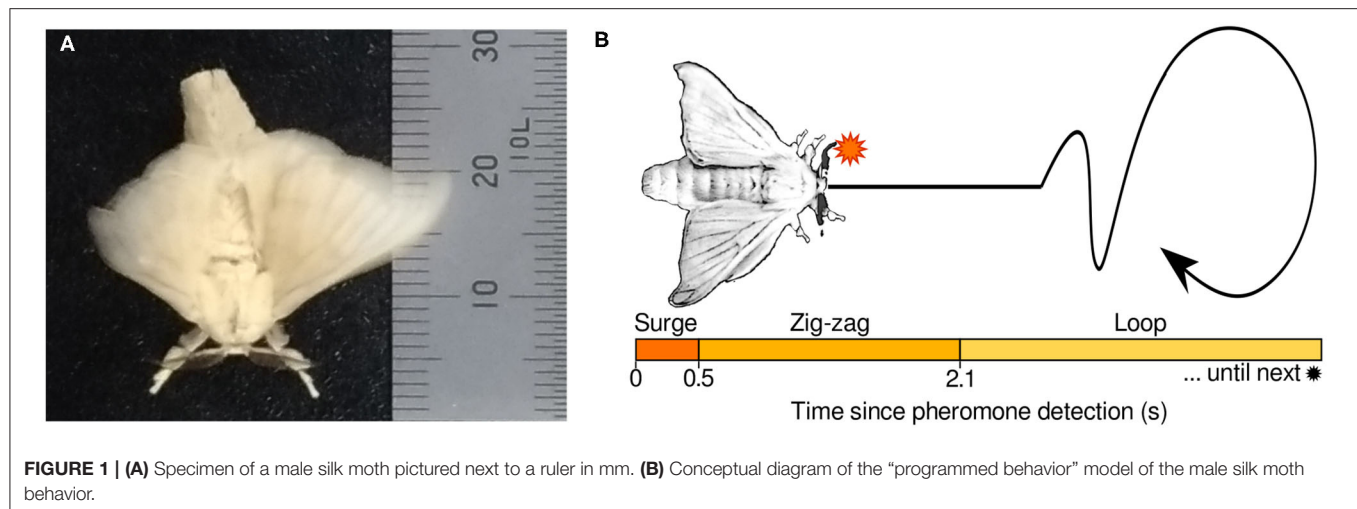
This paper is structured as follows: section 2 states the research questions of this paper. Section 3 describes the usage of optogenetic silk moths, the experimental virtual reality system to measure their behavior, and how to model it as infotaxis agents. Section 4 shows the results of the behavior measurement experiments and calculations of the information entropy of infotaxis-modeled silk moths. Section 5 discusses the contributions of this study and possible future areas of research.

2. PROBLEM STATEMENT

In this paper, we look for possible causes of adaptive mechanisms in the olfactory behavior of the silk moth, which are not represented in the programmed behavior model. Specifically, we investigate the following two hypotheses:

- Are deviations from the programmed behavior motivated by higher information gains?
- Can a probabilistic framework such as infotaxis explain how the male silk moth balances exploration and exploitation of olfactory information?

To test the first hypothesis, we need to measure the behavior of the silk moth in an olfactory environment that can be accurately reproduced in each experimental run. Therefore, in this paper we utilize a “virtual reality” behavioral measurement system in which we can subject moths to virtual odor plumes and measure their motor response to odor stimuli. However, such a system faces the challenge of an accurate stimulation of the moth antennae. In other words, stimulating the antennae with gaseous pheromone particles results in uncertain stimulation because such particles diffuse in the air; hence, they do not produce stimuli with the same intensity or duration each time. To overcome this, we employed genetically modified silkmooths that elicit their normal olfactory behavior response when subjected



to a blue light stimulus at their antennae; thus, we can present reproducible olfactory inputs.

To test the second hypothesis we modeled the trajectories of silkmoths as an agent that minimizes the information entropy of its probabilistic belief of the location of an odor source. Such a maximally informative agent is based in the infotaxis algorithm (Vergassola et al., 2007). We related the decrease in entropy of the infotaxis-modeled moth to the time steps in which the moth behavior matched or mismatched the programmed behavior model. Finally we determined whether infotaxis can explain the exploration-exploitation strategy of the silk moth behavior by evaluating the distribution of entropy reductions by either matching or mismatching behaviors.

3. MATERIALS AND METHODS

Here, we describe our methodology for conducting olfactory search experiments with optogenetic male silk moths and a non-invasive behavior measurement system. We also describe the method we used to represent the silk moth trajectories as those of an infotaxis agent. The silk moth experiments in this study were examined and approved by the Tokyo Institute of Technology Gene Recombination Experiments Safety Management Committee.

3.1. Virtual Reality System for Measurement of Moth Behavior

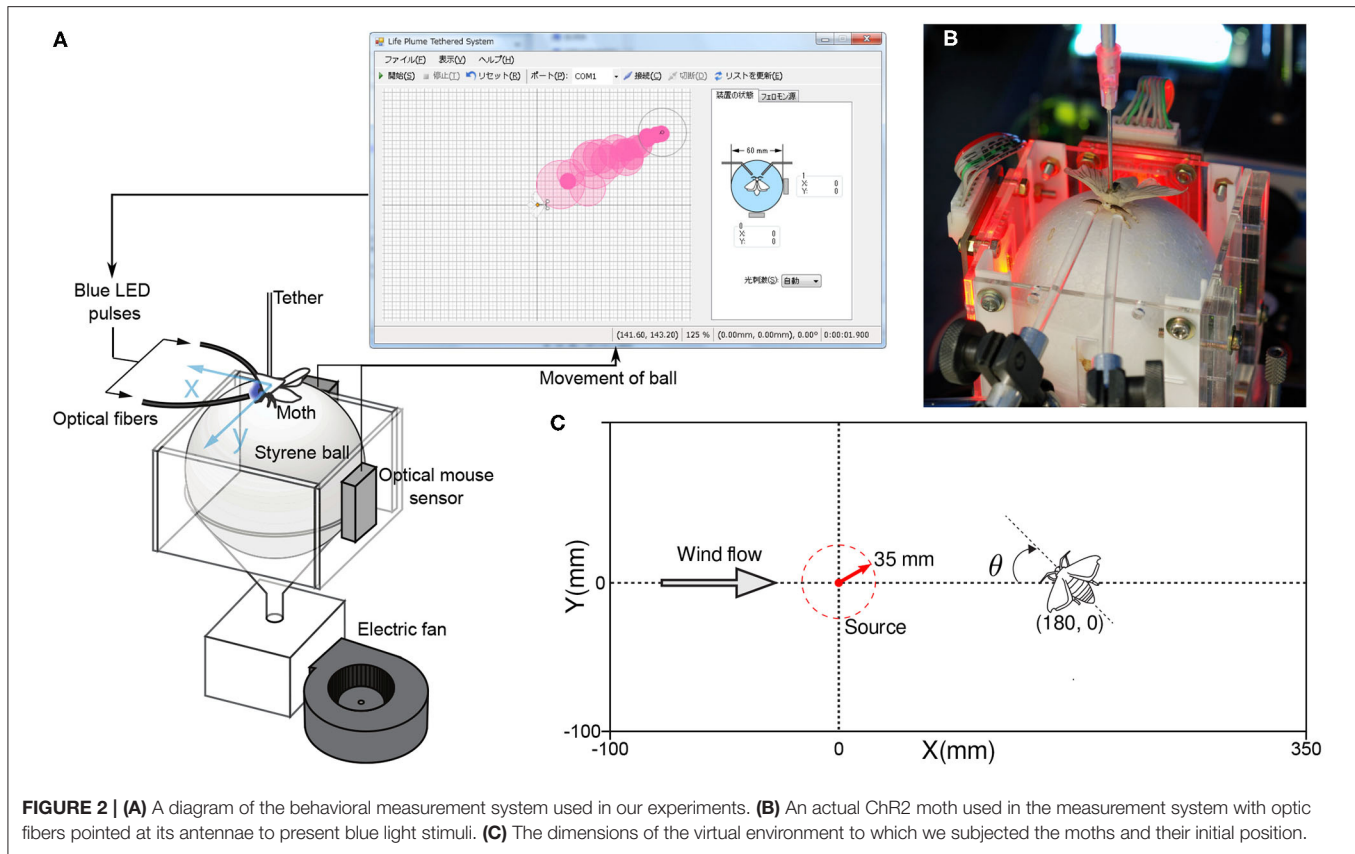
We conducted non-intrusive behavioral measurements on tethered male silk moths. Although similar systems to measure the olfactory behavior of insects have been used in the past (Shigaki et al., 2018a, 2019b), in this study we ensure that odor stimuli are accurately presented by using optogenetic silk moths. Using genetically modified specimens that react to blue light stimuli in the same way as normal specimens react to the pheromone bombykol, allowed us to present stimuli accurately and with reproducibility. This is because gaseous pheromones diffuse in the air; therefore, not all stimuli present the same amount of pheromone molecules to the antennae

of the moth. Furthermore, in this case, the response of the antennae is measured using an electroantennogram (EAG), which is technically challenging and subjected to electrical noise; in addition, damage to the antennae may occur. Our non-invasive behavior measurement system for the silk moth is shown in **Figure 2**, and fulfills the following purposes:

- Measuring the pose (x, y, θ) of the moths.
- Accurately presenting light stimuli to the antennae of the moth.
- Subjecting moths to a virtual odor plume to which we can alter the emission rate, wind speed, and other parameters.

To measure the pose of the silk moth, we fixed its back to a thin aluminum rod ($\varnothing$ 2 mm; length 150 mm) with glue (G17 Bond, Konishi K.K., Osaka, Japan) and placed it on a polystyrene sphere ($\varnothing$ 60 mm), which served as a two-dimensional treadmill. When the moth walked, the sphere moved in response because it was being levitated by the flow of wind from a small fan (FW1251-1051C2ALARX, ARX, Wanchai, Hong Kong). The movements of the sphere were detected using two optical sensors, such as those found in a computer mouse (ADNS-5030, Avago Technologies, California, USA), at a sampling rate of 20 Hz. They were then translated into translational and rotational movements of the moth, that is, the pose.

We developed a virtual representation of an odor plume by modeling the dispersion of white smoke in a wind tunnel. First, we recorded videos of the dispersion of smoke. We also calculated the statistics of the position and intensity of the pixels in the smoke video. Based on these statistics, we programmed a random process that generates virtual circular puffs that match the intensity and transit the positions of the real smoke puffs in the video. An example of a virtual plume is shown in **Figure 2A**. In addition to the virtual representation of the odor plume, we also programmed a virtual representation of a silk moth. As in the real world, the virtual moth reacts to the virtual plume and travels toward its source. By using a virtual odor plume environment, we can tune parameters such as wind speed, emission rate, and particle lifetime. Tuning such parameters is



particularly useful in infotaxis-based behavior modeling because it allows for faster testing of various plume structures and higher reproducibility; compared with real plume experiments. In summary, the following process describes the operation of our experimental device:

1. The moth in the virtual world encounters a puff of pheromone.
2. Blue light is shown to the real moth depending on which antenna of the virtual moth reacted.
3. The real moth moves after receiving the stimulus.
4. The movement of the real moth is sent to the virtual world.
5. The virtual moth reflects the movement of the real moth.
6. The loop is repeated until either the moth reaches the virtual source or until a predetermined time limit is passed.

3.2. Use of Optogenetic Moths for Accurate Antennae Stimulation

The presentation of accurate stimuli is important for the applied infotaxis-based analysis because updating the probability distribution of the source position; as well as the calculation of the expected entropy decrease, are directly affected by whether the agent experiences a hit or not at a given time step. In addition, reproducible odor stimuli are an overall useful property for an olfactory behavior measurement system because their duration and frequency can be finely tuned. Both properties have been reported to directly influence the olfactory behavior of moths (Celani et al., 2014) and other animals (Ache et al., 2016). To

present olfactory stimuli to the moth, previous studies have presented pheromones from glass tubes placed directly in front of the antennae of the moth. However, the amount of pheromone particles that effectively reach the antenna varies owing to their gaseous nature.

To ensure that each stimulus has the same intensity and is accurately sensed by the antennae, we utilized genetically modified moths. These BmOR1-GAL4/UAS-ChR2 silk moths (ChR2 hereinafter); express channelrhodopsin-2 in their olfactory receptor neurons. As a result, they execute their olfactory search behavior when their antennae encounter blue light, rather than pheromone particles. This property has been used in previous studies to ensure that all stimuli are reproducible with the same intensity and duration (Shigaki et al., 2018b, 2019a). To activate channelrhodopsin-2, i.e., blue light sensitivity in these moths, we injected all-trans retinal (ATR) into their abdomen on the day before the experiments; because insects do not intrinsically possess ATR. All behavior measurement experiments were conducted from 9:00 to 17:00 to reduce circadian effects (Tomioka et al., 1993). It is reported that brain serotonin level increases in the daytime and that serotonin enhances pheromones sensitivities in the silk moth (Gatellier et al., 2004).

We generated stimuli for the ChR2 silk moths with LEDs (LBW5AP-JYKY-35-Z; Osram Opto Semiconductors), which produced blue light with a 470 nm wavelength and a light intensity of more than 1.6 mW/mm². Such values of wavelength

and light intensity have been reported to reliably produce olfactory search responses in ChR2 moths (Tabuchi et al., 2013). On each LED, we attached optical fibers of 3 mm in diameter to ensure that blue light was directed only to each antenna, as seen in **Figure 2B**. In addition, moths are unable to make yaw turns because their back is glued to an aluminum rod. The only rotation they are able to make is on their neck (see **Supplementary Video**). However, this neck rotation is very small and it does not decrease the sensibility or the amount of stimulation to the antennae.

3.3. Modeling the Silk Moth as an Infotaxis Agent

Infotaxis was first proposed by Vergassola et al. (2007) as an odor source search algorithm for turbulent environments. In this algorithm, a point-mass agent is located at a position $\mathbf{r}$ and searches for an odor source by iteratively reducing its uncertainty about the distribution of possible source locations $\mathbf{r}_{src}$. The agent has knowledge of its trajectory, $\mathcal{T}_t$, which contains its sequence of positions as well as the odor “hits” it has experienced throughout the search. The agent also maintains a probability map $P(\mathbf{r}_{src}|\mathcal{T}_t)$ or “belief” (Thrun et al., 2005) about the location of the source. This belief spans all possible locations of the source $\mathbf{r}_{src}$ that in both the original infotaxis study and the present paper, consist of a two-dimensional lattice of discrete locations. The certainty of the belief $P(\mathbf{r}_{src}|\mathcal{T}_t)$ is represented by Shannon’s entropy as in Equation (1):

$$S_t = S[P(\mathbf{r}_{src}|\mathcal{T}_t)] = - \sum_{\mathbf{r}_{src}} P(\mathbf{r}_{src}|\mathcal{T}_t) \ln(P(\mathbf{r}_{src}|\mathcal{T}_t)) \quad (1)$$

The goal of infotaxis is to minimize the entropy of the belief $P(\mathbf{r}_{src}|\mathcal{T}_t)$; therefore, at every time step, the agent calculates the expected change of entropy by moving from its current position $\mathbf{r}_t$ to a future position $\mathbf{r}'$ as defined in Equation (2).

$$E[\Delta S(\mathbf{r}_t \mapsto \mathbf{r}')] = p^* \Delta S^* + (1 - p^*) \Delta S \quad (2)$$

Where p^* is the probability of finding the source at $\mathbf{r}'$, and ΔS^* and ΔS are the change in entropy if the source is found or not found at $\mathbf{r}'$, respectively. The agent then executes the move $\mathbf{r}_t \mapsto \mathbf{r}'$ with the largest negative value of $E[\Delta S]$, or; in other words, the move that causes the greatest reduction of uncertainty in the agent’s probability map of the possible source locations. **Figures 3A,B** show conceptual representations of the agent’s belief as well as the effect of odor detections on such belief. Detailed derivations of the infotaxis formulae are presented in **Appendix A** of this paper.

We modeled the body of the silk moth as a point agent with a radius of 10 mm (half of its average body length). We reduced the three degrees of freedom of the moth to (x, y) coordinates because an infotaxis agent moves in a two-dimensional grid ignoring the orientation. Furthermore, we considered as odor hits only those that occurred when the moth was facing upwind, that is, when $\cos(\pi - \theta + \theta_{src}) > 0$ (see **Figure 3C**), where θ and θ_{src} are the angle of the moth and the plume’s centerline, respectively. We considered this capture region because real moths limit the

odor hits to those coming from the front by flapping their wings (Loudon and Koehl, 2000).

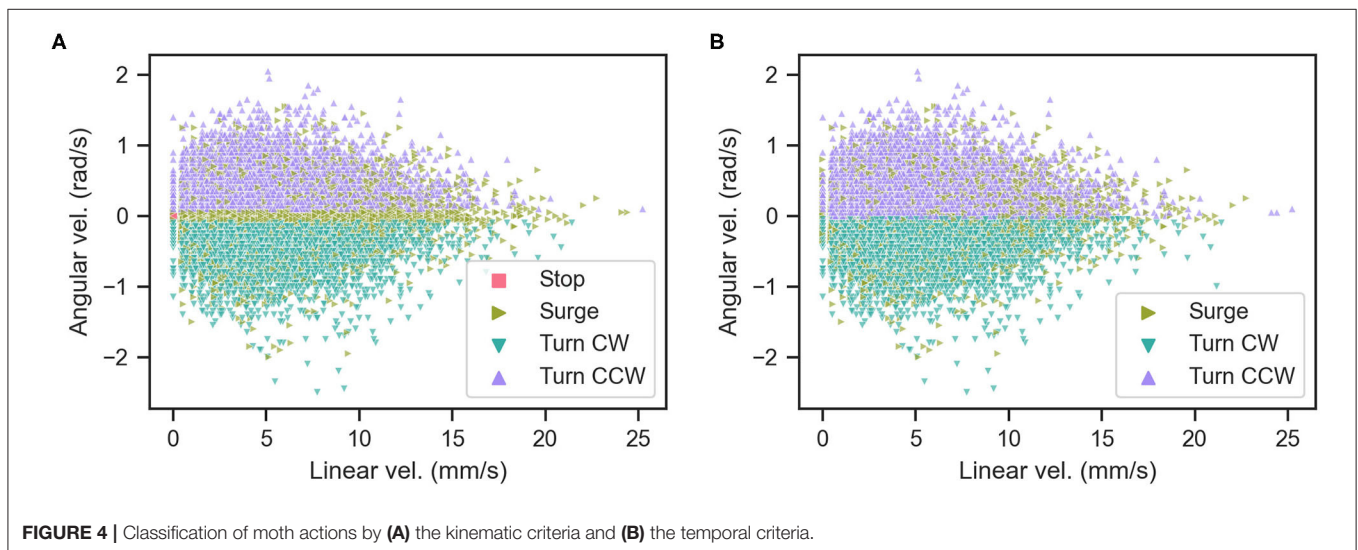
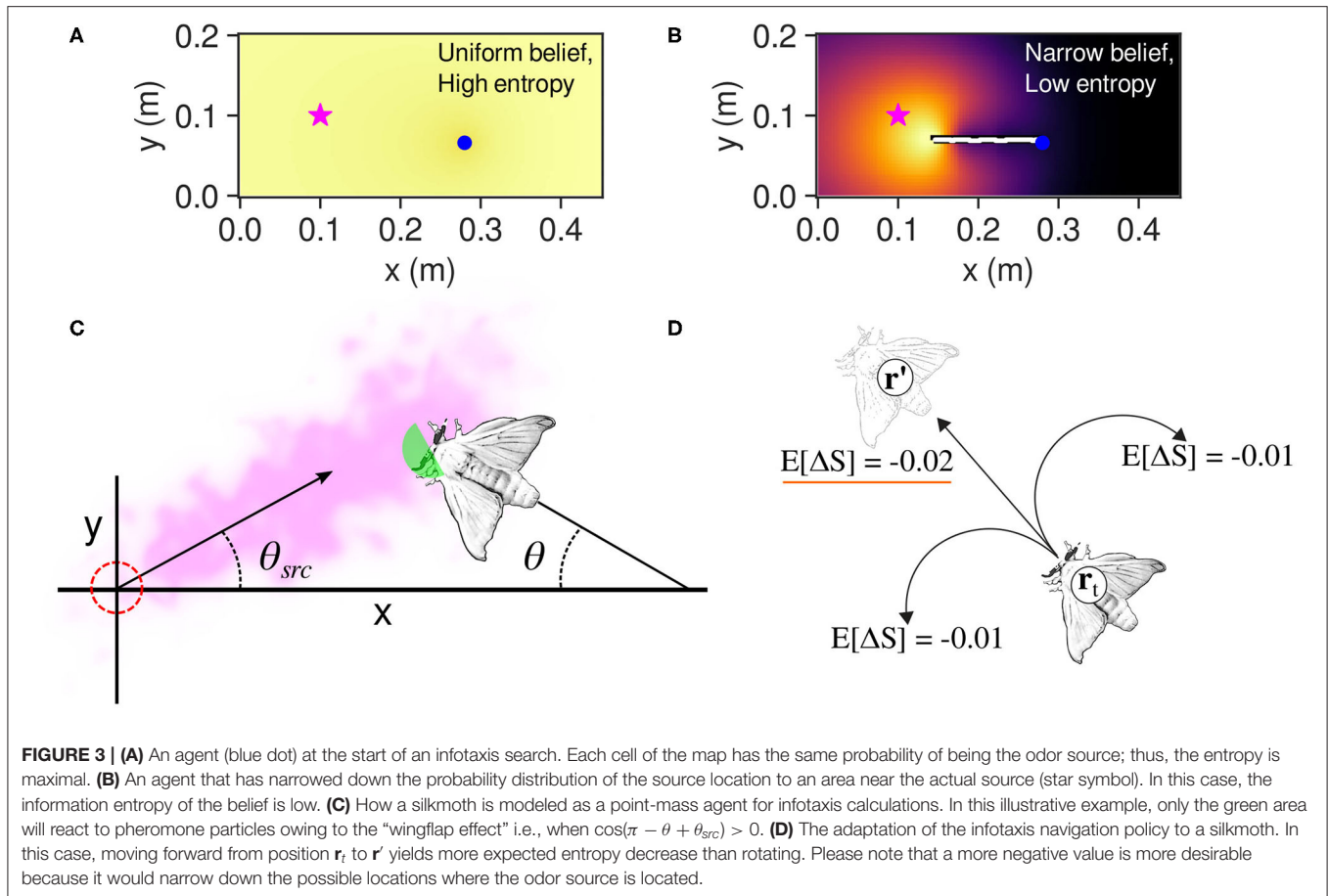
3.4. Classification of Variability in the Moth Behavior

We determined whether the behavior of the silk moth matches the definition of the programmed behavior (Kanzaki et al., 1992) by comparing it to the definition of Minegishi et al. (2012). Accordingly, we classified the maneuvers of the silk moth by simply considering the time elapsed since the last odor hit, which we call “blank duration” τ_b as in Celani et al. (2014). We also classified maneuvers according to both τ_b and the moth’s linear and angular velocities (v and ω , respectively) based on Minegishi et al. (2012). We denote the first and second classification as “temporal” and “kinematic,” respectively. **Table 1** shows a comparison of both schemes used to classify maneuvers and **Figure 4** shows the result of using each scheme. The blank duration threshold of 500 ms in the “temporal” classification of **Table 1** was selected because this is the average duration of surge motions after an odor hit as reported in Kanzaki et al. (1992). Throughout all olfactory search experiments, we classified the moth maneuvers by both schemes and labeled the state of the moth at each time step as “matching” if it matches the criteria of both schemes and “mismatching” if it only matches the “kinematic” criteria.

To determine whether “mismatching” behaviors are motivated by higher information gains, we analyze the value of the entropy change ΔS and the expected entropy change $E[\Delta S]$ regarding the rate of odor hits and the cumulative odor hits experienced by moths over a search. We are particularly interested in these variables because recent studies identified that they influence the decision-process of olfactory behaviors (Celani et al., 2014; Pang et al., 2018). We also evaluate whether the distribution of ΔS is different for “matching” and “mismatching” behaviors with a two-sample Kolmogorov-Smirnov test and by comparing their histograms. In addition, we calculate the cumulative density function (CDF) of ΔS and $E[\Delta S]$ to specifically determine whether “mismatching” behaviors have a higher probability of obtaining larger negative values of those variables, that is, greater information gains. Finally, we calculate the root mean squared error (RMSE) between the values of ΔS and $E[\Delta S]$ to determine what type of behavior is more similar to infotaxis, regarding the rate of odor hits and the cumulative sum of hits, which are our variables of interest. The following section presents the results of the calculations of ΔS and $E[\Delta S]$ regarding hit rate and cumulative hits, the histograms and CDFs, and the RMSE of “matching” and “mismatching” behaviors.

4. RESULTS

Here, we present the results of the VR odor source search experiments using optogenetic silkmooths. First, we present the trajectories of the moths as well as their information entropy. We then show the statistics of the matching versus mismatching states, followed by the relationship between those two states and the expected decrease in information entropy for each.



4.1. VR Olfactory Search Experiments

We subjected ChR2 silkmoths to olfactory search experiments. We conducted 20 trials in which the moth searched for a pheromone source in a 350 mm long by 200 mm wide virtual environment where the wind was blowing in the positive

x -direction at a mean speed of 0.1 m/s. The initial position of the moth in the virtual environment was $(x, y, \theta) = (180, 0, -\pi/6)$, where θ is in radians. Moths searched for a source located at $(x, y) = (0, 0)$ by entering a radius of 35 mm around it under a time limit of 180 s. The mean $\pm$ std. dev. of the time required to reach

TABLE 1 | Definitions for the maneuvers of silk moths when classified by either a temporal or a kinematic state.

	Temporal	Kinematic
Surge	$\tau_b \leq 500$ ms	$\tau_b \leq 500$ ms and $v > 0$ or $\tau_b > 200$ ms and $ \omega < 5\text{deg/s}$
Rotate	$\tau_b > 500$ ms	$\tau_b > 500$ ms and $ \omega > 0$
Stop	Otherwise	Otherwise

the source was 73.92 ± 46.5 s. **Figure 5A** shows the information entropy for the experiments where moths found the pheromone source. The solid line represents the average value, the shaded range represents the standard deviation, and the gray lines show the value for each trial. **Figure 5B** shows the moth trajectories of these successful trials. The color gradient represents the value of the information entropy. **Table 2** shows the statistics of the matching and mismatching moth states. Surge (temporal) and Rotate (kinematic) represent the proportion of time taken when the silk moths exhibited a mismatching state over the entire duration of the search experiments. In total we conducted 20 experiments with 10 specimens. Out of these, 12 trials from six specimens successfully found the odor source under the time limit; thus achieving a success rate of 60.0%. We considered only the data from the successful trials for the classification of matching and mismatching behaviors.

4.2. Relationship Between Behavior Variability and Information Gains

We investigated whether there is a relationship between mismatching maneuvers and a higher expected decrease in entropy $E[\Delta S(\mathbf{r}_t \mapsto \mathbf{r}')]$. **Figure 6** shows the actual rewards ΔS and expected rewards $E[\Delta S]$ of the match and mismatch behaviors. As can be seen in **Figures 6A,C**, matching and mismatching behaviors generate large decreases in entropy at low or high hit rates, respectively. In addition, the matching behaviors generated penalties (entropy increase) at high numbers of accumulated hits. Please note that entropy is non-monotonous (Hajieghrary et al., 2016; Rodríguez et al., 2017) and can increase on detection to non-detection sequences since the agent's belief is narrowed by the detection but broadens again at the non-detection. **Figures 6B,D** show that the expected rewards are greater at low or high hit rates for mismatching and matching behaviors, respectively. **Figures 7A,C** show histograms of the actual and expected rewards, respectively. We validated the statistical difference in the distributions of the matching and mismatching states (Kolmogorov-Smirnov test $p < 0.01$).

Figure 7B shows the cumulative density function of the actual rewards ΔS for matching and mismatching behaviors. As shown in the figure, mismatching behaviors have a higher probability of greater entropy reductions (particularly values of approximately 10^{-4} and 10^{-1}). Mismatching behaviors also have a higher probability of a larger decrease in entropy (values of approximately -4×10^{-3}) as shown in **Figure 7D**. **Figures 8A,B** show the cumulative odor hits and hit rate against the root mean squared error between the actual

ΔS and the expected reward $E[\Delta S]$. This was calculated as shown in Equation (3), where N is 20 because the sampling frequency of the behavioral measurement system is 20 Hz.

$$RMSE = \sqrt{\frac{1}{N} \sum_{i=1}^N (\Delta S_{i+1} - E[\Delta S_i])^2} \quad (3)$$

5. DISCUSSION

In this study, we investigated the possible causes of variability in the programmed behavior model of the male silk moth. Specifically, we asked whether such variability leads to higher information gains; in other words, if it minimizes the information entropy of the probability distribution of the moth regarding the location of an odor source. We also investigated whether the probabilistic framework of infotaxis can explain how the male silk moth selects maneuvers to balance the exploration and exploitation of the expected rewards.

5.1. Relationship Between Behavioral Variability and Information Rewards

In a recent study, Shigaki et al. (2019b) simultaneously measured the odor search behavior of male silkmoths and the neural activity from their lateral accessory lobe (LAL). The LAL generates motor commands in response to odor stimuli. That study found that silkmoths are less likely to “surge” (move forward) as the frequency of odor hits increases. In terms of infotaxis, this can be interpreted as moths preferring rotations (exploration) because, at high odor encounter rates, the expected decrease in entropy is less than at low rates. Our results found that matching and mismatching behaviors generate rewards at high and low hit rates, respectively (**Figure 6**). Thus, this leads us to believe that at high hit rates, silk moths prefer reactive or more exploitative behaviors, and at low rates, they prefer more stochastic or explorative behaviors such as rotations instead of straight forward moves. Furthermore, this tendency was observed on all specimens that reached the odor source.

An interesting interpretation of these results can also be made from the viewpoint of reinforcement learning (RL). In this field, an agent learns to behave according to an optimal policy with the highest expected accumulated reward over a time horizon. Nonetheless, many RL algorithms face the exploration and exploitation dilemma in which greedily selecting the actions with the highest reward can lead to suboptimal policies stuck in the local maxima. A common way to avoid this is to add stochasticity in the selection of actions; thus balancing exploration and exploitation, using methods such as ϵ -greedy algorithms (Sutton and Barto, 2018). An analogy can be made to the behavior of the silkmoth in the sense that some randomness in the selection of the “surge” maneuver leads to higher information gains and possibly a better odor source search performance. This can be clearly seen in **Figures 7B,D**, where

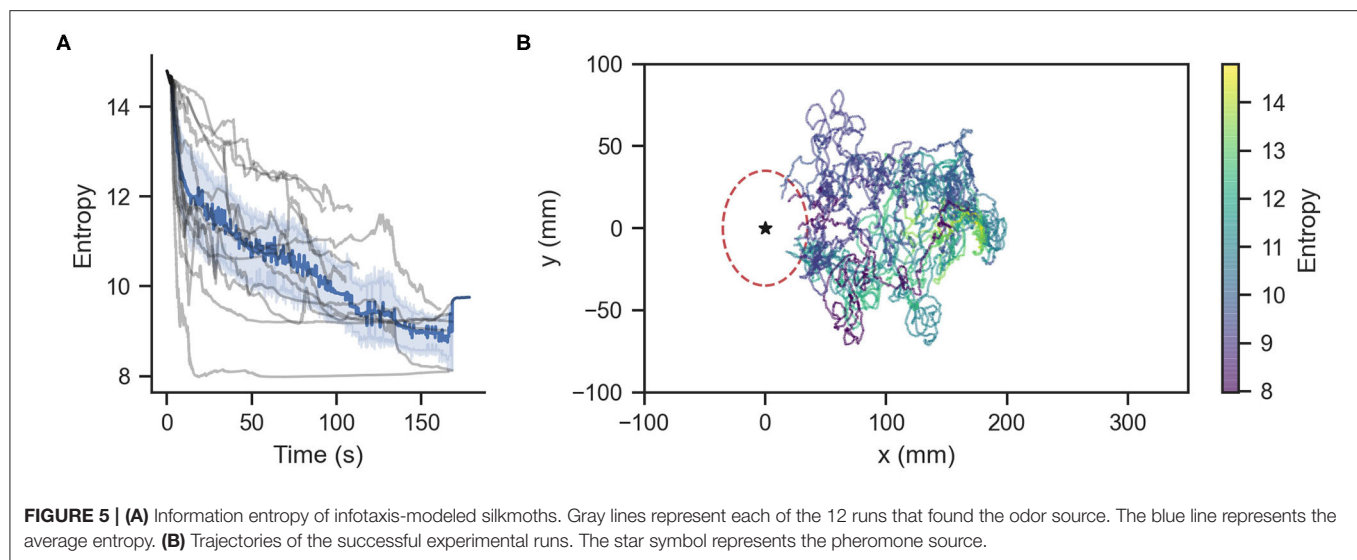


TABLE 2 | Normalized counts of each maneuver taken by the moths.

Kinematic	Temporal	
	Surge	Rotate
Surge	0.1597 ± 0.07	0
Rotate	$^{**}0.1939 \pm 0.11$	0.6464 ± 0.19

The “kinematic” classification scheme is based on the linear and angular velocities of the moths. The “temporal” scheme is based on the time since the last odor hit. The values with the asterisks indicate “mismatching” behaviors.

the probability of obtaining better rewards is higher for the mismatching behaviors.

5.2. Exploration and Exploitation in Silk Moth Behavior

We found that maneuvers that deviate from the programmed behavior model correspond to a larger expected decrease in entropy, that is, a higher expected reward in the terminology of reinforcement learning. Therefore, we demonstrated the capability of the infotaxis strategy to quantitatively express maneuvers that deviate from the programmed behavior as explorative and those that match it as exploitative.

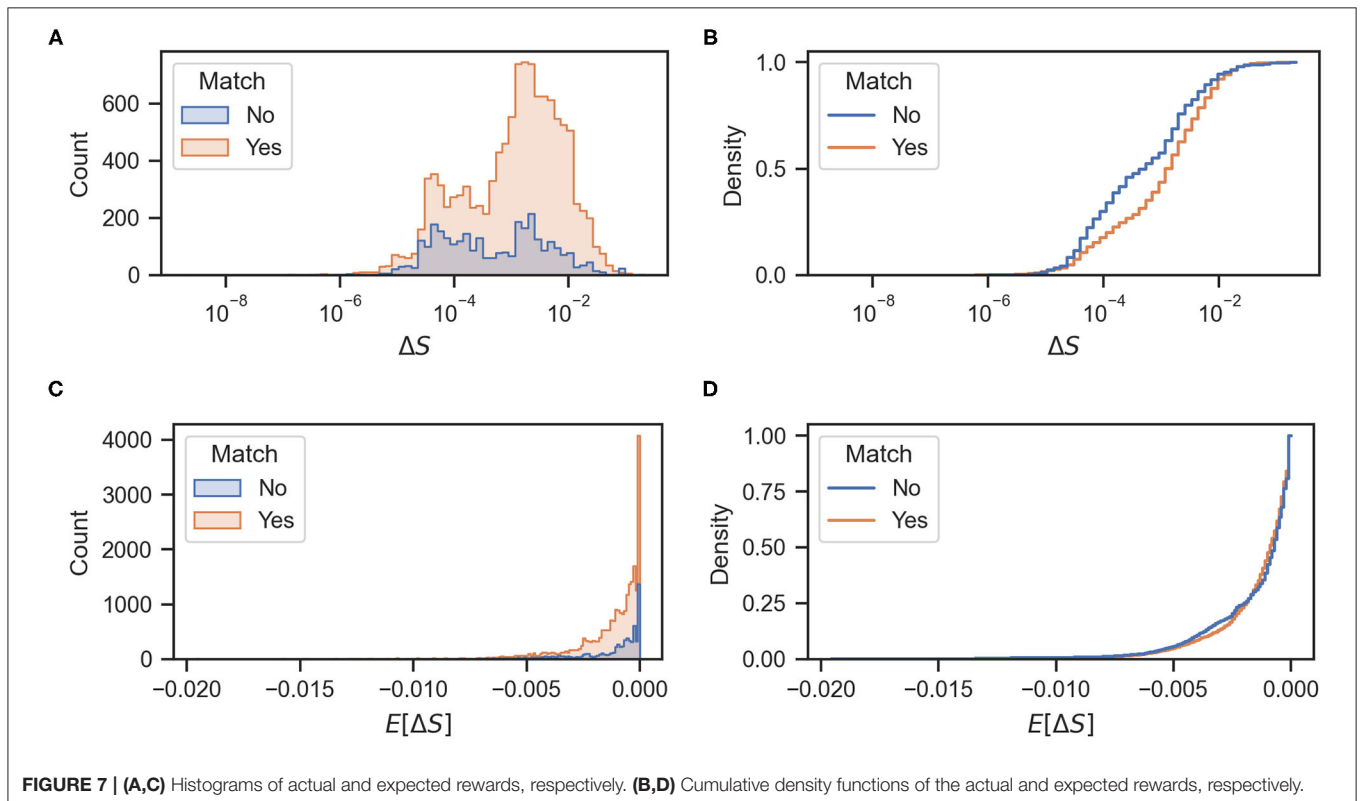
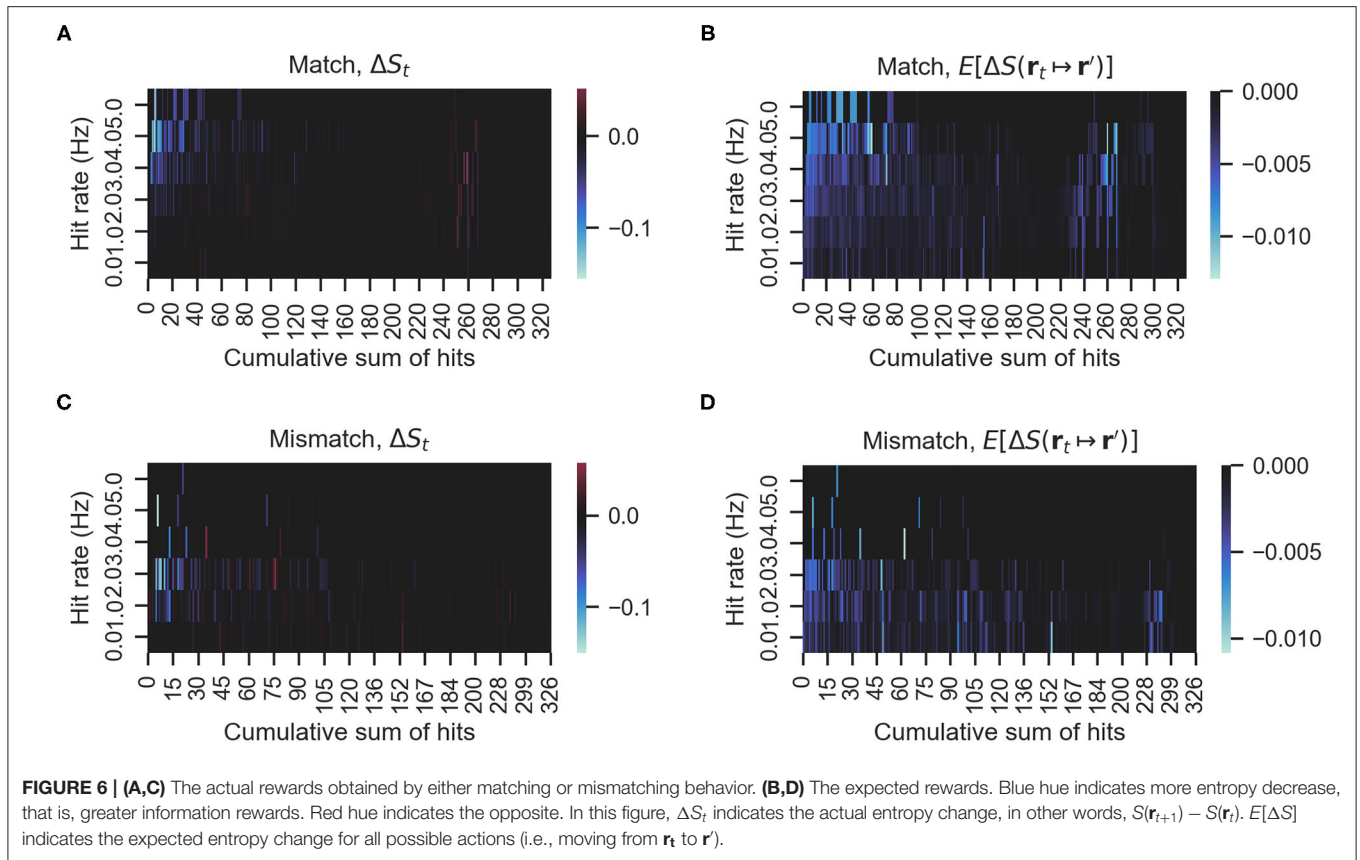
Another interesting point to note is the relationship between matching and mismatching behaviors with the root mean squared error (RMSE) of the real vs. expected rewards. As shown in **Figure 8A**, the error decreases proportionally to the accumulation of odor hits. This is relatively intuitive because more detections narrow down the belief of the source location. However, more RMSE occurs between real and expected rewards at times of high hit rates. Furthermore, the matching behaviors have a lower error than the mismatching behaviors. One possible interpretation for this is that matching behaviors are more

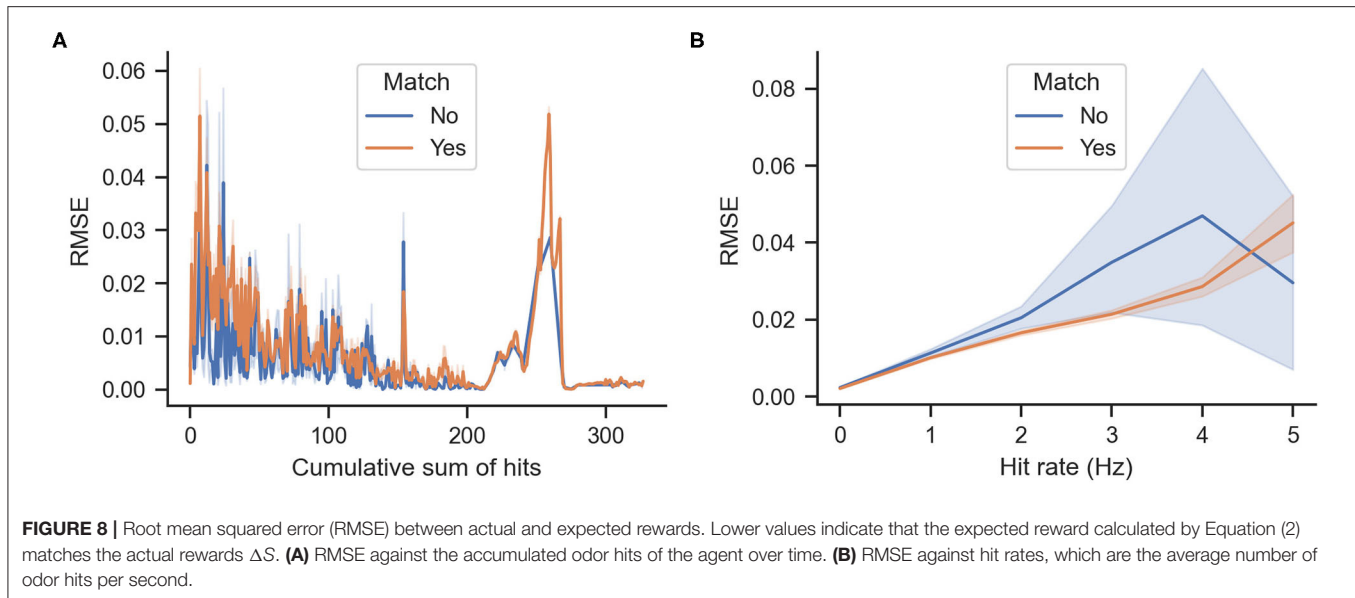
exploitative; thus they are more similar to the greedy infotaxis policy, whereas the mismatching behaviors are more explorative; hence, they differ from the expected reward of the infotaxis strategy.

We believe that being able to represent animal olfactory behavior through a method such as infotaxis is an important contribution to the fields of ethology and robotics because having a representation of the decision process of animals in terms of probabilistic beliefs and expected rewards facilitates the algorithmic implementation of these processes in robots. Furthermore, it allows for the refinement of these decision processes using tools such as machine and reinforcement learning.

6. CONCLUSION

In this study, we measured the behavior of moths using a virtual reality system that presents accurate and reproducible odor stimuli by using blue light and optogenetic moths. We then took trajectories from these measurements and modeled them as an infotaxis (Vergassola et al., 2007) strategy. We used infotaxis-based modeling to determine if variability in the silkmoth behavior is related to higher gains in information regarding the probabilistic distribution of the source location. We found that variations have a higher probability of obtaining larger information gains than “programmed behaviors” (i.e., reactive, exploitative behaviors). This suggests that silkmoths incorporate some stochasticity into their behavior to balance the exploration and exploitation of information gains. Future studies should be conducted to develop ways to extract decision-making mechanisms from free-running silkmoths. In this study, we used tethered moths walking on a treadmill, and, although such a device imposes minimal disturbances on the moth behavior, we believe it is necessary to study whether models from free-running experiments will differ from those in this specific study. It would also be useful to develop an olfactory search algorithm based on





the silkmoth exploration/exploitation mechanisms elucidated in this paper and then implement such an algorithm on a robot to test whether the search performance is improved compared with either the programmed behavior or the infotaxis strategy.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Files, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

CH-R, SF, SS, and DK contributed conception and design of the study. SF conducted the virtual reality silk moth experiments. CH-R performed the numerical analyses and wrote

the manuscript. TS, RK, and HS provided genetically modified silk moths. All authors read and approved the submitted version.

FUNDING

CH-R acknowledges funding from Instituto de Innovación y Transferencia de Tecnología (I2T2) and Consejo Nacional de Ciencia y Tecnología (CONACYT). This work was also partially supported by JSPS KAKENHI under Grant JP19H02104, JP19H04930, and JP19K14943.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fncom.2021.629380/full#supplementary-material>

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Conflict of Interest: SF was employed by MHPS Ltd.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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APPENDIX A: INFOTAXIS STRATEGY

Herein, we provide a more detailed explanation of the derivation of the infotaxis formulae. We based this explanation on the work of Pang (2018) and the original infotaxis strategy developed by Vergassola et al. (2007). The agent's belief in the source location $P(\mathbf{r}_{src}|\mathcal{T}_t)$ can be written using Bayes' theorem, as indicated in Equation (A1).

$$P(\mathbf{r}_{src}|\mathcal{T}_t) = \frac{P(\mathcal{T}_t|\mathbf{r}_{src})P(\mathbf{r}_{src})}{P(\mathcal{T}_t)} \propto P(\mathcal{T}_t|\mathbf{r}_{src})P(\mathbf{r}_{src}) \quad (\text{A1})$$

where $P(\mathcal{T}_t|\mathbf{r}_{src})$ is the likelihood of the source position and $P(\mathbf{r}_{src})$ is the prior distribution of the source. Infotaxis assumes that odor hits and misses are independent of one another and the likelihood of the source position takes the following form:

$$P(\mathcal{T}_t|\mathbf{r}_{src}) = \prod_t P(h(\mathbf{r}_t)|\mathbf{r}_{src}) \quad (\text{A2})$$

where $h(\mathbf{r}_t)$ is 1 if the agent detects an odor hit at time t and 0 if it detects a miss. The infotaxis strategy considers that the number of hits follows a Poisson distribution; hence, the probability of a hit or miss becomes the following:

$$P(h(\mathbf{r}_t) = 0|\mathbf{r}_{src}) = \exp[-R(\mathbf{r}_t|\mathbf{r}_{src})\Delta t] \quad (\text{A3})$$

$$P(h(\mathbf{r}_t) > 0|\mathbf{r}_{src}) = 1 - P(h(\mathbf{r}_t) = 0|\mathbf{r}_{src}) \quad (\text{A4})$$

where $R(\mathbf{r}_t|\mathbf{r}_{src})\Delta t$ is the mean rate of hits the agent expects at $\mathbf{r}_t$, during a time period of Δt , given a source position $\mathbf{r}_{src}$. The **Supplementary Material** of the original paper on infotaxis indicate that the hit rate is derived from the advection-diffusion equation of a turbulent plume and define it as follows:

$$R(\mathbf{r}|\mathbf{r}_{src}) = \frac{E}{\ln\left(\frac{\lambda}{\alpha}\right)} e^{\frac{(x_{src}-x)V}{2D}} K_0\left(\frac{|\mathbf{r}-\mathbf{r}_{src}|}{\lambda}\right) \quad (\text{A5})$$

$$\lambda = \sqrt{\frac{D\tau}{1 + V^2\tau/(4D)}} \quad (\text{A6})$$

where E is the emission rate of odor particles, which have an effective diffusivity D and, a finite lifetime τ , and are advected by a wind with mean velocity V that blows in the positive x -direction. K_0 is the modified Bessel function of order zero, and α is the radius of a round-shaped agent. In our calculations of the information entropy of the silkmoth we used the following parameters into Equation A6: $\alpha=10$ mm, $E=1$, $\tau=6.3$ s, $D=0.012$, and $V=0.1$ m/s to match the wind speed in the moth experiments. The range of possible values for the source location was a 1730×770 lattice; i.e. the size of each cell was 0.26 mm. For Equation A4 we set Δt to 50 ms; which is the same as the sampling period of the treadmill described in section 3.1. At each time step, the belief

of the source position distribution $P(\mathcal{T}_t|\mathbf{r}_{src})$ can be recursively updated as follows:

$$P(\mathbf{r}_{src}|\mathcal{T}_{t+1}) = P(h(\mathbf{r}_{t+1})|\mathbf{r}_{src})P(\mathbf{r}_{src}|\mathcal{T}_t) \quad (\text{A7})$$

At each time step, the agent considers five possible actions: moving forward, backward, left, right, or waiting. For each possible action, it calculates the probability p_* that the action will result in finding the source:

$$p_* = \sum_{\mathbf{r}_{src}} P(\mathbf{r}_{src}|\mathcal{T}_t) P(|\mathbf{r}' - \mathbf{r}_{src}| \approx 0) \quad (\text{A8})$$

Consequently, the probability of not finding the source is $1 - p_*$. If the source is found, then the entropy of the belief will become zero, that is, $\Delta S^* = (0 - S_t) = -S_t$. To balance the exploration and exploitation, the agent also considers the case in which it does not find the source after taking an action. In such case, it would sample from the environment either a miss with a probability p_m or a hit with a probability $p_h = 1 - p_m$. The probability of sampling a miss is the average of the miss probability over the range of possible source locations:

$$p_m = \sum_{\mathbf{r}_{src}} P_m(\mathbf{r}_{src}|\mathcal{T}_t) = \sum_{\mathbf{r}_{src}} P(h(\mathbf{r}') = 0|\mathbf{r}_{src})P(\mathbf{r}_{src}|\mathcal{T}_t) \quad (\text{A9})$$

where $\mathbf{r}'$ is the future position of the agent after taking an action. The agent also estimates how its source position belief, as well as its entropy, would change after moving. The change in entropy after sampling a miss or a hit at $\mathbf{r}'$ would be the following:

$$\Delta S_m = - \sum_{\mathbf{r}_{src}} P_m(\mathbf{r}_{src}|\mathcal{T}_t) \ln(P_m(\mathbf{r}_{src}|\mathcal{T}_t)) - S_t \quad (\text{A10})$$

$$\Delta S_h = - \sum_{\mathbf{r}_{src}} P_h(\mathbf{r}_{src}|\mathcal{T}_t) \ln(P_h(\mathbf{r}_{src}|\mathcal{T}_t)) - S_t \quad (\text{A11})$$

Overall, the agent calculates the expected change of entropy by moving from $\mathbf{r}_t$ to $\mathbf{r}'$ as follows:

$$E[\Delta S(\mathbf{r}_t \mapsto \mathbf{r}')] = p^*(0 - S_t) + (1 - p^*)(p_m \Delta S_m + p_h \Delta S_h) \quad (\text{A12})$$

where the terms on the left and right sides of the sum are the change in entropy if the source is found or not found at $\mathbf{r}'$, respectively. Finally, the agent chooses the action a with the largest expected decrease in entropy (see **Figure 3D**) as:

$$a = \arg \min_{\mathbf{r}'} (E[\Delta S(\mathbf{r}_t \mapsto \mathbf{r}')]) \quad (\text{A13})$$

After making a move, the agent encounters either a miss or a hit from the odor plume and updates the probability distribution of the source location. The agent then repeats the navigation policy process iteratively until it finds the source.



Self-Learning Event Mistiming Detector Based on Central Pattern Generator

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Received: 15 November 2020

Accepted: 11 January 2021

Published: 04 February 2021

Citation:

Szadkowski R, Prágr M and Faigl J
(2021) Self-Learning Event Mistiming
Detector Based on Central Pattern
Generator.
Front. Neurobot. 15:629652.
doi: 10.3389/fnbot.2021.629652

A repetitive movement pattern of many animals, a gait, is controlled by the Central Pattern Generator (CPG), providing rhythmic control synchronous to the sensed environment. As a rhythmic signal generator, the CPG can control the motion phase of biomimetic legged robots without feedback. The CPG can also act in sensory synchronization, where it can be utilized as a sensory phase estimator. Direct use of the CPG as the estimator is not common, and there is little research done on its utilization in the phase estimation. Generally, the sensory estimation augments the sensory feedback information, and motion irregularities can reveal from comparing measurements with the estimation. In this work, we study the CPG in the context of phase irregularity detection, where the timing of sensory events is disturbed. We propose a novel self-supervised method for learning mistiming detection, where the neural detector is trained by dynamic Hebbian-like rules during the robot walking. The proposed detector is composed of three neural components: (i) the CPG providing phase estimation, (ii) Radial Basis Function neuron anticipating the sensory event, and (iii) Leaky Integrate-and-Fire neuron detecting the sensory mistiming. The detector is integrated with the CPG-based gait controller. The mistiming detection triggers two reflexes: the elevator reflex, which avoids an obstacle, and the search reflex, which grasps a missing foothold. The proposed controller is deployed and trained on a hexapod walking robot to demonstrate the mistiming detection in real locomotion. The trained system has been examined in the controlled laboratory experiment and real field deployment in the Bull Rock cave system, where the robot utilized mistiming detection to negotiate the unstructured and slippery subterranean environment.

Keywords: locomotion, central pattern generator, Hebbian learning, phase estimation, radial basis function neuron, reflexes, hexapod walking robot, bio-inspired robotics

1. INTRODUCTION

Maintaining fluent gait motion in a body with a high degree of freedom while continually reacting to terrain irregularities is a challenging problem that, however, can be observed in nature (Bekey, 1996). During the gait, the legged locomotion control sustains the regular repetitive motion using reflexive reactions triggered by detected motion irregularities. In nature, animals demonstrate stunning adaptability to motion disruptions through reflexes (Pearson and Franklin, 1984; Duysens et al., 2000). Many of such reflexes are wired in neural circuits located close to the legs inside the vertebrates' spine or thoracic ganglia of many invertebrates. The spinal neural circuits must

recognize an irregularity in the locomotion through proprioception to trigger a reflex (Bekey and Tomovic, 1986). Hence, the irregularity recognition needs a model of regularity to which a measured state is compared. In this work, we focus on phase irregularities, where the timing of the measured event is compared to its estimate. The tool for phase modeling is a neural structure that centrally generates rhythms, the Central Pattern Generator (CPG).

CPGs play an essential role in gait locomotion control. The CPG's rhythmic patterns are combined with the sensory-motor neural circuits and stabilize the gait periodicity. The CPG activity and spinal neural control can generally be controlled by descending (e.g., from the brain) signals. Interestingly, the locomotion can be sustained without the brain's participation and sensory input in virtual locomotion (Brown, 1912), since the CPG sustains its rhythmic signals even if it is disconnected from its sensors and effectors. This suggests the CPG can work in an open-loop mode, and thus the CPG provides the motor control even without input excitations. On the other hand, if the CPG is synchronized to the sensory signals, the CPG acts as an estimator of the sensory phase (Kuo, 2002).

We can identify that some signals are tightly coupled to the gait motion and thus inherit the gait period, such as swing stop or ground contact. The CPG that synchronizes to such a periodic signal continually estimates the signal phase. The estimated and measured sensory phase should be the same during a regular motion. However, a regular motion disturbed by unexpected dynamics, elevations, and depressions can induce disturbances in the sensory signal. Hence the motion irregularities can be detected by comparing the measured sensory phase with its estimation (Miall and Wolpert, 1996). Any difference between the timing of the measured and estimated sensory events can be utilized for mistiming detection (Goldschmidt et al., 2014), which is insufficiently researched within the context of plastic CPG-based neural networks.

In this paper, we propose a trainable CPG-based event mistiming detector integrated into gait controller architecture introduced in Szadkowski and Faigl (2020). Unlike common architectures that model the phase of sensed (input) signal and motor (output) signal with one CPG, the employed architecture models each signal with either the motor CPG, generating the motor signal phase, or sensory CPG, estimating the phase of the sensory signal. We propose to utilize the sensory CPG for the detection of irregularities in the sensory phase. We couple a plastic Radial Basis Function (RBF) neuron to each sensory CPG, which learns to anticipate sensory events. The difference in timing of anticipated and measured events is the phase error. The error is integrated by Leaky-Integrate-and-Fire (LIF) neuron, which learns to distinguish the regular phase error induced by regular measurement imperfections, and fires on irregular phase error detecting the event mistiming. Two types of event mistiming are distinguished: event absence, which occurs when the sensory event is delayed, and event disruption occurs when the sensory event is too early; see **Figure 1**. Both types of event mistiming are detected by the

proposed CPG-based mistiming detector that augments the sensory feedback information.

We demonstrate the benefits of the proposed mistiming detector using the detection as a trigger of two reflexes: the elevator and search reflexes. The elevator reflex elevates the leg to avoid an obstacle detected during the leg swing phase. The search reflex is a behavior where the leg searches for supporting ground after not detecting the expected support at the end of the swing phase. Hence, the elevator reflex is triggered by the early stop of the swinging leg, and the escape reflex is triggered by ground contact absence. Finally, even though the focus of this work is plastic mistiming detection, we also extend the motor control of our previous work to control multiple motion phases with position and maximum torque commands.

The proposed CPG-based controller is deployed on a real hexapod walking robot. The robot is trained to walk tripod gait on flat terrain. First, the robot self-learns to estimate the sensory phase needed for mistiming detection in a regular environment. Then, we demonstrate the mistiming detector by guiding the robot over elevations and depressions in two scenarios. In the first scenario, the robot walks in a controlled environment, where the detections are isolated and thus easily observable. The second scenario tests the proposed controller's limits in the Bull Rock cave system, which provides highly unstructured terrain depicted in **Figure 1A**.

The rest of the paper is organized as follows. The following section is dedicated to related work. In section 3, the phase estimation problem is described within the context of gait control and the theoretical foundations for the event mistiming detection. The CPG-based controller is presented in section 4, where the sensory prediction and mistiming detection system is described, followed by the description of the motor control and reflex system. The experimental deployment is described in section 5 and further discussed in section 6. Finally, the paper is concluded in section 7.

2. RELATED WORK

CPG-based gait controllers were proposed for many robots and body models, where the controller implementations vary in architecture. In this section, we provide a brief overview of existing related CPG-based controller architectures. In particular, we focus on whether the CPG represents the phase of a sensory signal (input), motor/control signal (output), or both. Existing CPG-based controllers primarily use the CPG as a generator of the motor phase. For example, the CPG in the controller presented in Maufroy et al. (2008) determines whether the leg is in the extension or flexion phase to select a subnetwork that controls the respective actuator. Similarly in limbless locomotion, a chain of coupled CPGs controls the flexion rhythm of each servomotor in a modular lamprey-like robot (Li et al., 2014). Locomotion patterns can be changed by altering the parameters of the CPG. In Yu et al. (2020), the frequency of the CPG oscillation is temporarily increased as a part of reflexive behavior, where the leg performs fast spiral motions. Switching the topology of coupling between CPGs changes the gait pattern,

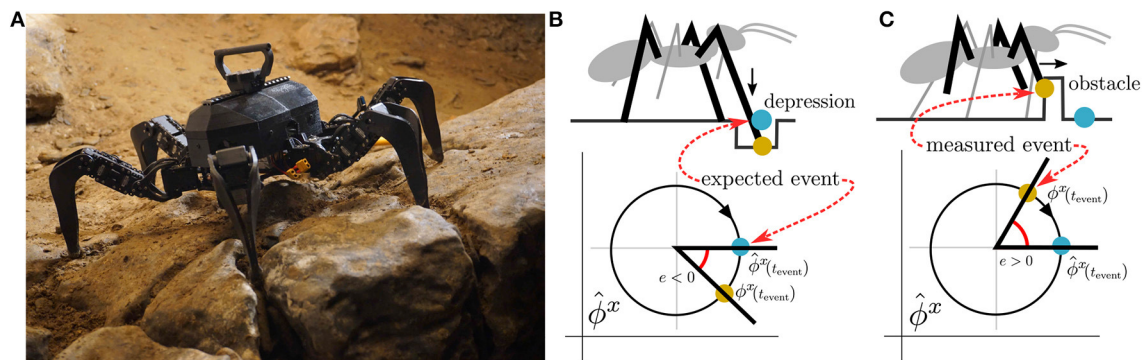


FIGURE 1 | (A) The utilized hexapod walking robot in Bull Rock cave. The unstructured environment causes motion disturbances, which result in sensory event mistiming. The sensory phase ϕ^x measurement is compared to its estimation $\hat{\phi}^x$, where their difference is the phase error e . We distinguish two types of phase error: event absence, $\phi^x > \hat{\phi}^x$, and disruption, $\phi^x < \hat{\phi}^x$. An example of event absence is illustrated in **(B)**, where at the beginning of the stance phase, the front leg finds itself in a depression (orange dot) and thus detects the ground contact later than expected (blue dot). In the disruption example **(C)**, at the end of the swing phase, the front leg hits elevated terrain (orange dot) and thus detects the ground contact sooner than expected (blue dot).

which is used in Wang et al. (2014) where CPG network generates multiple gaits for a fish-like robot, such as forward and backward swimming and turning. Besides the motor signal generation, a CPG can also be used as a sensory phase estimator. A CPG that is entrained by a periodic sensory signal can become synchronized with the signal where the phases of the CPG and its entraining signal evolve at the same rate (except for a short transient behavior) (Pikovsky et al., 2001). In Kuo (2002), Kuo proposes the CPG synchronization to model the sensory signal phase continuously. He showed that the actuator controller that uses the CPG's sensory estimate, is more stable than a controller using a raw sensory signal.

The difference between a motor CPG and a sensory CPG is that the former represents an actuator phase, while the latter represents a phase of the entraining sensory signal. Assuming the sensor and motor phases are the same, a single CPG can represent both phases. In Yan et al. (2017), it is assumed that the gait phase is a function of the sensory phase, e.g., a function of the hip joint angle. Thus the gait phase is estimated by the CPG synchronized to sensory events, such as maximum hip flexion. The functional dependence between the sensory and motor variables is implicitly assumed by synchronizing the CPG to the sensory input and using the same CPG as the motor phase generator (Fukuoka et al., 2003; Endo et al., 2004; Righetti and Ijspeert, 2006). However, such an architecture needs some prior knowledge about the robot morphology, where it must be determined which motors and sensors are functionally dependent. On the other hand, the morphology agnostic approach is not to assume any functional dependence and model each phase, be it sensory or motor, with its respective CPG. The controller presented in Hélot and Espiau (2008) is composed of a layer of the sensory CPGs estimating the phase that is fused and fed into the central motor CPG, which controls the gait phase. A more general approach is presented in our previous work (Szadkowski and Faigl, 2020), where both the sensory and the motor variables have their own CPGs forming a layer of sensory CPGs, which is connected to a layer of the motor CPGs. Hence, the CPGs in biomimetic controllers have two basic

roles: motor phase generator and the sensory phase estimator. In the rest of this section, we focus on the sensory CPGs only, as the proposed approach enriches their utilization.

A sensory model that estimates the sensory state can help in the detection of motion disturbances. In the context of animal locomotion, such disturbances can be small obstacles, depressions, slippage, and others, to which the animal reacts with reflexes documented in Pearson and Franklin (1984) and Duysens et al. (2000). The reflexes are triggered by proprioceptive events such as increased load on a muscle or tensile sensing (Bekey and Tomovic, 1986; Duysens et al., 2000), which indicates a motion disturbance. Motion disturbance detection is implemented in a number of biomimetic reflex controllers, where each reflex has to be triggered by such a disturbance. The disturbance detection can be realized by comparing the estimated values with the measured ones; if the difference is too high, a disturbance is detected. In the context of periodic sensory signals, two differences can be measured: difference in amplitude and difference in phase. The amplitude trigger is simple; the detector directly measures a value above (or below) a certain threshold, which triggers the reflex reaction. For example, the reflexive slip responses can be triggered by detecting leg movement while the leg is on the ground (Boone and Hodgins, 1995). The elevator reflex, where the leg avoids an obstacle blocking its protraction during a swing motion, can be triggered by a significant angle error in the protractor motor, as shown in Klaassen et al. (2002). The author of Bläsing (2006) shows that the search reflex, where the leg tries to find support during the stance, can be triggered by lowering the leg under the threshold, which indicates a gap. Besides, the search and elevator reflexes are implemented in multiple other controllers (Espenschied et al., 1996; Li et al., 2018; Yu et al., 2020). However, the above-mentioned reflex triggers are hand-tuned and thus dependent on the robot body morphology. Generally, the robot morphology can change in time or is not entirely known, and thus the disturbance detection algorithm must adapt. A simple, adaptive mechanism is used

in Lewinger and Quinn (2010), where the system remembers the depressor motor position during the last stance. Another learning algorithm is presented in Kirkwood et al. (1989), where the controller is trained to fuse multiple sensor inputs into a given reflex trigger.

The presented amplitude-based detectors are dependent on measuring unusual sensory values directly, where the value crosses a threshold. However, some disturbances do not change the sensory signal's amplitude but a phase, causing a sensory mistiming, such as the absence of anticipated foot contact or protraction stopping too early. The event mistiming can be detected from the difference between the phase measurement and phase estimation provided by the internal model. Generally, the internal model estimates the sensory feedback either by directly processing the current sensory measurement or processing the copy of motor command (so-called efference copy) (Miall and Wolpert, 1996). In Goldschmidt et al. (2014) the efference copy from a motor CPG is processed into a ground contact phase estimation, where the absence of ground contact triggers the search reflex. Maffei et al. pointed out that the sensory model that maps the efference copy onto sensory estimation is sensitive to the specific controller configuration. The authors propose to adapt the sensory model directly to the sensory feedback (Maffei et al., 2017). In the context of phase estimation, the CPG entrained to the sensory feedback estimates the sensory phase. The idea of phase estimating CPGs introduced in Kuo (2002) is expanded in Dzeladini et al. (2014), where the difference between the measured and estimated sensory phase is used as a corrective term that participates in motor activity regulation. However, the authors use one CPG per actuator and select the entraining sensory feedback using prior knowledge.

In the proposed approach, we leverage the sensory/motor CPG distinction presented in Szadkowski and Faigl (2020) and design a self-learning mistiming detector on the sensory CPG layer. Hence, the main expected advantage of the proposed motion irregularity detection is that no prior knowledge about sensory-motor relation is needed.

3. PROBLEM STATEMENT

The sensory mistiming detection is based on the periodicity of the sensory signal, which is entrained by the repetitive gait motion. The repetitive motion pattern arises from the rhythmical motor actuation. The motor actuation is controlled by the *control signal* $\mathbf{u}(t)$ which has period T^{gait} during the regular motion. The periodically actuated body interacts with the environment, and the effects of the interactions are measured by sensors. We focus on such a *sensory signal* $\mathbf{x}(t)$ that inherits the actuation periodicity T^{gait} . The motor $\phi^{\mathbf{u}}$ and sensory $\phi^{\mathbf{x}}$ phases are defined as variables that grow linearly with time at the rate $\omega^{\text{gait}} = 2\pi(T^{\text{gait}})^{-1}$ during the regular motion, formally $\dot{\phi}^{\mathbf{x}} = \dot{\phi}^{\mathbf{u}} = \omega^{\text{gait}}$; see Figure 2. Likewise, we define the sensory amplitude $A^{\mathbf{x}}$ as a variable that does not change, i.e., $\dot{A}^{\mathbf{x}} = 0$ and similarly for the motor amplitude $A^{\mathbf{u}}$; however, this work is focused on the phase variables.

The *phase difference* between sensory and motor phases $\Delta\phi^{\mathbf{ux}} = \phi^{\mathbf{u}}(t) - \phi^{\mathbf{x}}(t)$ is not changing in regular environments with $\Delta\dot{\phi}^{\mathbf{ux}} = \dot{\phi}^{\mathbf{u}} - \dot{\phi}^{\mathbf{x}} = 0$, but it is dynamic in irregular environments, which cause disturbance of the motion. The motion disturbances propagate into the controller through the sensory signal, and the controller needs to react to sustain the regular gait.

The disturbance in a sensory signal can be assessed by comparing the sensory signal with the *sensory estimation* $\hat{\mathbf{x}}(t)$. Focusing on the phase, the *sensory phase estimation* $\hat{\phi}^{\mathbf{x}}(t)$ yields the phase of a sensory signal during regular motion: $\hat{\phi}^{\mathbf{x}}(t) = \omega^{\text{gait}}t + \Phi$, where Φ is the sensory phase at $t = 0$. During the regular motion, the phase difference between estimated and measured phase, referred to as *phase error*, is $e(t) = \phi^{\mathbf{x}}(t) - \hat{\phi}^{\mathbf{x}}(t) = 0$. However, the phase error can be non-zero due to sensory signal disturbances caused by irregular motion. The authors of Pikovsky et al. (2001) describe the disturbance in dynamic systems with stable periodicity as perturbations in the phase and amplitude of the system. The perturbations can be approximately formalized as $\dot{A}^{\mathbf{x}}(t) = p^A(t)$ and $\dot{\phi}^{\mathbf{x}}(t) = \omega^{\text{gait}} + p^{\phi}(t)$, where $p^A(t)$ and $p^{\phi}(t)$ are amplitude and phase perturbations, respectively. The phase error then gains dynamics driven by the phase perturbation $\dot{e}(t) = \omega^{\text{gait}} + p^{\phi}(t) - \omega^{\text{gait}} = p^{\phi}(t)$. Hence, the positive error $e(t) > 0$ represents sensory signal being ahead of time while negative $e(t) < 0$ is being delayed, which is illustrated in Figures 1B,C. If the phase error accumulated over one gait cycle exceeds a given threshold, $\int_{\tau-T^{\text{gait}}}^{\tau} |e(t)| dt > \theta$, then the *sensory mistiming* is detected at the time τ .

There are two necessary tools for detecting the sensory mistiming: the sensory phase estimator $\hat{\phi}^{\mathbf{x}}(t)$ and the phase error threshold θ . Moreover, the sensory phase is rarely measured continually, as pointed out in Héliot and Espiau (2008). Instead, it is measured as a short periodic event, and only during this sensory event, the phase measurement can be compared to the phase estimation. In this work, the i -th sensory input $x_i(t) \in [0, 1]$ is a binary signal, where its high level $x_i(t) \approx 1$ indicates the *event*. However, since each sensor has a different sensitivity and the sensory events have different duration, the estimator and the error threshold must be self-learned for each sensor input. The proposed neurodynamic approach for self-learnable mistiming detection and its utilization in gait locomotion is presented in the next section.

4. THE GAIT LOCOMOTION CONTROLLER

This section presents the proposed sensory event mistiming detector that is integrated within the CPG-based gait controller. The overall architecture of the gait controller, depicted in Figure 3, can be described as two coupled sub-controllers: the *phase control*, which estimates the phase of sensory input and generates the motor phase, and the *amplitude control*, which generates the command values for the actuators. The phase controller is composed of two CPG layers: the *sensory CPGs* that estimate the phase for each i -th sensory input $\phi_i^{\mathbf{x}}$, and the *motor CPGs* that generate the motor phase of each j -th actuator

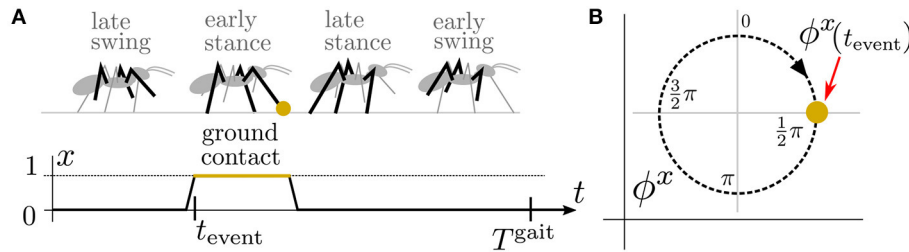


FIGURE 2 | (A) An illustration of an ant during the tripod gait, a motion pattern where three legs propel the body while the other three legs swing forward. During the tripod gait, the ant puts a front leg on the ground and senses the ground contact with $x(t_{\text{event}}) = 1$ at the fourth of the gait period $t_{\text{event}} = \frac{1}{4}T_{\text{gait}}$. During the regular motion, such an event occurs periodically with $x(t_{\text{event}} + nT_{\text{gait}}) = 1$ for any $n \in \mathcal{N}$. Therefore, **(B)** for the sensory signal x , we define the sensory phase ϕ^x on which we can map the event occurrence at $\phi^x(t_{\text{event}} + nT_{\text{gait}}) = \frac{1}{2}\pi$ for any $n \in \mathcal{N}$. Notice that the sensory phase is directly measured only at t_{event} , and there is no sensory phase measurement for the rest of the gait cycle.

ϕ_j^u . The sensory CPGs provide a continuous estimation of the sensory input phases utilized by the motor CPG. The motor CPGs generate the phase of the motion for each actuator. Based on the motor phase, the amplitude control generates the control signal u_j for each j -th actuator, which performs the regular motion. In this work, the amplitude control is extended with reflex reactions to motion disturbances triggered by mistiming detection. The mistiming detector is an extension of the sensory CPG layer utilizing the provided sensory phase estimation.

4.1. Central Pattern Generator as Phase Estimator

The CPG provides a stable periodic rhythm that can be synchronized with an input signal. In the gait motion context, the periodic stability sustains the motion periodicity while the synchronization is utilized for the sensory phase estimation. The synchronization is a property of CPGs modeled as a dynamic system with a limit-cycle attractor (Pikovsky et al., 2001). The employed CPG can be formalized as follows.

Let $\dot{\mathbf{y}} = f(\mathbf{y}, c(t)) \in \mathbb{R}^D$ be the CPG dynamics in the D -dimensional space with the input signal $c(t)$. The limit-cycle $\mathbf{Y} \subset \mathbb{R}^D$ is a closed trajectory in the phase space to which the unperturbed dynamic system $\mathbf{y}(t)$ converges. After the convergence, the unperturbed CPG produces a stable periodic signal with the natural frequency ω^{CPG} . If the CPG is entrained by the periodic signal $c(t)$ with a frequency close to the natural frequency $\omega \approx \omega^{\text{CPG}}$, the CPG synchronizes the input signal. The synchronization is a phase relation, where the phase difference between the CPG output and the entraining signal $\Delta\phi^{yc} = \phi^y(t) - \phi^c(t)$ becomes stable. Note that the stable phase difference implies that the entrained CPG frequency becomes the same as the entraining signal frequency $\omega^{\text{CPG}} = \omega$, and if the phase of the input signal shifts, the phase of the CPG shifts as well. Hence, the phase of the synchronized CPG continuously estimates the phase of the entraining signal: $\hat{\phi}^c(t) = \phi^y(t) - \Delta\phi^{yc}$. However, since neither the phase difference $\Delta\phi^{yc}$, nor the function that maps the CPG state $\mathbf{y} \in \mathbf{Y}$ onto the CPG phase $\phi^y(t)$ are known in general, the explicit value of the CPG phase $\phi^y(t)$ cannot be directly used in practice. Instead, we exploit the fact that there exists one-to-one mapping between the CPG phase $\phi^y(t) \in [0, 2\pi)$ and the

limit-cycle points $\mathbf{Y}(\phi^y) = \mathbf{y}$. Thus, since $\mathbf{Y}(\phi^y - \Delta\phi^{yc}) = \mathbf{Y}(\hat{\phi}^c)$ is one-to-one mapping, each point on the limit-cycle $\mathbf{y} \in \mathbf{Y}$ represents the phase of the entraining signal $\hat{\phi}^c$. This limit-cycle representation of the input signal phase is the essential CPG property in the proposed approach.

We employ Matsuoka's neural oscillator (Matsuoka, 1987) as the CPG

$$\dot{\mathbf{y}} = f(\mathbf{y}, c(t)) = \begin{bmatrix} \tau \dot{y}_1 \\ \tau \dot{y}_2 \\ \gamma \dot{y}_3 \\ \gamma \dot{y}_4 \end{bmatrix} = \begin{bmatrix} h(y_3) - y_1 \\ h(y_4) - y_2 \\ -y_3 - h(y_4)\alpha - y_1\beta + 1 \\ -y_4 - h(y_3)\alpha - y_2\beta + 1 + c(t)\lambda \end{bmatrix}, \quad (1)$$

$$h(z) = \max(z, 0), \quad (2)$$

where the parameters $\alpha = 2.5$, $\beta = 2.5$, $\tau = 0.5$, and $\gamma = 0.25$ define the limit-cycle $\mathbf{Y} \subset \mathbb{R}^4$ to which $\mathbf{y}$ converges; and the parameter $\lambda = 0.5$ scales the input signal $c(t)$. The input signal of the sensory CPG is the sensory signal $c(t) = x(t)$; thus, the limit-cycle $\mathbf{Y}$ represents the sensory phase.

4.2. Sensory Event Mistiming Detection

The mistiming detection module, depicted in **Figure 4**, is composed of the CPG estimating the sensory phase, Radial Basis Function (RBF) neuron estimating the sensory event, and Leaky-Integrate-and-Fire (LIF) neuron, which fires on the integrated mistiming error. For each sensory input, the detector is trained to recognize two types of mistiming error: the sensory event absence and disruption.

Event mistiming occurs when a sensory event unexpectedly transpires, or no event happens when the sensory phase estimator expects it. The phase estimation is provided by the sensory CPG entrained by its respective sensory signal $\dot{\mathbf{y}}_i^{\text{sense}} = f(\mathbf{y}_i^{\text{sense}}, x_i(t))$. Assuming the natural CPG frequency and gait frequency are similar $\omega^{\text{CPG}} \approx \omega^{\text{gait}}$, the CPG synchronizes to the sensory signal and thus estimates the phase of the sensory signal continuously.

The sensory event phase estimation is utilized by the RBF neuron, which learns to anticipate the sensory event, when $x(t) \approx 1$. The RBF neuron activity coupled to the CPG represents a

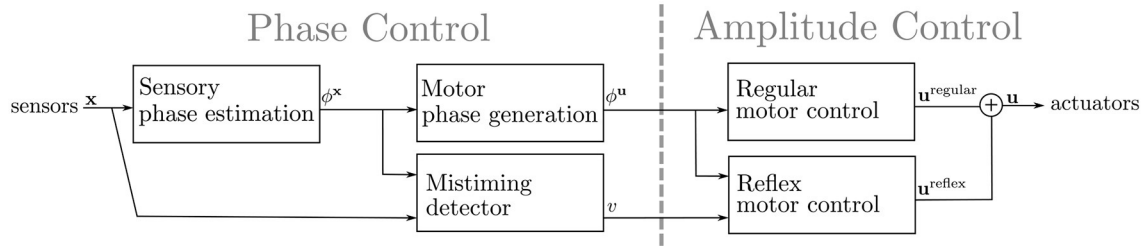


FIGURE 3 | The proposed gait controller architecture takes the sensory signal x as the input and outputs the control signal u . The gait controller is composed of two sub-controllers: (i) Phase Control, which detects the mistiming and regulates the phase of the gait, and (ii) Amplitude Control, which maps the motor phase ϕ^u and mistiming detections v into actuator commands u . The phase control is CPG-based, where a coupled ensemble of CPGs estimates the sensory phase ϕ^x and generates the motor phase ϕ^u . The mistiming detector compares the sensory phase estimation ϕ^x to sensory input x , and self-learns to detect sensory phase errors v . The mistiming detection v and generated motor phase ϕ^u flow into the amplitude control, which transforms the inputs into the control signal u . There are two modules of the amplitude control: the regular control and the reflex control that modifies the regular control if triggered by mistiming detection.

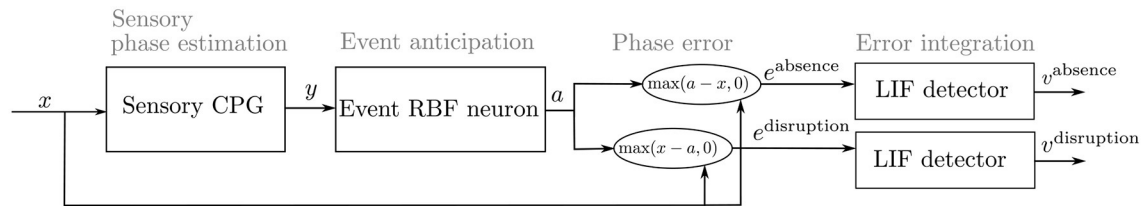


FIGURE 4 | The architecture of the proposed mistiming detector with the sensory phase estimator. The sensory CPG synchronizes the sensory signal x and thus estimates the sensory phase ϕ^x . The RBF neuron learns the phase during which the event occurs; the RBF neuron is active, $a \approx 1$, during the anticipated event. A difference between the RBF neuron activation and sensory signal gives two types of mistiming error: e^{absence} and $e^{\text{disruption}}$. Each error excites its respective LIF neuron, where each LIF neuron learns the activation threshold during the regular motion. If the sensory signal contains disturbances, the LIF activation v exceeds the threshold and fires. The LIF firing detects the mistiming.

particular phase interval, be it motor phase (Pitchai et al., 2019) or sensory phase. The RBF neuron uses the activity function

$$\varphi(\mathbf{y}; \mathbf{m}) = \exp(-\varepsilon \|\mathbf{y} - \mathbf{m}\|^2), \quad (3)$$

where $\mathbf{y}$ is the CPG state and $\mathbf{m}$ is the center parameter. Hence, the RBF neuron is excited if the CPG state is near the RBF center. The excitation timing is learned to be the same as the timing of the regular sensory event using the periodic Grossberg learning rule $\dot{m}_i = v(t)x_i(t)(\mathbf{y}_i - \mathbf{m}_i)$. The periodic Grossberg rule pushes the RBF center near the point on the CPG limit cycle $\mathbf{Y}_i^{\text{sense}}$ that represents the phase during the signal event $x_i(t) \approx 1$. Therefore, the RBF activation $\varphi(\mathbf{y}_i^{\text{sense}}(t); \mathbf{m}_i^{\text{sense}}) = a_i(t)$ anticipates the binary sensory event $x_i(t) \approx 1$.

Motion disturbances can perturb the timing of the sensory event. Then, the perturbed sensory event does not overlap the imitated event $|a_i(t) - x_i(t)| > 0$ and thus generates the phase error. Two types of mistiming errors are used to measure the lack of overlap: the *disruption error* (4) and *absence error* (5):

$$e_i^{\text{disruption}}(t) = h(x_i(t) - a_i(t)), \quad (4)$$

$$e_i^{\text{absence}}(t) = h(a_i(t) - x_i(t)). \quad (5)$$

The disruption error is non-zero $e_i^{\text{disruption}}(t) > 0$ when the RBF neuron does not anticipate the event occurrence, while the absence error is non-zero $e_i^{\text{absence}}(t) > 0$ when the event is anticipated but does not occur.

The mistiming errors indicate the phase perturbation; however, they can also be non-zero during the regular motion in practice. In particular, since the waveforms of the signals $a_i(t)$ and $x_i(t)$ are generally different; thus, there is always some mistiming error even during the regular motion. Moreover, false sensory events may occur due to sensory processing or measurement imperfections. Hence, in practice, the integral of the mistiming error (i.e., the absence or disruption) over one gait period $E(\tau) = \int_{\tau-T^{\text{gait}}}^{\tau} e(t)dt$ might be non-zero even during the regular gait, $E(\tau^{\text{regular}}) > 0$. We assume that if the motion is disturbed during the gait, the integrated mistiming error is greater than the regular error $E(\tau^{\text{disturbed}}) > E(\tau^{\text{regular}})$. Therefore it is possible to set the threshold $\theta = E(\tau^{\text{regular}})$ which delimits the regular sensory input error from irregular.

We propose approximating the integration with the LIF neuron and adapting the firing threshold θ using a learning rule. The LIF neuron with activation dynamics $\dot{v}_i = -v_i\gamma + e_i$ fires when the neuron activation v_i reaches the threshold θ_i . Since the threshold depends on many factors, such as the sensory variance and the shape of the CPG limit-cycle, the threshold must be

parameterized for each sensory input x_i . A similar LIF threshold parametrization problem is described in Diehl and Cook (2015), where authors introduce a learning rule for threshold adaptation. The adaptation mechanism increases the threshold during LIF firing and then slowly decays when LIF is at a non-firing activity. The LIF fire rate is then lower, and it is more likely that LIF fires at an irregular input. We employ the idea of the threshold adaptation in the following dynamics:

$$\dot{\theta}_i = v(t)(h(v_i + \gamma - \theta_i) - (\theta_{\min} - \theta_i)), \quad (6)$$

where γ adds margin to the threshold and $\theta_{\min}$ sets the default threshold value. The threshold is adapted only during learning $v(t) > 0$, when LIF is fed by a regular input; therefore, the LIF threshold is adapted to regular integrated phase error. For each i -th signal input, there are two LIF neurons. The first is for the disruption error $v_i^{\text{disruption}}, \theta_i^{\text{disruption}}$ and the second is for the absence error $v_i^{\text{absence}}, \theta_i^{\text{absence}}$. If a motion irregularity occurs, the integrated mistiming error (the absence or disruption) in the LIF neuron exceeds the respective threshold θ_i , and the neuron fires. Thus, the firing activity of the LIF neuron v_i indicates the mistiming detection, which can trigger a reflex reaction modifying the regular motor control.

4.3. Amplitude Motor Control

The amplitude controller generates a control signal combining the regular gait motion, which produces the tripod gait, and the reflexive motion triggered by sensory event mistiming. The regular motion of an actuator is divided into four phases: first, the (i) early and (ii) late swing phases, and then the (iii) early and (iv) late stance phases, illustrated in **Figure 2**. Each phase defines the joint angle and torque limit set into the actuator during the motion. If a disturbance is detected, the respective reflex reaction modifies the joint angle and torque limit for a short period. Hence, the modification of the regular control causes a reflex behavior.

4.3.1. Control of Regular Motion

The regular motor phase of the j -th actuator is generated by the motor CPG

$$j_j^{\text{motor}}(t) = f(y_j^{\text{motor}}, c_j^{\text{motor}}(t)). \quad (7)$$

Four motor RBF neurons are trained with periodic Grossberg rule to be excited at the corresponding k -th motor phase $\Phi_{j,k}^u$, see **Figure 5A**. For the training, we generate *target binary signals* $d_{j,k}(t) \in [0, 1]$ for six-legged robot walking a tripod gait, where two triplets of legs alternate in stance. Thus, four motor phases $k \in \{1, 2, 3, 4\}$ and legs of the first group $j \in \{\text{actuators of the left front/hind and right middle legs}\}$, the signals are defined as

$$d_{j,k}(t) = \begin{cases} 1 & \text{if for any } n \in \mathbb{N} : t \in [(n + (k - 1)/4)T^{\text{gait}}, \\ & (n + (k - 1)/4 + 0.05)T^{\text{gait}}], \\ 0 & \text{else.} \end{cases}$$

The target signals for actuators of the second group j' are shifted $d_{j',k}(t) = d_{j,k}(t + T^{\text{gait}}/2)$. The four motor phases on the limit-cycle $\mathbf{Y}_j^{\text{motor}}$ are approximated by four RBF centers learned with the periodic Grossberg rule $\dot{m}_{j,k}^{\text{motor}} = v(t)d_{j,k}(t)(y_j^{\text{motor}} - \mathbf{m}_{j,k}^{\text{motor}})$. During the learning, the motor CPG is entrained by the first target signal $c_j^{\text{motor}}(t) = d_{j,1}(t)$ to keep the limit-cycle consistent through multiple learning episodes; see **Figure 5C**. After the learning, the RBF activities $a_{j,k}^{\text{motor}} = \varphi(y_j^{\text{motor}}; \mathbf{m}_{j,k}^{\text{motor}})$, see (3), generate peaks, where each peak indicates the particular motor phase $\Phi_{j,k}^u$.

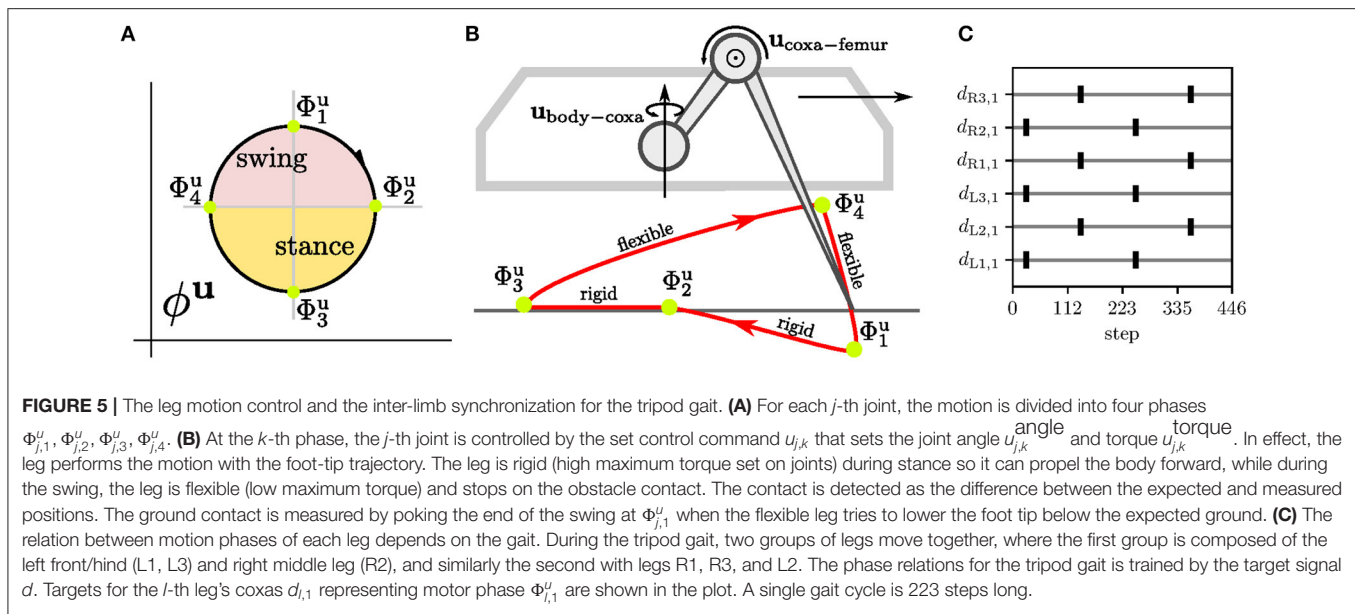
The regular motor control transforms the motor phase into regular actuator commands, see **Figure 3**. Commands of each j -th actuator are $u_j^{\text{angle}} = \sum_{k=1}^{K=4} a_{j,k}^{\text{motor}} u_{j,k}^{\text{angle}}$ and $u_j^{\text{torque}} = \sum_{k=1}^{K=4} a_{j,k}^{\text{motor}} u_{j,k}^{\text{torque}}$ for joint angle and maximum torque, respectively; where $u_{j,k}^{\text{angle/torque}}$ are the set parameters. The motion command parameters are set up so that the leg performs stance and swing, depicted in **Figure 5B**. The swing is designed to be flexible and protracts the leg over the ground. If the leg hits an obstacle, the leg stops due to its flexibility caused by a low torque limit. On the other hand, during the stance, the leg becomes rigid and pushes the body forward by retracting the leg. Three legs move together during the stance, the ipsilateral front, hind legs, and the contralateral middle, creating the tripod gait.

4.3.2. Control During Irregular Motion

The controller provides two mechanisms reacting to the phase error: sensory-motor phase difference stabilization and reflexes. The phase difference stabilization (introduced in the base work Szadkowski and Faigl, 2020) couples the sensory and motor CPGs using a layer of sensory RBFs. Each motor CPG is connected to all sensory CPGs through RBF neurons, each trained by the target signal $d_{j,1}(t)$ to find the corresponding phase on the sensory CPG. Effectively, each sensory RBF center encodes the phase difference between the particular sensory CPG and motor CPG. The averaged sensory RBF activity entrains the motor CPG, and thus the sensory-motor phase difference is stabilized.

The sensory-motor phase difference stabilization is used to handle the long term phase errors. However, reflexes represent a more suitable tool for critical errors since they affect the amplitude control by modifying the regular commands; thus, creating the reflexive behaviors. Two reflexes are implemented in this work: the search reflex and the elevator reflex. The search reflex is triggered by the absence of the ground contact event, and its reaction is the leg's rapid elevation and protraction.¹ The elevator reflex is triggered by a disruption of the protraction stop event, where the leg rapidly retracts and elevates, and then continues the protraction. Both reflexes utilize the presented sensory event mistiming detection and demonstrate the proposed approach in a practical deployment from which results are reported in the next section.

¹It is a simplified version of the search reflex observed in a locust (Pearson and Franklin, 1984), where the insect searches for the foothold with circular motions.



5. DEPLOYMENT AND EMPIRICAL VALIDATION

The proposed CPG-based controller has been deployed on the real hexapod walking robot depicted in **Figure 6A**. The setup of the deployment is detailed in section 5.1. The robot controller learns the motor control for the tripod gait and the mistiming detector; see the description provided in section 5.2. The trained controller has been examined in two scenarios. Section 5.3 reports on the first scenario, where the robot encounters two obstacles, detects mistiming events, and performs the elevator and search reflexes. The robustness of the proposed controller has been examined in the second scenario, described in section 5.4, in which the robot traverses highly unstructured terrain in the Bull Rock cave system. Further, the found insights are discussed in section 6.

5.1. Setup and Deployment

The proposed mistiming detector is deployed on the hexapod walking robot shown in **Figure 6**, a six-legged robot where each leg is formed from three Dynamixel AX-12 servomotors (Faigl and Čížek, 2019). In this work, we control two servo motors per leg: the body-coxa and coxa-femur joint servomotors; the third servomotor, femur-tibia joint, is set to a static angle. The servomotors provide the joint angle measurements processed into sensory signals for leg protraction stops and ground contact events. Both events occur during the swing when the leg is flexible. The stop of the l -th leg protraction x_l^{stop} occurs at Φ_4^u (see **Figure 5B**), where the body-coxa servomotor position change is near zero. If the leg encounters an obstacle, the body-coxa stops sooner due to low torque. The ground contact of the l -th leg x_l^{contact} occurs at the end of Φ_1^u , where the coxa-femur servomotor cannot lower the leg anymore because of the ground, and the position error therefore grows. On the other hand, if

there is a depression in the ground, the coxa-femur servomotor continues to lower the leg, and the contact event occurs later than usual, or not at all if the leg does not reach a foothold. Each leg generates a pair of sensory signals, x_l^{stop} and x_l^{contact} , fed into the controller during both phases: the learning and deployment.

The dynamics of the proposed controller described by the differential equations are numerically solved by the Euler method with the step size of 0.01. The execution of 100 steps was measured to be 5.15s long ($T^{\text{gait}} = 223 \text{ steps} \approx 11.5\text{s}$).

5.2. Tripod Gait Training and Mistiming Detection Learning

The controller has been learned in two parts with the hexapod walking robot on flat ground. First, the robot is trained to generate the motor phase. In the second part, the robot learns to detect sensory mistiming. The reflexive behavior is turned off during the learning. The individual training parts are detailed as follows.

5.2.1. Tripod Gait Training

The motor phase generation has been trained for 30,000 steps on a flat terrain by the given target signal d for each joint, as shown in **Figure 5C**. Four motor RBFs are trained to be active during their respective motion phases, which determine the hand-tuned configuration of the control commands, see **Figure 7A**. The regular control signal u^{regular} for body-coxa and coxa-femur joint angles, shown in **Figure 7B**, follows the general foot-tip trajectory depicted in **Figure 5B**. The maximum torque u^{torque} is set to 1.25 N m (rigid) during stance and 0.5 N m (flexible) during swing. The reflex control signal u^{reflex} is hand-tuned to perform the elevator and search reflexes, plotted in **Figures 7C,D**, respectively. The example of joint angle evolution is shown in **Figure 7E**, where both reflexes occur within five gait-cycles. During any reflex, the coxa-femur servomotor, affecting the leg

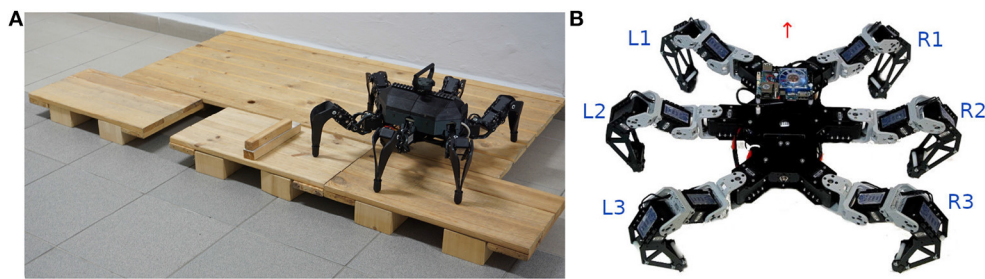


FIGURE 6 | (A) Photo of the hexapod walking robot in the laboratory test track. The robot has six legs, each comprising three Dynamixel AX-12 servomotors; however, only the body-coxa and coxa-femur servomotors are controlled in experiments presented in this work. The servomotors also provide the joint angle measurement, which is further processed into swing stop and ground contact events for each leg. **(B)** Leg schema.

elevation, is rigid, while the body-coxa servomotor is flexible. The inter-leg phase relations given by the target $\mathbf{d}(t)$ are learned by the motor phase generator, and the hexapod robot walked the tripod at the end of the gait training. The walking hexapod robot interacts with the environment that generates the regular sensory signal, which trains the mistiming detector.

5.2.2. Mistiming Detection Self-Learning

The mistiming detection is learned during 13000 steps of walking tripod gait in the regular environment, as shown in **Supplementary Video 1**.

We first let the robot learn to anticipate the sensory events for 8,000 steps with the learning rate $\nu(t)$ linearly decreasing from one to zero. As can be seen in **Figure 8**, the event RBF neurons find their respective phase represented by a limit-cycle $\mathbf{Y}^{\text{sense}}$. At the end of the anticipation learning, the event RBF neurons anticipate the sensory events with high accuracy, as shown in **Figure 8D**.

After the event anticipation learning, the robot adapts the LIF thresholds during 5,000 steps, where the learning rate $\nu(t)$ linearly decreases from one to zero. At the start, mistiming error causes LIF to fire, as it is shown in **Figures 9A,B**, which increases the threshold with dynamics (6). Then, the threshold slowly decays. On some occasions, the threshold descends too close to the regular LIF activity and fires again, increasing the threshold. However, since the learning rate $\nu(t)$ converges to zero, the threshold increments are smaller as the learning progresses.

At the end of the learning, the thresholds are adapted so LIFs do not fire in the regular environment, see **Figures 9C,D**. The thresholds are also close to the LIF activity maxima; therefore, LIF fires and detects the phase mistiming if there is more error accumulated due to the motion disturbances.

5.3. Walking Over Obstacles

The proposed mistiming detection is demonstrated in the deployment of the robot on track depicted in **Figure 6A**, where the mistiming detector triggers reflexes. The robot's left legs must negotiate one obstacle and one depression to continue its gait. The obstacle is 7 cm high and 4 cm long, which is higher than the maximum elevation during the regular swing. Hence, the leg is stopped by the swing, and the event disruption is detected, which triggers the elevator reflex, see **Figure 10A**. After avoiding the obstacle, the leg encounters a depression 10 cm deep, and

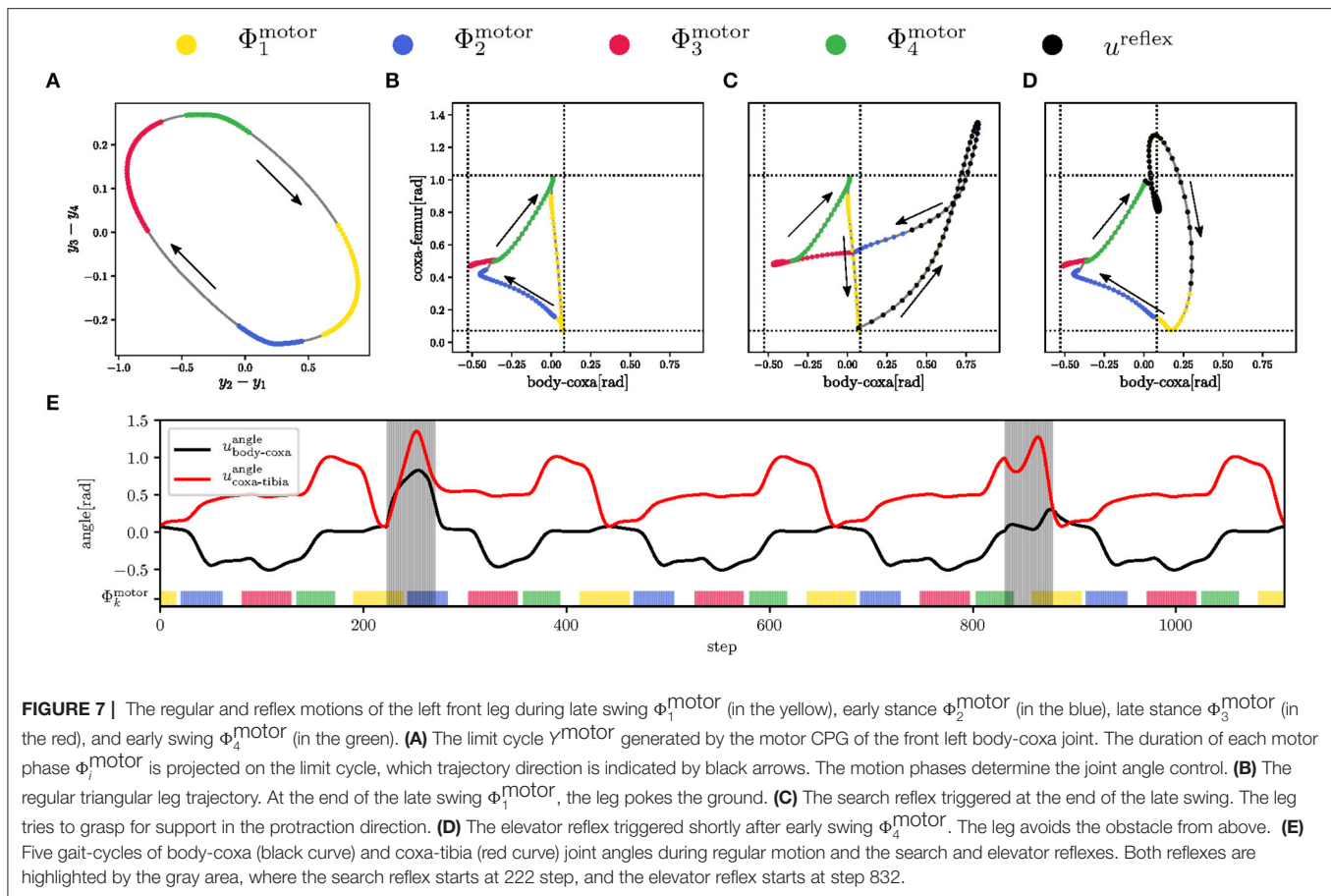
5 cm long, which is further than the leg reaches during regular motion. Since the leg is not stopped by the ground as anticipated, an absence of the ground collision is detected, which triggers the search reflex, see **Figure 10B**. The searching leg grasps the far away support, and the motion continues. In **Figure 10C**, we can see the right legs moving regularly as no obstacle was detected. The record of the robot walking over obstacles is provided in **Supplementary Video 2**.

5.4. Irregular Locomotion in Bull Rock Cave

Limits of the proposed controller have been tested during the field deployment in Bull Rock cave, where the robot crawled over highly unstructured terrain with a wet slippery surface and cracks, see **Figure 1A**. In such an environment, multiple reflexes are triggered at once; see **Figure 11C** and **Supplementary Video 3**, which changes the locomotion of the whole body and, in some cases, detects event mistiming when there is seemingly none. For example, the combination of triggered reflexes toggles the robot on the left side, and thus when the right leg enters the stance, it touches the ground later, which triggers the search reflex. On the other hand, the elevator reflex works in unintended situations, that have been observed for a leg is stuck in a crack, which is documented in **Figures 11A,B**. In such a situation, the leg does not move during the swing, and thus the elevator reflex is triggered, which frees the leg. Overall, the hexapod walking robot with the proposed locomotion control traversed the highly irregular terrain multiple times and detected parallelly multiple phase mistiming, supporting the expected advantage of the mistiming detector in a real cave environment.

6. DISCUSSION

The proposed controller has been trained to perform the tripod gait. During the tripod gait on flat terrain, the hexapod walking robot learned to anticipate the ground contact and swing stop with accuracy shown in **Figure 8**. LIFs then adapt the regular difference between sensory anticipation and measurement. The thresholds are upper-bound of the regular LIF activity, see **Figure 9**; therefore, LIFs are at rest during regular motion. The benefit of mistiming detection is further demonstrated in two deployment scenarios where mistiming detection triggers the designed reflex reactions. The reflexes allowed the robot to



locomote through terrains that are otherwise untraversable with the regular gait. From this perspective, the expected advantage of the proposed idea has been fulfilled.

On the other hand, in some cases, the reflexes were triggered even though there was no obstacle nor depression. In the testbed scenario visualized in **Figure 10C**, the middle left leg performs the elevator reflex at step 1100, albeit the leg already cleared the obstacle at step 900. The elevator reflex at step 1,100 has been triggered by detected early swing stop, which has not been caused by an obstacle, but by the search reflex of the front left leg triggered at step 1,050. Such behavior can also be observed in **Figure 11C**, where the search reflex of the front legs causes the elevator reflex of the middle legs. The search reflex leaves the robot body slightly tilted, which causes the adjacent middle leg to stop the swing earlier. Thus, the middle left leg detects the search reflex of the adjacent leg. It is a cautionary tale that the interpretation of mistiming detection, or generally any sensory error, is dependent on the context in which the robot is. The direct interpretation of the situation in which an obstacle stops the swing is correct only if the robot's current state is close to the state of the regular motion. Sustaining the regular gait motion improves not only the locomotion but also the interpretability of the sensory input. Therefore, improving the gait control, e.g., adding balancing reflex, is one strategy preventing incorrect interpretation of the sensory input. Another strategy can be based

on fusing multiple sensory inputs as it is less likely that each of the sensory input provides incorrect interpretation at the same time.

The proposed mistiming detector relies on the CPG providing the sensory phase estimation; thus, the mistiming detector inherits the robustness of the CPG dynamics but also its drawbacks. While short-term changes of sensory signal properties have little effect on the CPG, if the change is lasting, then the CPG behavior changes as well. Consider that the sensory signal changes in phase or frequency. If the sensory signal changes in phase, the sensory CPG shifts its phase and maintains the stable phase difference between the signal and the CPG. However, there are more possible outcomes if the sensory signal frequency of ω^c changes. The CPG has a range of detuning $\Delta\omega = \omega^c - \omega^{\text{CPG}}$ where the CPG can synchronize with the input signal (Pikovsky et al., 2001). Outside the synchronization range, the phases of the CPG and input signal evolve with different speeds; therefore, if the detuning is too high², the sensory CPG does not estimate the sensory phase.

² In particular, the synchronization range depends on the input signal strength, which is set to $\lambda = 0.5$ in this work. The range gets smaller with lesser input strength creating a structure in the λ - $\Delta\omega$ plane called the Arnold tongue. In general, the Arnold tongue cannot be found analytically, yet there must be some small synchronization region around $\Delta\omega = 0$ for high enough λ .

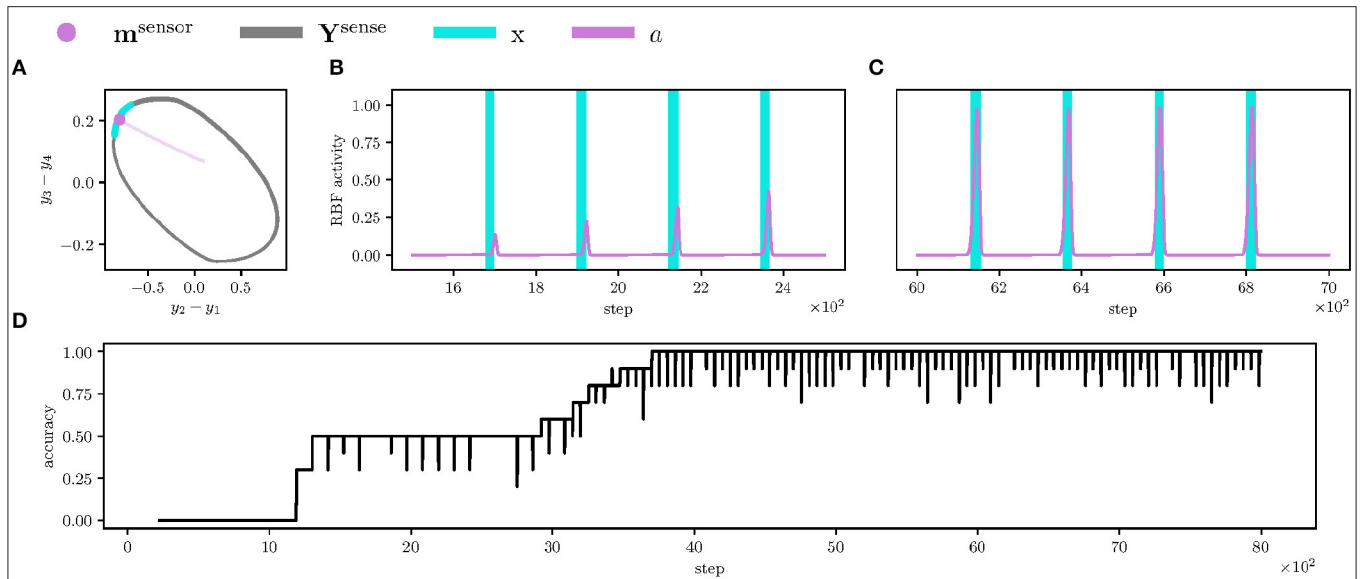


FIGURE 8 | Detail of learning the left leg's contact event anticipation and the overall anticipation accuracy. **(A)** Projected CPG limit-cycle γ^{sense} (in the gray) and the event RBF weight m^{sensor} trajectory (in the magenta) of the front left leg's contact event. During the learning, the RBF weight approaches the limit-cycle segment, during which the left leg senses contact $x > 0$ (in the blue). At the end of the learning, the RBF weight (the magenta dot) is close to the limit-cycle segment; therefore, the RBF activity a spikes during the phase segment can be seen in the following plots. **(B)** At the start of the learning, the RBF activity a (in the magenta) is low and peaks outside of the left leg contact event $x > 0$ (in the blue). **(C)** However, at the end of the learning, the RBF activity peaks are close to the maximum possible activity (one), and the peaks overlap with the events. Ideally, the total number of such overlaps during one gait-cycle is twelve, one per each sensory input. **(D)** The plotted sum of the anticipation-event overlaps over a sliding window of the size $\tau_{\text{gait}} = 223$ divided by the number of sensory inputs (12). At step 4,000, all RBF neuron anticipations overlap with the measured sensory events.

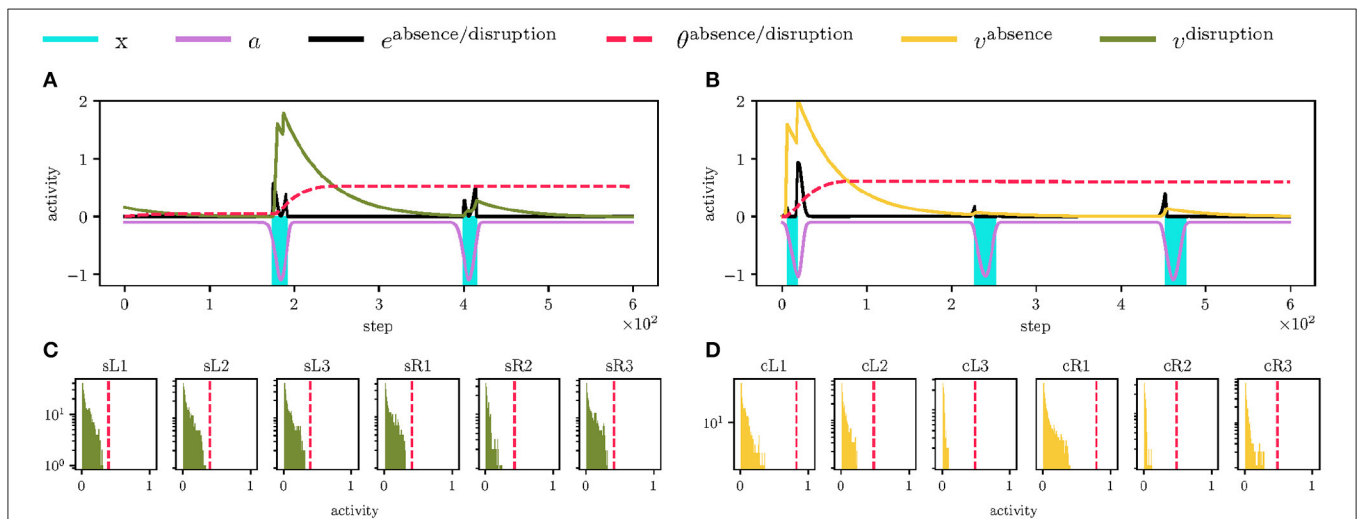


FIGURE 9 | Adaptation of the firing threshold θ . **(A)** Detail of the LIF threshold $\theta^{\text{disruption}}$ (visualized as the red dashed line) adaptation for the left leg's early swing stop. Initially, the threshold is set to zero, thus LIF fires (in the green) at the first non-zero error $e^{\text{disruption}}$ (in the black), where the error is rectified difference between the early stop event x (in the blue) and RBF anticipation a (in the magenta), $h(x - a)$. During the LIF firing, the threshold rapidly grows; therefore, the next LIF non-zero activity at step 400 is below the threshold, and LIF does not fire. The threshold slowly decays (not observable in plots). **(B)** The LIF detector (in the yellow) for the left leg's contact absence behaves similarly. The last thousand steps of the LIF neuron activations are aggregated in histograms, where it is shown that the respective thresholds are upper-bound of the regular activations. **(C)** The swing stop perception is precise during the regular motion; thus, the LIF activity (in the green) is similar for all legs, and so are the thresholds (shown as the red dashed line). **(D)** However, the ground contact perception differs for each leg (probably due to different loads on the legs during the stance) and is less precise (the leg sometimes did not detect the ground contact). It resulted in the increased variance of the ground contact absence thresholds across the legs. Note that the contra-lateral legs (e.g., cL1 and cR1) have similar thresholds.

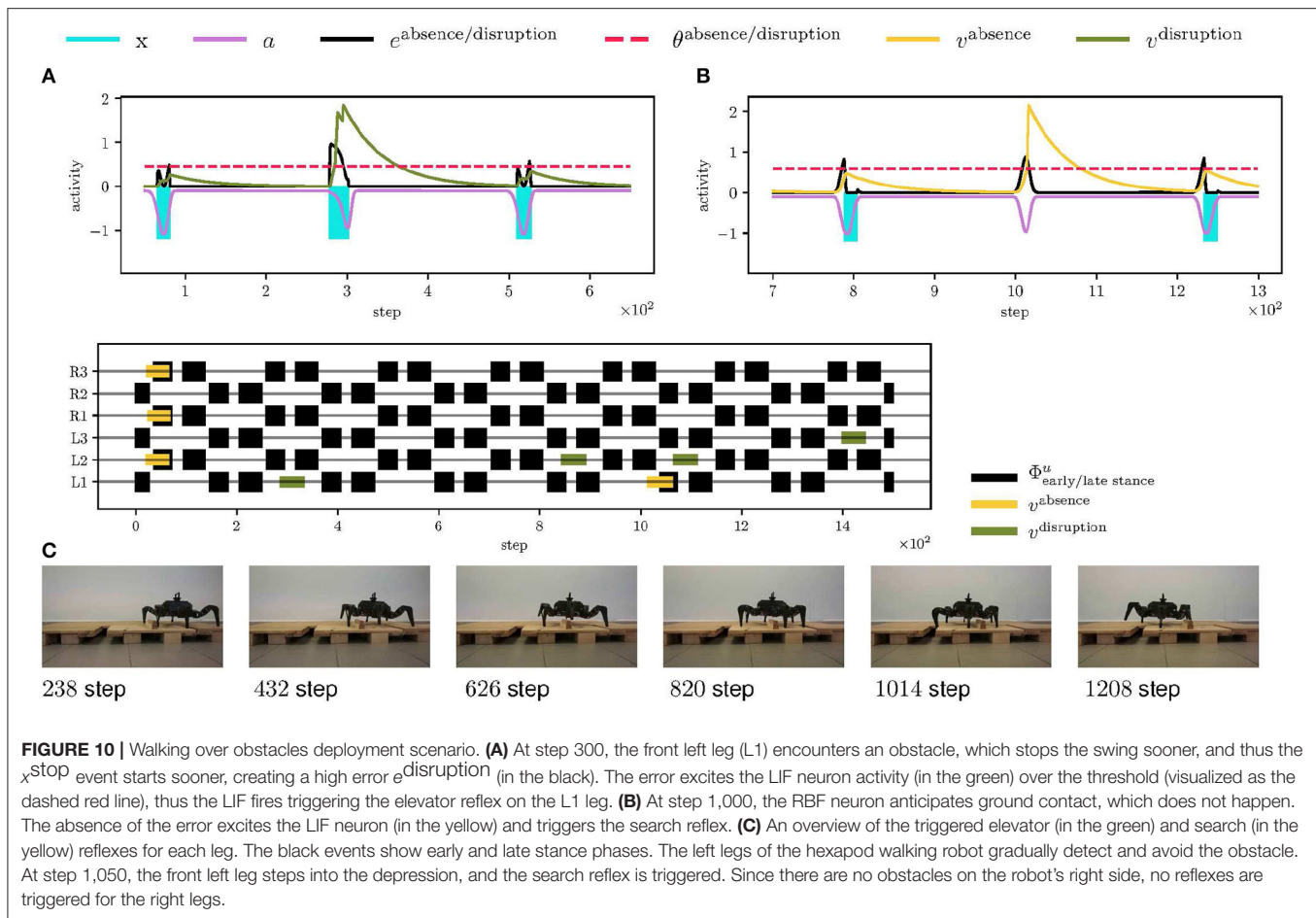


FIGURE 10 | Walking over obstacles deployment scenario. **(A)** At step 300, the front left leg (L1) encounters an obstacle, which stops the swing sooner, and thus the x^{stop} event starts sooner, creating a high error $e^{\text{disruption}}$ (in the black). The error excites the LIF neuron activity (in the green) over the threshold (visualized as the dashed red line), thus the LIF fires triggering the elevator reflex on the L1 leg. **(B)** At step 1,000, the RBF neuron anticipates ground contact, which does not happen. The absence of the error excites the LIF neuron (in the yellow) and triggers the search reflex. **(C)** An overview of the triggered elevator (in the green) and search (in the yellow) reflexes for each leg. The black events show early and late stance phases. The left legs of the hexapod walking robot gradually detect and avoid the obstacle. At step 1,050, the front left leg steps into the depression, and the search reflex is triggered. Since there are no obstacles on the robot's right side, no reflexes are triggered for the right legs.

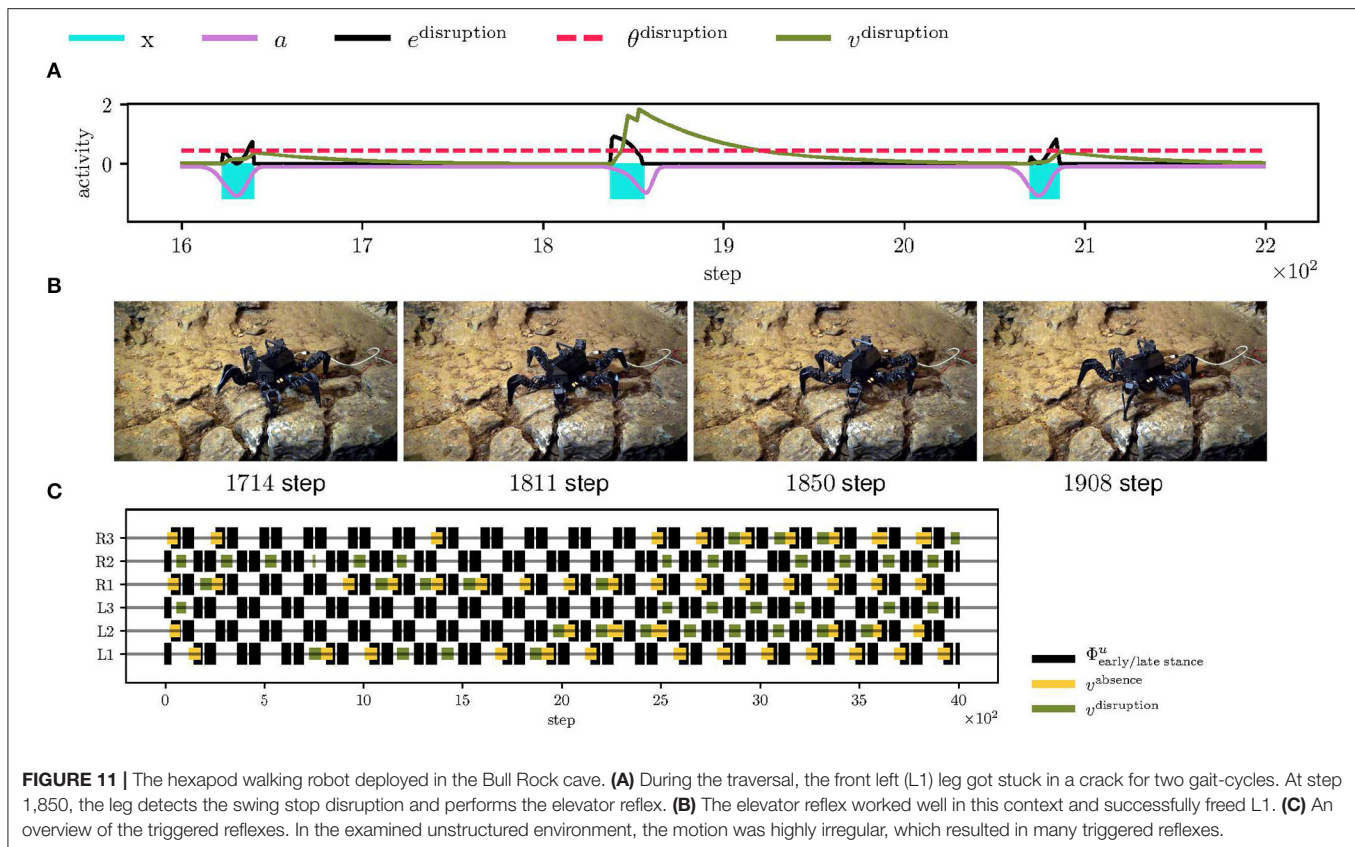
In the gait control context, the sensory inputs for the mistiming detector are a consequence of the interaction between the environment and periodic motor activity. A persistent change in motor activity can induce a change in the sensory signal, influencing the sensory CPGs, as described above. The terrain in Bull Rock cave is a source of such persistent change, see **Figure 11**, where the rough terrain caused a change in the motor activity by triggering one reflex after another. Although it was not observed during the short span of the Bull Rock cave deployment, the change of the sensory CPG properties (phase or frequency) influences the motor phase generation (see **Figure 3**), which may compromise the gait pattern. Therefore, the presented gait controller can generate a disturbed motion pattern if it operates in a highly unstructured environment. Such disturbances can be prevented by adding more reflexes, which would stabilize the regular motion, or the controller can react to an unstructured environment by a switch to a different gait. For both cases, the mistiming detector provides the means to recognize a highly irregular environment.

The mistiming detection adds an alternative to usual amplitude error detection, where the measured sensory value rises above some threshold. Notice, from a practical

point of view, the ground contact absence and the swing stop detections are implemented simply from reading the position from the Dynamixel AX-12 servomotors, without the need for any additional sensory equipment. Generally, the proposed mistiming error augments the information gained from the measured sensory input, and further utilization of the augmentation is a subject of our future work.

7. CONCLUSION

In this paper, we present a novel learnable CPG-based event mistiming detection. We propose to combine CPG with the RBF neuron into a sensory event estimator and compare the estimation with measurement to assess the phase error. The phase error is integrated by the LIF neuron, which detects the irregularity in the timing of event occurrence. The proposed mistiming detection is self-learned with dynamic Hebb-like learning rules by the robot on which the system is deployed. We integrated the mistiming detection with the CPG-based gait controller, where the detection triggers reflexive behavior. An



absence of the ground contact triggers the search reflex, while the elevator reflex is triggered by detecting an obstacle during the swing. The CPG-based controller is deployed on a real hexapod walking robot, which is trained to walk using a tripod gait and learns the properties of twelve sensory signals. The learned controller has been examined in two deployment scenarios. In the laboratory testbed, the robot encounters a depression and an obstacle on flat terrain, where each leg reacts independently with corresponding reflexes. In the second scenario, we demonstrate the robustness of the proposed controller in Bull Rock cave, where the robot traverses slippery and highly unstructured terrain. The proposed plastic CPG-based mistiming detection enhances the information gained from the periodic sensory signal, which can be utilized not only for reflex control but also can serve as an input for other control centers.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

RS conceived and designed the study. RS and MP performed the experiments and processed the data. With the support of MP and

JF, RS wrote the manuscript. All the authors contributed to the manuscript and approved the submitted version.

FUNDING

The work was supported by the Czech Science Foundation (GAČR) under research project No. 18-18858S.

ACKNOWLEDGMENTS

We would like to acknowledge the support of the speleologist branch organization ZO 6-01 for providing access to the Bull Rock cave testing site. We also thank Jan Bayer and Petr Čížek for their help with the hexapod walking robot maintenance.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fnbot.2021.629652/full#supplementary-material>

Supplementary Video 1 | The hexapod walking robot self-learns the mistiming detector.

Supplementary Video 2 | The hexapod walking robot walks over obstacles.

Supplementary Video 3 | The hexapod walking robot deployed in Bull Rock cave.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Descending and Ascending Signals That Maintain Rhythmic Walking Pattern in Crickets

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OPEN ACCESS

Edited by:

Amir Ayali,
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Reviewed by:

Daniel Knebel,
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University of Cologne, Germany

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Specialty section:

This article was submitted to
Computational Intelligence in
Robotics,
a section of the journal
Frontiers in Robotics and AI

Received: 02 November 2020

Accepted: 01 March 2021

Published: 29 March 2021

Citation:

Naniwa K and Aonuma H (2021)
Descending and Ascending Signals
That Maintain Rhythmic Walking
Pattern in Crickets.
Front. Robot. AI 8:625094.
doi: 10.3389/frobt.2021.625094

The cricket is one of the model animals used to investigate the neuronal mechanisms underlying adaptive locomotion. An intact cricket walks mostly with a tripod gait, similar to other insects. The motor control center of the leg movements is located in the thoracic ganglia. In this study, we investigated the walking gait patterns of the crickets whose ventral nerve cords were surgically cut to gain an understanding of how the descending signals from the head ganglia and ascending signals from the abdominal nervous system into the thoracic ganglia mediate the initiation and coordination of the walking gait pattern. Crickets whose paired connectives between the brain and subesophageal ganglion (SEG) (circumesophageal connectives) were cut exhibited a tripod gait pattern. However, when one side of the circumesophageal connectives was cut, the crickets continued to turn in the opposite direction to the connective cut. Crickets whose paired connectives between the SEG and prothoracic ganglion were cut did not walk, whereas the crickets exhibited an ordinal tripod gait pattern when one side of the connectives was intact. Crickets whose paired connectives between the metathoracic ganglion and abdominal ganglia were cut initiated walking, although the gait was not a coordinated tripod pattern, whereas the crickets exhibited a tripod gait when one side of the connectives was intact. These results suggest that the brain plays an inhibitory role in initiating leg movements and that both the descending signals from the head ganglia and the ascending signals from the abdominal nervous system are important in initiating and coordinating insect walking gait patterns.

Keywords: locomotion, rhythmic movement, cricket, gait, descending signal, ascending signal

INTRODUCTION

One of the common issues between biologists and robotics scientists is revealing the mechanisms underlying adaptive locomotion in animals. It is generally believed that insects appeared on the earth roughly 400 million years ago and that approximately 1,000,000 insect species are living on the earth. One of the reasons why insects have successfully evolved to spread across the earth may be the development of adaptive locomotion. Locomotion is the act of moving from place to place and is a crucial behavior for insects to obtain resources such as foods, territories, to find mating partners, to avoid predators, and so on. Revealing the neuronal mechanisms underlying locomotion in insects can aid in understanding the evolution of insect behaviors, as well as accelerate the development of novel design and control laws for legged robots.

This study focuses on cricket locomotion. Cricket is one of the ideal experimental animals to investigate neuronal mechanisms underlying varieties of behaviors such as locomotion [walking

(Owaki et al., 2021), flight (Schul and Schulze, 2001; Pollack and Martins, 2007), swimming (Matsuura et al., 2002), aggressive behavior (Stevenson et al., 2000; Sakura et al., 2012; Rillich and Stevenson, 2014, 2017), escape behavior (Jacobs et al., 2008; Yono and Aonuma, 2008), mating behavior (Nagao et al., 1991; Ureshi et al., 2002; Nagamoto et al., 2005; Killian et al., 2006), learning and memory (Matsumoto et al., 2006), phonotaxis (Baden and Hedwig, 2008; Pollack and Kim, 2013), circadian rhythm (Saifullah and Tomioka, 2002) and so on]. On the other hand, in the robotics field, cricket inspired robots are made where design and control law of autonomous robots are investigated [the locomotion of micro-cricket robot: (Birch et al., 2000), phonotaxis robot: (Lund et al., 1997; Reeve et al., 2005), group behavior: (Funato et al., 2008, 2011), cricket-robot interaction: (Guerra et al., 2010; Kawabata et al., 2013a, Kawabata et al., 2013b)]. Some of the robotics scientists struggle to make hexapod robots that move like an insect (Delcomyn and Nelson, 2000; Meyer et al., 2020). However, probably because they employed centralized control, it seems hard to realize a robot that behaves adaptively like an insect. Other robotics scientists employ sensory-feedback-based control to realize adaptive locomotion (Owaki et al., 2017). But still, it seems difficult to realize exploratory behavior like an insect. To establish suitable design and control law for adaptive robots, it is one of the effective strategies to understand the adaptive behavior of insects using biological approaches.

Exploratory behavior to identify resources is initiated by the command signals generated in the brain. Thus, descending signals from the brain are necessary for the initiation of voluntary walking in both vertebrates and invertebrates (Kagaya and Takahata, 2011). External and internal signals are associated with the initiation of various behaviors. Chemical cues initiate exploratory behavior in insects because they are attracted by the chemical components of food and pheromones (Dethier, 1947). Auditory signals are another type of cue for attracting conspecific insects. For example, female crickets express phonotaxis to the calling song stridulated by males (Alexander, 1961; Nagao and Shimozawa, 1987; Jacob and Hedwig, 2016). Internal signals also function to initiate behaviors. Starvation and thirst can increase the motivation to initiate exploratory behavior for food and water, indicating that food digestion and the excretion system are associated with initiating behaviors in insects.

Insects are hexapod animals and most of them exhibit a tripod gait pattern, whereby the foreleg and hind leg on one side move in synchrony with the midleg on the other side (Wilson, 1966; Bender et al., 2011; Smolka et al., 2013; Ramdya et al., 2017). Descending signals via the central complex in the brain are important for initiating walking in insects (Strausfeld, 1999; Bender et al., 2010; Emanuel et al., 2020). The central complex is one of the important neuropils in the brain where multi kinds of sensory information are converged and processed, such as visual and olfactory information, auditory information (Homberg, 2008; Pfeiffer and Homberg, 2014). It is believed that the key role of the central complex is locomotor control (Strauss, 2002; Bender et al., 2010; Ritzmann et al., 2012), spatial orientation (Neuser et al., 2008; Triphan et al., 2010; Homberg et al., 2011), visual memory (Liu et al., 2006; Ofstad et al.,

2011), and various forms of arousal (Lebestky et al., 2009; Kong et al., 2010). The local centers of the leg movements lie within the thoracic ganglia, where oscillatory neuronal activities, which are known as central pattern generators (CPGs), contribute to rhythmic leg movements (Borgmann et al., 2009). Descending information from the brain into the thoracic ganglia is necessary to coordinate the movement of the legs (Heinrich, 2002; Emanuel et al., 2020). The subesophageal ganglion (SEG) plays a crucial role in walking (Knebel et al., 2018). However, our previous study demonstrated that headless crickets do not exhibit voluntary walking, except following defecation (Naniwa et al., 2019). After-defecation walking is initiated by ascending signals from the terminal abdominal ganglion. This suggested to us that ascending signals from abdominal ganglia may also contribute to coordinated walking. Indeed, cricket elicits avoidance walk by responding to air displacement that is detected by circus (Camhi et al., 1978; Shimozawa et al., 2003; Dupuy et al., 2011). The sensory signals from the circus are converged and processed in the terminal abdominal ganglion (Kanou and Shimozawa, 1984; Yono and Aonuma, 2008). Activation of ascending giant interneurons introduce activation of motor control in the thoracic ganglia to initiate avoidance walk (Ritzmann and Camhi, 1978; Ritzmann and Pollack, 1986). It is also demonstrated that abdominal ganglia in the cricket control the timing of the calling song pattern (Jacob and Hedwig, 2016). These indicate that the ascending signals from the abdominal ganglia can mediate neuronal activities of the thoracic ganglia. Thus, understanding the roles of ascending signals from the abdominal ganglia must be necessary to reveal the neuronal mechanism underlying adaptive locomotion in insects.

In this study, we aimed to determine how the ascending signals from the abdominal nervous system and the descending signals from the brain and SEG influence the coordinated walking gait pattern. To investigate this issue, we surgically cut the connectives of the ventral nerve cord at different positions and analyzed the walking gait pattern of the field cricket. To determine the roles of the brain in initiating and regulating the walking gait, either the paired connectives or one side of the connectives between the brain and SEG were cut. To investigate the roles of the SEG, either the paired connectives or one side of the connectives between the SEG and prothoracic ganglion were cut. Furthermore, to investigate the roles of the ascending signals from the abdominal nervous system, either the paired connectives or one side of the connectives between the metathoracic ganglion and first free abdominal ganglion were cut. Based on these results, we demonstrated that both the descending signals and the ascending signals into the thoracic ganglia play an important role in maintaining a coordinated walking pattern.

MATERIALS AND METHODS

Animals

The cricket *Gryllus bimaculatus* (De Geer) used in this study were raised in a laboratory colony. They were reared on a 14 h:10 h light and dark cycle (lights on at 6:00 h) at $28 \pm 2^\circ\text{C}$. They were fed a diet of insect food (Sankyo Lab, Tokyo, Japan) and

water *ad-libitum*. Adult male crickets that had molted within 2 weeks before the experiments were randomly selected for use in this study.

Behavioral Experiments

The crickets used were randomly selected from the colony. A cricket was placed on a handmade passive treadmill using a floating ball to observe its walking pattern. The treadmill ball was composed of a Styrofoam sphere ($\phi 150$ mm) that hovered over a stream of air flowing beneath it. Each cricket was anesthetized with CO₂ gas for 10 s and was then placed on the ball. A steel rod ($\phi 100$ μ m) was attached to the thorax of the cricket using dental wax (Shofu, Kyoto, Japan). The rod was inserted into a plastic tube ($\phi 500$ μ m) that was fixed to a manipulator, by means of which the cricket was placed in the exact desired position on the Styrofoam sphere (floating ball). The behavioral experiment was performed 1 h after the cricket was placed on the ball so that it adapted to the new circumstances. A cricket on the ball could walk as well as change its orientation and ground clearance freely.

To investigate the roles of either the ascending or descending signals into the thoracic ganglia, where the premotor signals for locomotion are generated, the intersegmental connectives between the brain and SEG, between the SEG and prothoracic ganglion, and between the metathoracic ganglion and abdominal ganglia were cut using a razor blade. Surgical treatment was performed after administering anesthesia. A cricket held by hand was placed under the dissection microscope (SZX-12, Olympus, Tokyo Japan), and then a small square window was opened on the head to cut the intersegmental connectives. The cuticle cut off was replaced, and the hemolymph clotted quickly to close the window. Behavioral experiments were performed 3 h after surgical treatment.

The locomotion patterns of the crickets were observed and recorded using a high-speed camera (800 $\times$ 600 pixels, 300 fps, HAS-L1, DITECT, Japan). Intact crickets and the crickets whose intersegmental connectives between thoracic ganglia and abdominal ganglia were cut initiated voluntary walking on the ball. In contrast, the cricket whose paired circumesophageal connectives were cut did not walk without external stimulation. To initiate walking, the cercus of the cricket was stimulated by touching with a paintbrush. The detail of the touching stimuli is described in the previous study (Aonuma, 2020). Tactile stimuli were applied once or twice using a paintbrush in each trial and intertrial interval was varied between 1 and 5 min to prevent habituation. Continuous walking-period was shortened in connective-cut crickets compared to intact one (see **Table 1**). Therefore, we focused on a continuous walking-period to analyze gait patterns. The images were saved as sequential JPEG files on a Windows PC for subsequent analysis.

Data Analysis

To analyze and evaluate the leg movement patterns, we drew polar histograms (Naniwa et al., 2020), in which we focused on the leg movement direction. In brief, we defined the power stroke as the thrust produced when the angle between the femur and tibia increased in the case of the hindleg, or when the angle between the femur and trunk increased in the case of the foreleg

and midleg. During the recovery stroke, the angle between the femur and tibia decreased for the hindleg or the angle between the femur and trunk decreased for the foreleg and midleg. The stroke mode was obtained manually from the video data. The condition of each leg in a frame was compared to those of the adjacent frames to determine whether it was a power or recovery stroke.

In the definition of the phase for each leg, t is a certain time and t_n is the start time of the power stroke directly before the n th step of the leg of interest.

The phase ϕ at a time t is defined as

$$\phi(t) = \frac{t - t_n}{t_{n+1} - t_n} 360(\text{deg}).$$

Therefore, the leg phase is defined as the period between the beginning of two consecutive power strokes. In this case, ϕ_{object} , ϕ_{subject} are the phases of an arbitrary leg, where the subscripts object and subject indicate the leg positions (e.g., LF, RM).

The leg phase difference of the subject leg relative to the object leg at a time t is expressed as

$$\bar{\phi}_{\text{object-subject}}(t) = \begin{cases} \phi_{\text{object}}(t) - \phi_{\text{subject}}(t) & (\phi_{\text{object}} \geq \phi_{\text{subject}}) \\ \phi_{\text{object}}(t) - \phi_{\text{subject}}(t) + 360 & (\phi_{\text{object}} < \phi_{\text{subject}}) \end{cases}$$

This method aims to provide an intuitive and precise representation of the rhythmic pattern corresponding to the variations in the cricket legs owing to movement. Therefore, even in a polar representation, in which the area represents the ratio of frequencies, the height of a bar is the value of the square root of the frequency that it represents. As a result, the total area of the bar is 1 in a polar histogram (Nemec, 1988). The phase difference between the legs can be calculated for each frame. The polar histogram of the experimental results represents a summary of the frequencies of leg phases for all individuals and all frames in each experimental pattern. In an ideal tripod, the leg phase difference between adjacent legs (e.g., LF and RF or LF and LM) is always 180°.

In the polar histogram, the phase mean Φ is calculated as:

$$Re^{i\Phi} = \frac{1}{N} \sum_t e^{i\bar{\phi}(t)},$$

where R is the mean resultant length of each histogram, N is the total amount of sample data, and i is an imaginary number.

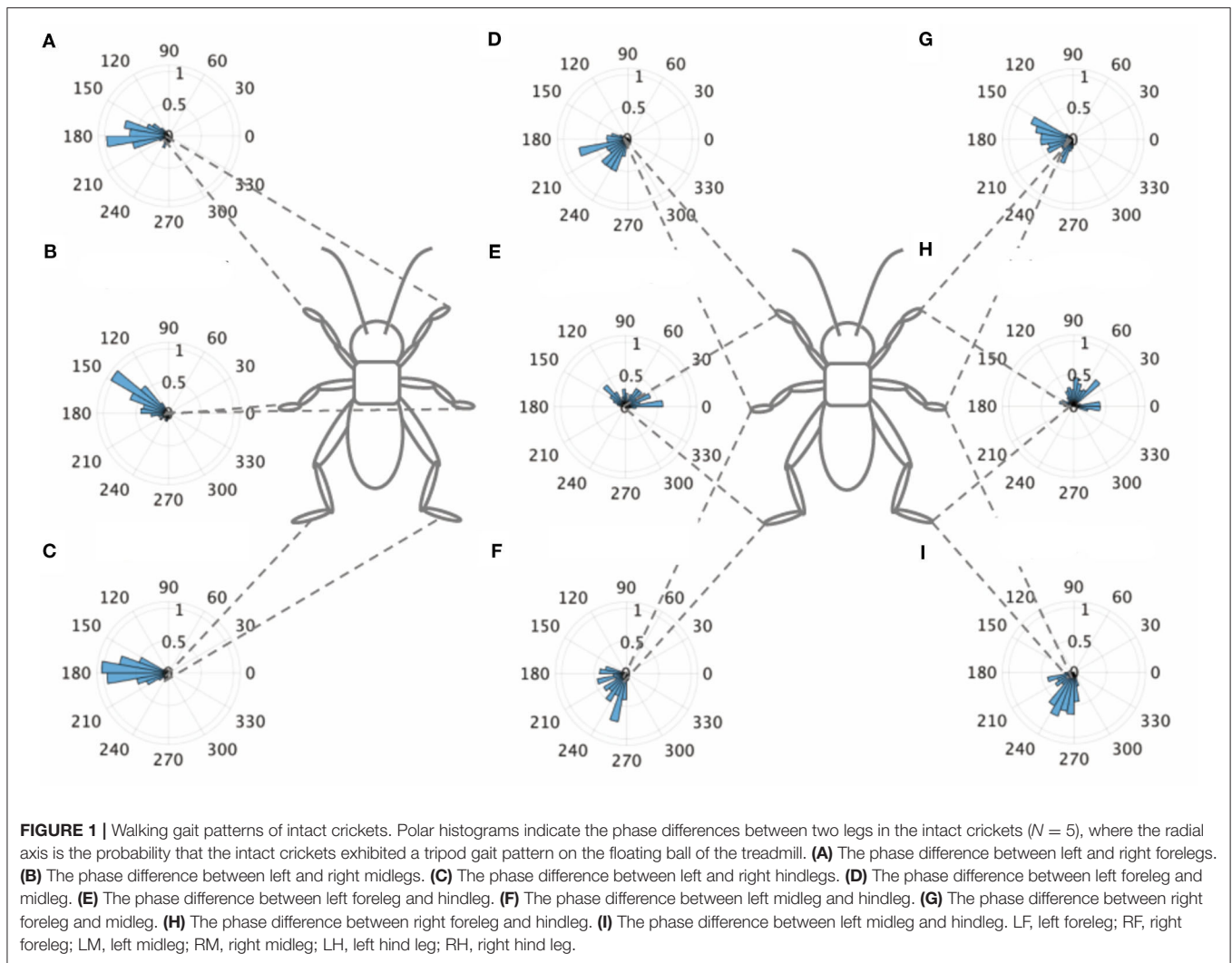
The circumferential dispersion s and circumferential standard deviation ν of the circumferential data are defined as follows:

$$s \equiv 1 - R \quad (0 \leq s \leq 1) \\ \nu \equiv \sqrt{-2 \log(R)}.$$

TABLE 1 | Summary of the results.

Specimens	Number of specimens	Average time analyzed [sec]	Average number of steps analyzed $\pm$ SD[step]	Combination of legs	Sample size: total number of steps analyzed [step]	ϕ [deg]	ν [deg]	R	d	Power	Kuiper test vs. intact Kuiper statistic	V-test for 180 V Statistic
(A)	$N = 5$	3.06	11.3 ± 3.0	LF-RF	113	185	39.6	0.79			-	9.97 [†] $P < 0.01$
				LM-RM	113	165	47.6	0.71			-	9.00 [†] $P < 0.01$
				LH-RH	114	180	28.9	0.88			-	12.1 [†] $P < 0.01$
				LF-LM	112	212	42.2	0.76			-	8.98 [†] $P < 0.01$
				LM-LH	113	225	42.6	0.76			-	6.76 [†] $P < 0.01$
				LF-LH	114	68.7	62.1	0.56			-	-2.50 $P = 0.99$
				RF-RM	114	194	35.1	0.83			-	9.96 [†] $P < 0.01$
				RM-RH	114	241	29.3	0.88			-	4.14 [†] $P < 0.01$
				RF-RH	114	71.7	57.9	0.60			-	-2.45 $P = 0.99$
(B)	$N = 5$	2.46	5.8 ± 2.3	LM-RM	57	193	55.5	0.63	0.54	0.90	0.18 $P = 0.87$	5.45 [†] $P < 0.01$
(C)	$N = 5$	3.30	6.2 ± 2.6	LM-RM	57	187	131	0.07	0.22	0.27	0.57 $P < 0.01$	-2.12 $P = 0.98$
(D)	$N = 5$	11.5	0.7 ± 0.6	LM-RM	-	-	-	-	-	-	-	-
(E)	$N = 5$	2.86	11.1 ± 3.5	LM-RM	109	165	37.3	0.81	0.00	0.05	0.23 $P = 0.56$	9.53 [†] $P < 0.01$
(F)	$N = 5$	8.47	12.2 ± 3.7	LM-RM	121	109	108	0.17	0.67	0.99	0.59 $P < 0.01$	-1.38 $P = 0.92$
(G)	$N = 5$	6.43	6.4 ± 2.7	LM-RM	63	87.5	110	0.16	0.91	1.00	0.58 $P < 0.01$	-3.46 $P = 1.00$
(H)	$N = 5$	3.26	7.6 ± 2.7	LM-RM	71	199	108	0.17	0.41	0.74	0.41 $P < 0.01$	1.65 $P = 0.05$
(I)	$N = 5$	1.71	4.1 ± 1.5	LM-RM	51	180	55.7	0.62	0.29	0.38	0.23 $P = 0.56$	4.12 [†] $p < 0.01$

(A) Intact crickets. (B) Crickets whose paired circumesophageal connectives were cut. (C) Crickets whose left side of the circumesophageal connective were cut. (D) Crickets whose paired connectives between SEG and prothoracic ganglion were cut. (E) Crickets whose left side of the connective between SEG and prothoracic ganglion was cut. (F) Crickets whose left side connective between brain and SEG, and left side connective between SEG and prothoracic ganglion were cut. (G) Crickets whose right side connectives between brain and SEG, and left side connectives between SEG and prothoracic ganglion were cut. (H) Crickets whose paired connectives between metathoracic ganglion and 1st free abdominal ganglion were cut. (I) Crickets whose left side connective between metathoracic ganglion and 1st free abdominal ganglion was cut. ϕ , mean phase difference; ν , circular standard deviation; R , mean resultant length; d , effect size. Kuiper statistic is a descriptive statistic for a two-sample Kuiper test with intact crickets. The significance level $\alpha = 0.05$; V statistic is a descriptive statistic based on the V-test for 180. It tests the null hypothesis that there is no tendency for leg phase differences to be distributed around 180. Significance level $\alpha = 0.05$. [†]the V statistic is greater than the rejection threshold at $\alpha = 0.05$ (Batschelet, 1981).



The rank statistics of the measured circumference data $\bar{\phi}(t)$, sorted in ascending order in the range of $0 \leq \phi < 2\pi$, are represented by $\{\bar{\phi}_{(1)}^*, \bar{\phi}_{(2)}^*, \dots, \bar{\phi}_{(N)}^*\}$.

In this case, the empirical distribution function $S(\phi)$ can be expressed as

$$S(\bar{\phi}_{(n)}^*) = n/N, \quad n = 1, 2, \dots, N.$$

The variations in the phase differences between legs could be intuitively understood by comparing the shapes of the empirical distribution functions. In this study, the empirical distribution function of the leg phase difference between the midlegs in each experiment is illustrated as a representative example. The phase distribution of the midlegs was tested. G*Power (Version 3.1.9.6) was used to conduct a *post-hoc* analysis of effect size d and power—the significance level $\alpha = 0.05$. The two-sample Kuiper test was performed for comparison with midleg phase distribution of intact cricket. The two-sample Kuiper test assesses the anomaly of continuous, one-dimensional

probability distributions (Kuiper, 1960; Paltani, 2004). The V-test was performed to confirm that the midleg phases were in the opposite phase. It tests the null hypothesis that there is no tendency for leg phase differences to be distributed around 180. The number of specimens used in each experimental condition was five. The samples used for the tests were the leg phase at the timing of each leg grounding ($n = 51-121$).

RESULTS

An intact cricket was anesthetized and placed on the floating ball of the treadmill. After recovered from anesthesia, voluntary evoked walking of the cricket was observed and recorded for 10 min, and then the periods of continuously walking were focused to analyze the gait pattern. The intact crickets exhibited a tripod gait pattern during walking on the floating ball of the treadmill ($N = 5$, Table 1A, Figure 1, Supplementary Video 1). The polar histogram indicates the phase difference between two of the six legs. The phase difference between the left and right forelegs occurred in an almost anti-phase manner. The mean of

the foreleg phase difference Φ_{LF-RF} was 185° , with a standard deviation ν_{LF-RF} of 39.6° . The mean vector length R_{LF-RF} was 0.79. Similarly, the left and right midlegs moved in an anti-phase manner. The mean of the midleg phase difference Φ_{LM-RM} was 164° , with a standard deviation ν_{LM-RM} of 47.6° . The mean vector length R_{LM-RM} was 0.71. The left and right hindlegs also moved in an anti-phase manner. The mean of the midleg phase difference Φ_{LH-RH} was 180° , with a standard deviation ν_{LH-RH} of 28.9° . The mean vector length R_{LH-RH} was 0.88. The foreleg and midleg on the same side moved in an almost anti-phase manner (Φ_{LF-LM} : 212° , ν_{LF-LM} : 42.2° , R_{LF-LM} : 0.76, Φ_{RF-RM} : 194° , ν_{RF-RM} : 35.1° , R_{RF-RM} : 0.83), and the foreleg and hind leg on the same side moved slightly later than in-phase (Φ_{LF-LH} : 68.7° , ν_{LF-LH} : 62.1° , R_{LF-LH} : 0.56, Φ_{RF-RH} : 71.7° , ν_{RF-RH} : 57.9° , R_{RF-RH} : 0.60). A V-test for 180° was also performed on the inter-leg phase differences of the intact crickets. The leg phases tended to be concentrated at 180° , between the adjacent legs in the tripod gait [LF-RF: $n = 113$, V statistic for 180° : 9.97, LM-RM: $n = 113$, V statistic for 180° : 9.00 ($P < 0.01$), LH-RH: $n = 114$, V statistic for 180° : 12.1, LF-LM: $n = 112$, V statistic for 180° : 8.98 ($P < 0.01$), LM-LH: $n = 113$, V statistic for 180° : 6.76 ($P < 0.01$), RF-RM: $n = 114$, V statistic for 180° : 9.96 ($P < 0.01$), RM-RH: $n = 114$, V statistic for 180° : 4.14 ($P < 0.01$), **Table 1A**]. However, the degree of concentration varied. These results indicate that the legs did not maintain a perfectly coordinated relationship with one another during the tripod gait in the intact crickets. The intact crickets maintained the leg-phase relationship characteristic of a tri-pod gait with a certain degree of variability.

To investigate the manner in which the ordinary tripod gait pattern is regulated by descending signals from the brain or ascending signals from the abdominal nervous system, the connectives of the ventral nerve cord were surgically disconnected. The central nervous system of insects has a symmetric structure. The brain (protocerebrum, deutocerebrum, and tritocerebrum) is joined by paired nerve connectives to the SEG, which is, in turn, linked to the thoracic and abdominal ganglia by paired connectives.

Disconnection of Circumesophageal Connectives

The cricket whose paired circumesophageal connectives were cut did not show voluntary evoked walking. To investigate the walking gait pattern of the surgically treated cricket, we touched the cercus using a fine paintbrush to evoke walking. The disconnection of the paired circumesophageal connectives did not change the walking gait pattern of the test crickets, which walked on the floating ball with a tripod gait ($N = 5$, **Figure 2A**, **Supplementary Video 2**). The test crickets did not respond to tactile stimuli on the antennae, although they responded to tactile stimuli on the cercus while walking. This indicates that the descending signals from the brain into the SEG were shut down. The crickets mainly walked straight forward and did not turn voluntarily. The phase difference between the left and right midlegs occurred in an anti-phase manner (**Figure 2Ab**). In the intact crickets, the mean midleg phase difference Φ_{LM-RM} was

164° , with a standard deviation ν_{LM-RM} of 47.6° . The mean vector length R_{LM-RM} was 0.71. In contrast, in the test crickets, the mean of the midleg phase difference Φ_{LM-RM} was 193° , with a standard deviation ν_{LM-RM} of 55.5° . The mean vector length R_{LM-RM} was 0.63. The shape of the empirical distribution function of the midlegs of the test crickets was similar to that of the intact crickets (**Figure 2B**). The inter-leg phase difference of the midlegs of the test cricket was not significantly different from that of intact cricket and was concentrated in an anti-phase manner [LM-RM: $n = 57$, Kuiper statistic vs. intact LM-RM: 0.18 ($P = 0.87$), V statistic for 180° : 5.45 ($P < 0.01$), **Table 1B**]. In contrast, leg frequencies tended to be lower than those of intact crickets (**Supplementary Figure 1**). This indicates that the gait pattern of the test cricket is classified as a tripod gait although its walking pattern is slightly different from that of the intact cricket.

However, the crickets in which only the left side of the circumesophageal connectives was cut did not walk straight forward but continued to turn clockwise (**Supplementary Video 3**). This kind of surgically treated crickets showed voluntary evoked walking without tactile stimuli. Their gaits did not exhibit an ordinary tripod pattern ($N = 5$, **Figure 3**). The polar histogram of these test crickets indicates that the phase differences between the left and right legs were not consistent (**Figure 3A**). In the test crickets, the mean of the midleg phase difference Φ_{LM-RM} was 187° , with a standard deviation ν_{LM-RM} of 131° (**Table 1C**). The mean vector length R_{LM-RM} was 0.07. The shape of the empirical distribution function of the midlegs in the test crickets was different from that of the intact crickets [LM-RM: $n = 57$, Kuiper statistic vs. intact LM-RM: 0.57 ($P < 0.01$), V statistic for 180° : -2.12 ($P = 0.98$), **Table 1C**, **Figure 3B**]. This analysis also demonstrates that the walking pattern was far from the ordinary tripod gait (**Figure 3C**). The gait chart diagram of the test crickets reveals that the duration of the left leg movements appeared to be rhythmic, similar to that of the intact crickets. The duration of the right legs touching the floor was much longer than that of the left legs. The frequency of the right legs was lower than that of the left side, and the stroke angle of the right legs was smaller than that of the left side (**Supplementary Figure 1C**). This indicates that the left legs moved more than the right legs, making the cricket continue to turn clockwise. Similarly, when the right side of the circumesophageal connective was cut, the test crickets continued to turn counterclockwise and did not exhibit a tripod walking gait pattern (**Supplementary Video 4**).

Disconnection of Connectives Between SEG and Prothoracic Ganglion

To investigate the role of the SEG, the paired connectives between SEG and prothoracic ganglion in the crickets were surgically cut. The behavior of these test crickets was the same as those of the headless crickets previously reported (Naniwa et al., 2019). The test crickets did not show voluntary evoked walking on the ball, except during defecation. They did not respond with walking to the tactile stimuli using the paintbrush. Therefore, the gait chart diagrams indicate that all legs of the crickets were always on the ground ($N = 5$,

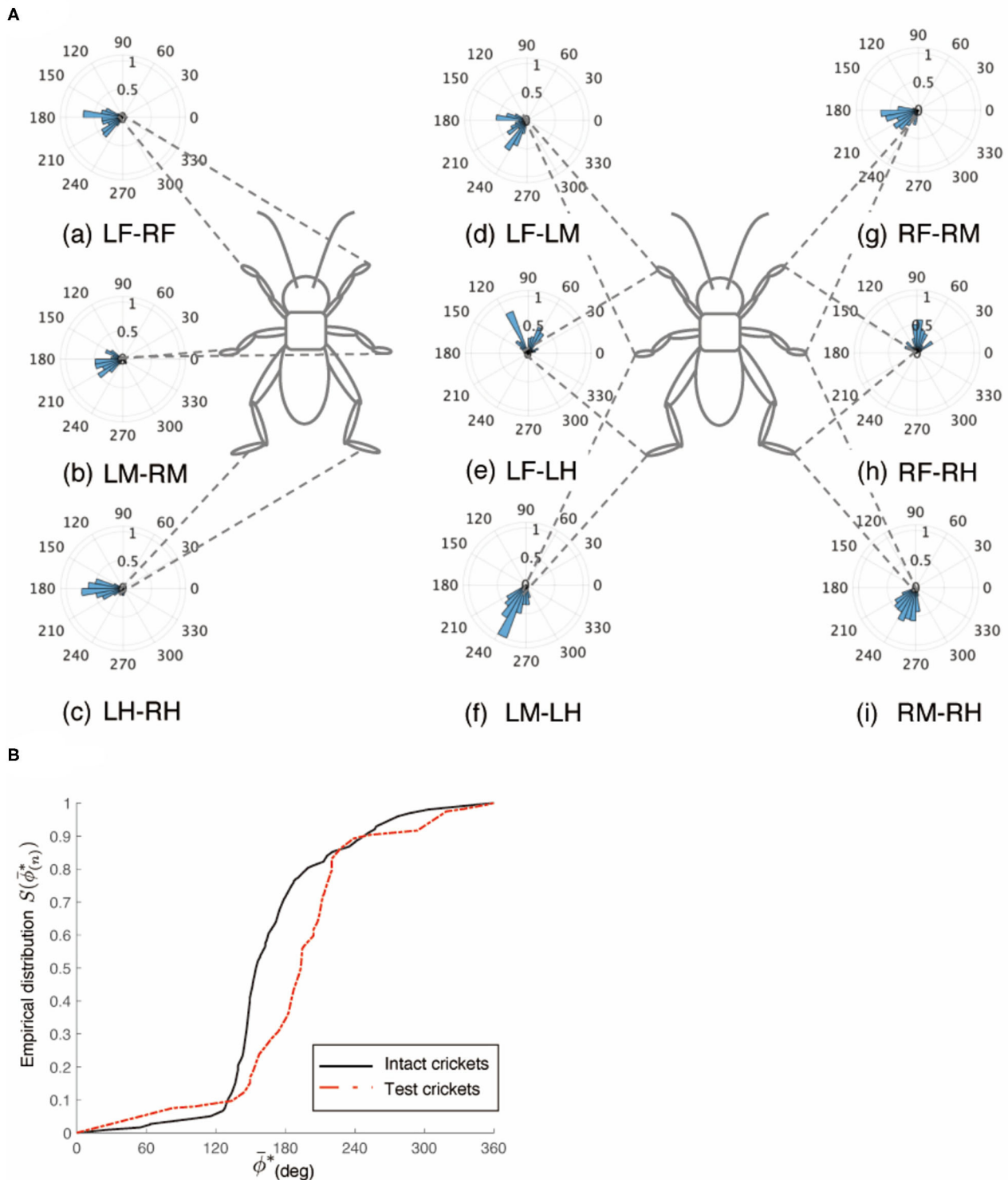


FIGURE 2 | Walking gait pattern of crickets in which paired nerve connectives between brain and SEG were cut. **(A)** Polar histograms indicate phase differences between two legs in test crickets ($N = 5$). The polar histograms demonstrate that the test crickets exhibited a tripod gait pattern on the floating ball of the treadmill. (a–i) Phase differences between pairs of legs. **(B)** Comparison of the empirical distribution function of leg phase differences between left and right legs $\bar{\phi}_{LM-RM}$. The black line indicates the empirical distribution function of the intact crickets and the red line indicates that of the crickets in which the pair of connectives between the brain and SEG was cut. LF, left foreleg; RF, right foreleg; LM, left midleg; RM, right midleg; LH, left hind leg; RH, right hind leg.

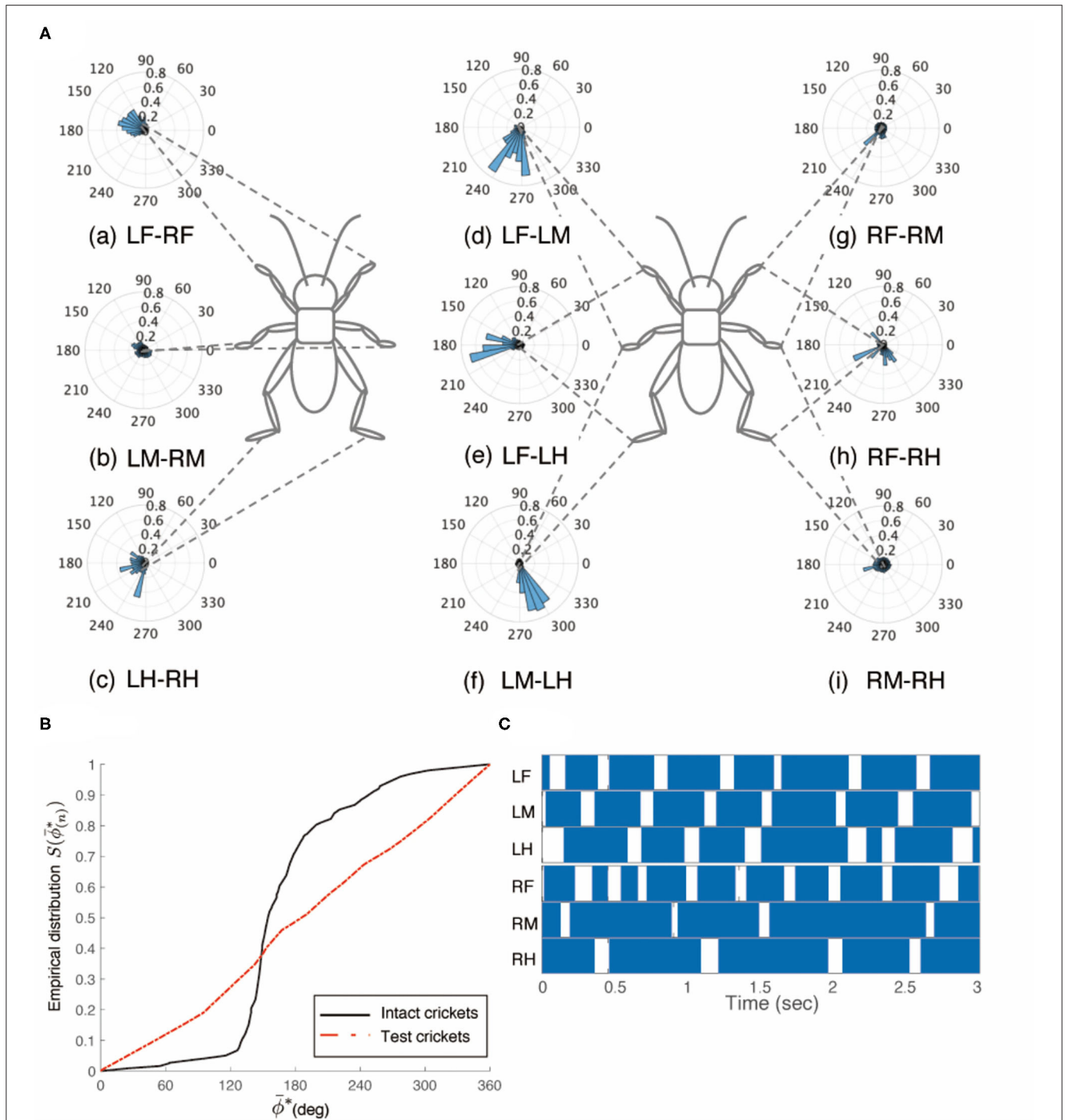


FIGURE 3 | Walking gait patterns of crickets in which left side of nerve connectives between brain and SEG was cut. **(A)** Polar histograms indicate phase differences between two legs in test crickets ($N = 5$). The test crickets continued to turn clockwise. The polar histograms demonstrate that the walking pattern was not a tripod gait. (a–i) Phase differences between pairs of legs. **(B)** Comparison of the empirical distribution function of leg phase differences between left and right legs $\bar{\phi}_{LM-RM}$. The black line indicates the empirical distribution function of the intact crickets and the red line indicates that of the test crickets. **(C)** Gait chart diagram of test cricket. The filled part indicates the duration of the power stroke period and the blank part indicates the duration of the recovery stroke. This also demonstrates that the walking pattern was not a tripod gait in the test cricket. LF, left foreleg; RF, right foreleg; LM, left midleg; RM, right midleg; LH, left hind leg; RH, right hind leg.

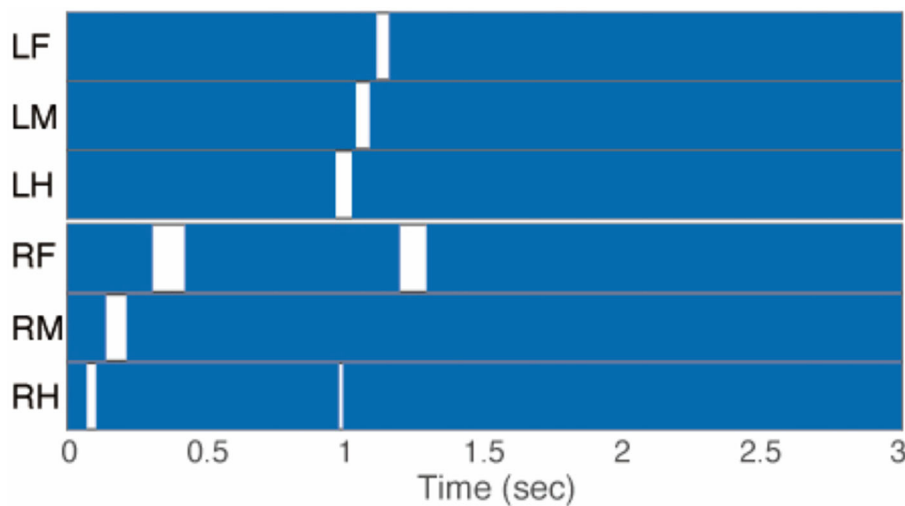


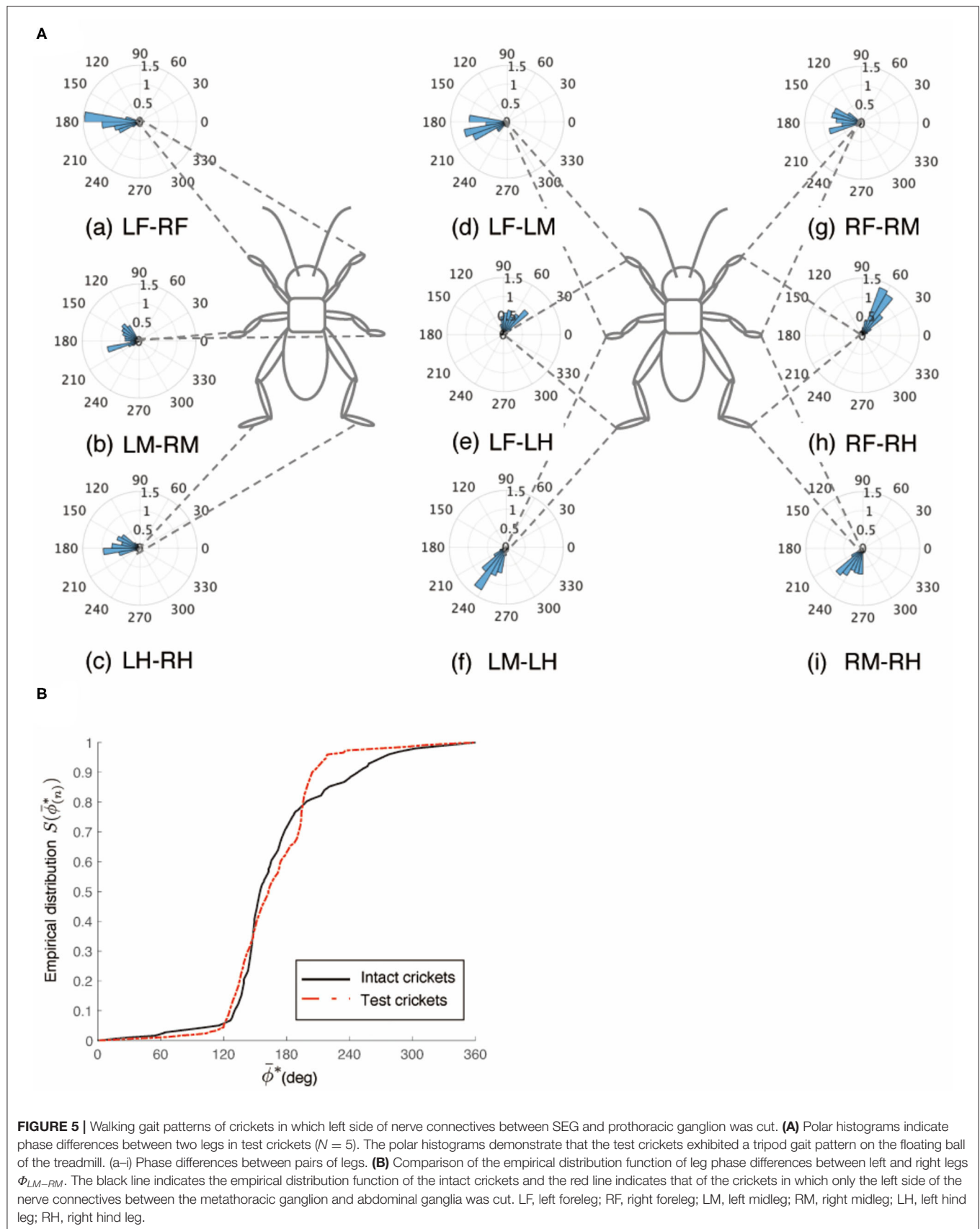
FIGURE 4 | Gait chart diagram of cricket in which paired nerve connectives between SEG and prothoracic ganglion were cut. The filled parts indicate that the tip of the legs touched the floor, demonstrating that the cricket did not walk on the floating ball of the treadmill. LF, left foreleg; RF, right foreleg; LM, left midleg; RM, right midleg; LH, left hind leg; RH, right hind leg.

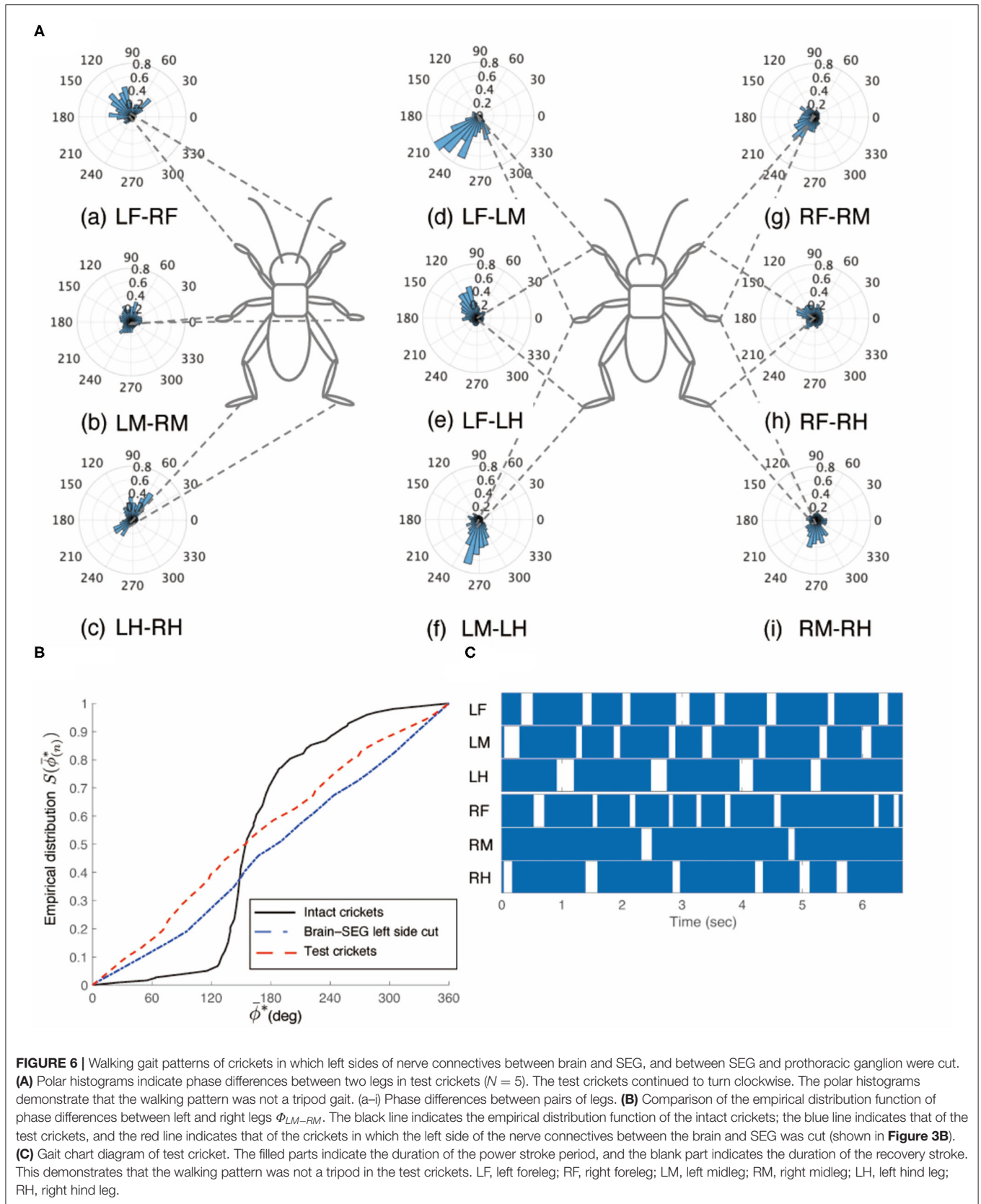
Figure 4, Supplementary Video 5). All test crickets did not walk a sufficient number of steps to analyze leg phase difference, frequency, and amplitude (average $n = 0.7$, **Table 1D**). However, if only one of the connectives between the SEG and prothoracic ganglion was cut, the crickets exhibited intact-like walking. The test crickets in which the left-side connective between the SEG and prothoracic ganglion was cut could walk with a tripod gait ($N = 5$, **Figure 5, Supplementary Video 6 0:00–1:15**). The crickets showed voluntary evoked walking. We focused on the periods of continuously walking to analyze the gait pattern. The phase differences between the left and right legs occurred in an anti-phase manner (**Figures 5Aa–c**). The foreleg and midleg of the same side moved in an anti-phase manner, whereas the foreleg and hindleg of the same side moved in an in-phase manner (**Figures 5Ad–i**). In the test crickets, the mean of the midleg phase difference Φ_{LM-RM} was 165° , with a standard deviation ν_{LM-RM} of 37.3° . The mean vector length R_{LM-RM} was 0.81. The shape of the empirical distribution function of the pair of midlegs of the test crickets was similar to that of the intact crickets (LM-RM: $n = 109$, Kuiper statistic vs. intact LM-RM: 0.23 ($P = 0.56$), V statistic for 180° : 9.53 ($P < 0.01$), **Table 1E, Figure 5B**). Neither leg frequency nor stroke angle was significantly different from that of intact crickets under this experimental condition (**Supplementary Figure 1D**). We also examined the behavior when only the right-side connective between the SEG and prothoracic ganglion was cut. The results were quite similar to those of the crickets with the left-side connective cut (**Supplementary Video 6 1:15–2:12**).

The crickets in which the left-side connectives between both the brain and SEG, and the SEG and prothoracic ganglion were cut did not walk straight forward, but continued to turn clockwise ($N = 5$, **Supplementary Video 7 0:00–1:06**). The walking of the crickets was evoked without tactile stimuli. We focused on the periods of continuously walking to analyze the gait pattern. The

gaits in these test crickets did not exhibit an ordinary tripod pattern (**Figure 6**). The polar histogram of the test crickets indicates that the phase differences between the left and right legs were not consistent (**Figure 6A**). In the test crickets, the mean of the midleg phase difference Φ_{LM-RM} was 109° , with a standard deviation ν_{LM-RM} of 108° . The mean vector length R_{LM-RM} was 0.17. The shape of the empirical distribution function of the midlegs of the test crickets was different from that of the intact crickets [LM-RM: $n = 121$, Kuiper statistic vs. intact LM-RM: 0.59 ($P < 0.01$), V statistic for 180° : -1.38 ($P = 0.92$), **Table 1F, Figure 6B**]. The gait chart diagram of the test crickets demonstrates that the duration of the left leg movements appeared to be rhythmic, as in the intact crickets (**Figure 6C**). Compared with intact crickets, the frequencies of leg movements were rather low. In addition, the frequencies of the movement in the midleg and hind legs on the right side were smaller than those on the left side (**Supplementary Figure 1E**). The duration of the right legs touching the floor was much longer than that of the left legs. The angular stroke of the left midleg was not significantly different from that of intact crickets, while the angular stroke of the right midleg was suppressed. As a result, the test crickets turned in the clockwise direction. We also investigated the behavior of the crickets in which the right-side connectives between both the brain and SEG, and between the SEG and prothoracic ganglion were cut. These crickets continued to turn counterclockwise and did not exhibit a tripod gait (**Supplementary Video 7 1:06–2:12**).

The behavior of the crickets in which the left-side connective between the brain and SEG, and the right-side connective between the SEG and prothoracic ganglion were cut was the same as that of the crickets in which the left-side connectives between the brain and the SEG, and between the SEG and prothoracic ganglion were cut. The walking of the crickets was evoked without tactile stimuli. Again, the test crickets did





not walk straight forward, but continued to turn clockwise ($N = 5$, **Supplementary Video 8** 0:00–0:55). The gait pattern of these test crickets did not exhibit a tripod (**Figure 7**). The polar histogram of the test crickets indicates that the phase differences between the left and right legs were not consistent (**Figure 7A**). In the test crickets, the mean of the midleg phase difference Φ_{LM-RM} was 87.5° , with a standard deviation ν_{LM-RM} of 110° . The mean vector length R_{LM-RM} was 0.16. The shape of the empirical distribution function of the midlegs of the test crickets was different from that of the intact crickets [LM-RM: $n = 63$, Kuiper statistic vs. intact LM-RM: 0.58 ($P < 0.01$), V statistic for 180° : -3.46 ($P = 1.00$), **Table 1G**, **Figure 7B**]. The gait chart diagram of the test crickets demonstrates that the duration of the left leg movements appeared to be rhythmic, as in the intact crickets, but the right legs were not coordinated (**Figure 7C**). Compare to intact crickets, the frequencies of the leg movements were rather low. In addition, the frequencies of the leg movement on the right side were smaller than those on the left side (**Supplementary Figure 1F**). The angular stroke of the left midleg was not significantly different from that of intact crickets, while the angular stroke of the right midleg was suppressed. As a result, the test crickets turned in the clockwise direction. When the right-side connective between the brain and SEG, and the left-side connective between the SEG and prothoracic ganglion were cut, the test crickets continued to turn counterclockwise (**Supplementary Video 8** 0:55–2:12).

Disconnection of Connectives Between Metathoracic Ganglion and Abdominal Ganglia

The crickets in which the pair of connectives between the metathoracic ganglion and first free abdominal ganglion was cut did not exhibit a tripod gait ($N = 5$, **Figure 8A**, **Supplementary Video 9**). The crickets showed voluntarily evoked walking although they did not respond with walking to the tactile stimuli of the cercus. The phase differences between the left and right midlegs were not consistent (**Figure 8Aa**). In the test crickets, the mean of the midleg phase difference Φ_{LM-RM} was 199° , with a standard deviation ν_{LM-RM} of 108° . The mean vector length R_{LM-RM} was 0.17. The shape of the empirical distribution function of the midlegs of the test crickets was far from that of the intact crickets [LM-RM: $n = 71$, Kuiper statistic vs. intact LM-RM: 0.41 ($P < 0.01$), V statistic for 180° : 1.65 ($P = 0.05$), **Table 1H**, **Figure 8B**]. The frequency of the movements in all legs and the amplitude of the movement in the midleg were slightly lower than those of the intact cricket (**Supplementary Figure 1G**). However, the walking gait pattern in the crickets in which the left-side connective between the metathoracic ganglion and first free abdominal ganglion was cut exhibited an ordinary tripod gait pattern (**Figure 9A**, **Supplementary Video 10** 0:00–1:06). The walking was evoked voluntarily. The polar histogram of the test crickets in which the left-side connective was cut indicates that the phase differences between the left and right legs occurred in an anti-phase manner (**Figure 9Aa**). In the test crickets, the mean of the midleg phase difference Φ_{LM-RM} was 180° , with a standard deviation ν_{LM-RM}

of 55.7° . The mean vector length R_{LM-RM} was 0.62. The shape of the empirical distribution function of the midlegs of the test crickets was similar to that of the intact crickets [LM-RM: $n = 51$, Kuiper statistic vs. intact LM-RM: 0.23 ($P = 0.56$), V statistic for 180° : 4.12 ($P < 0.01$), **Table 1I**, **Figure 9B**]. The frequency of movements in all legs was slightly lower than those of the intact cricket (**Supplementary Figure 1H**). Similarly, when the right-side connective between the metathoracic ganglion and third abdominal ganglion was cut, the test crickets exhibited an intact-like tripod gait walk (**Supplementary Video 10** 1:06–2:20).

DISCUSSION

Crickets walk with a tripod gait pattern on a flat floor. Although the tripod gait is typical in insect walking, the gait patterns are not always fixed, but rather, change flexibly depending on the ground surface structure. The walking gait patterns may also vary if the body structure is changed; for example, owing to a loss of legs as a result of an accident (Full and Tu, 1991; Owaki et al., 2021). To evaluate the changes in the gait patterns, gait chart diagrams of insects have been drawn in many previous studies (Wilson, 1966). A gait chart diagram has also been used to evaluate the gait pattern of legged robots (Owaki et al., 2017). Such a diagram expresses the movements of each leg and clearly indicates a snapshot of the position of each leg. Moreover, polar histograms describing gait patterns evaluate the phase differences of a given pair of legs during walking (Naniwa et al., 2020). One of the advantages of using a polar histogram is that it enables us to evaluate the gait patterns of not only individuals but also a group of animals and legged robots. We investigated the effects of the loss of either the descending signals or ascending signals into the thoracic ganglia on regulating the cricket gait pattern.

Descending Signals Into Thoracic Ganglia to Initiate Walking

Although the crickets in which the paired circumesophageal connectives were cut could walk, they did not change their direction while walking on the floating ball. The polar histograms of the treated crickets demonstrated that their gait was very close to the typical tripod pattern of the intact crickets in terms of inter-leg phase difference. As voluntary walking is initiated by descending signals originating in the brain (Kien and Altman, 1992; Kagaya and Takahata, 2011), the walking of the treated crickets was different from voluntary walking but could be initiated by receiving exteroceptive stimuli. The crickets responded to either tactile stimuli or air puffing on the cerci while walking. Crickets detect air currents using filiform hairs that are arranged on the surface of the cerci of the abdomen and respond with rapid avoidance movement when they are deflected (Edwards and Palka, 1974). Information on air movements is processed and integrated into the terminal abdominal ganglion, and the signals are transferred to the thoracic ganglia to initiate avoidance walking (Mendenhall and Murphey, 1974; Aonuma et al., 2008; Yono and Aonuma, 2008). Furthermore, the ascending signals from the abdominal nervous system also contribute to the initiation of walking; for example,

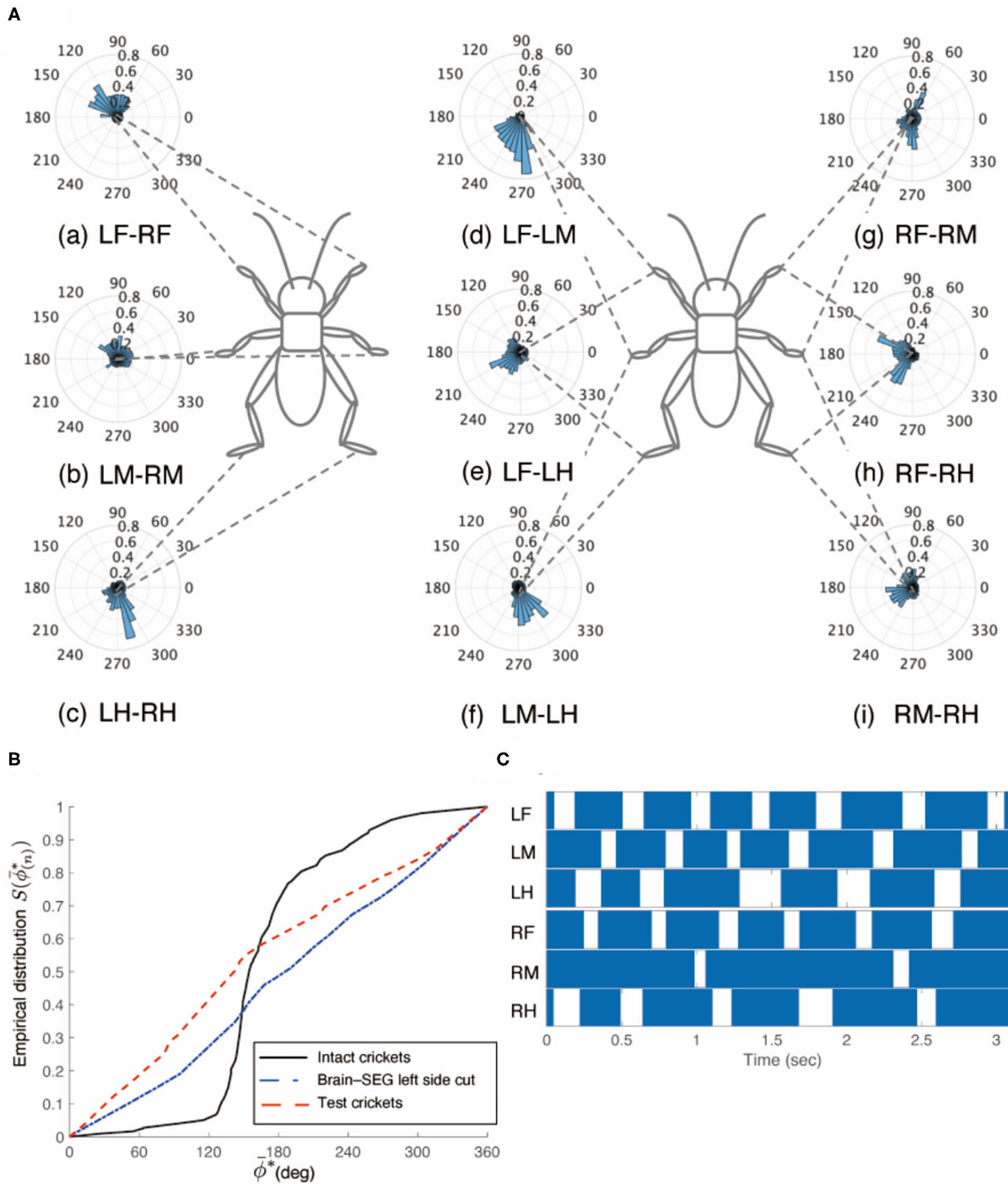


FIGURE 7 | Walking gait patterns of crickets in which left side of nerve connectives between brain and SEG, and right side of connective between SEG and prothoracic ganglion were cut. **(A)** Polar histograms indicate phase differences between two legs in test crickets ($N = 5$). The test crickets continued to turn clockwise. The polar histograms demonstrate that the walking pattern was not a tripod gait. **(a–i)** Phase differences between pairs of legs. **(B)** Comparison of the empirical distribution function of phase differences between left and right legs ϕ_{LM-RM} . The black line indicates the empirical distribution function of the intact crickets; the blue line indicates that of the test crickets, and the red line indicates that of the crickets in which the left side of the nerve connectives between the brain and SEG was cut (shown in **Figure 3B**). **(C)** Gait chart diagram of test cricket. The filled parts indicate the duration of the power stroke period, and the blank part indicates the duration of the recovery stroke. This demonstrates that the walking pattern was not a tripod gait in the test crickets. LF, left foreleg; RF, right foreleg; LM, left midleg; RM, right midleg; LH, left hind leg; RH, right hind leg.

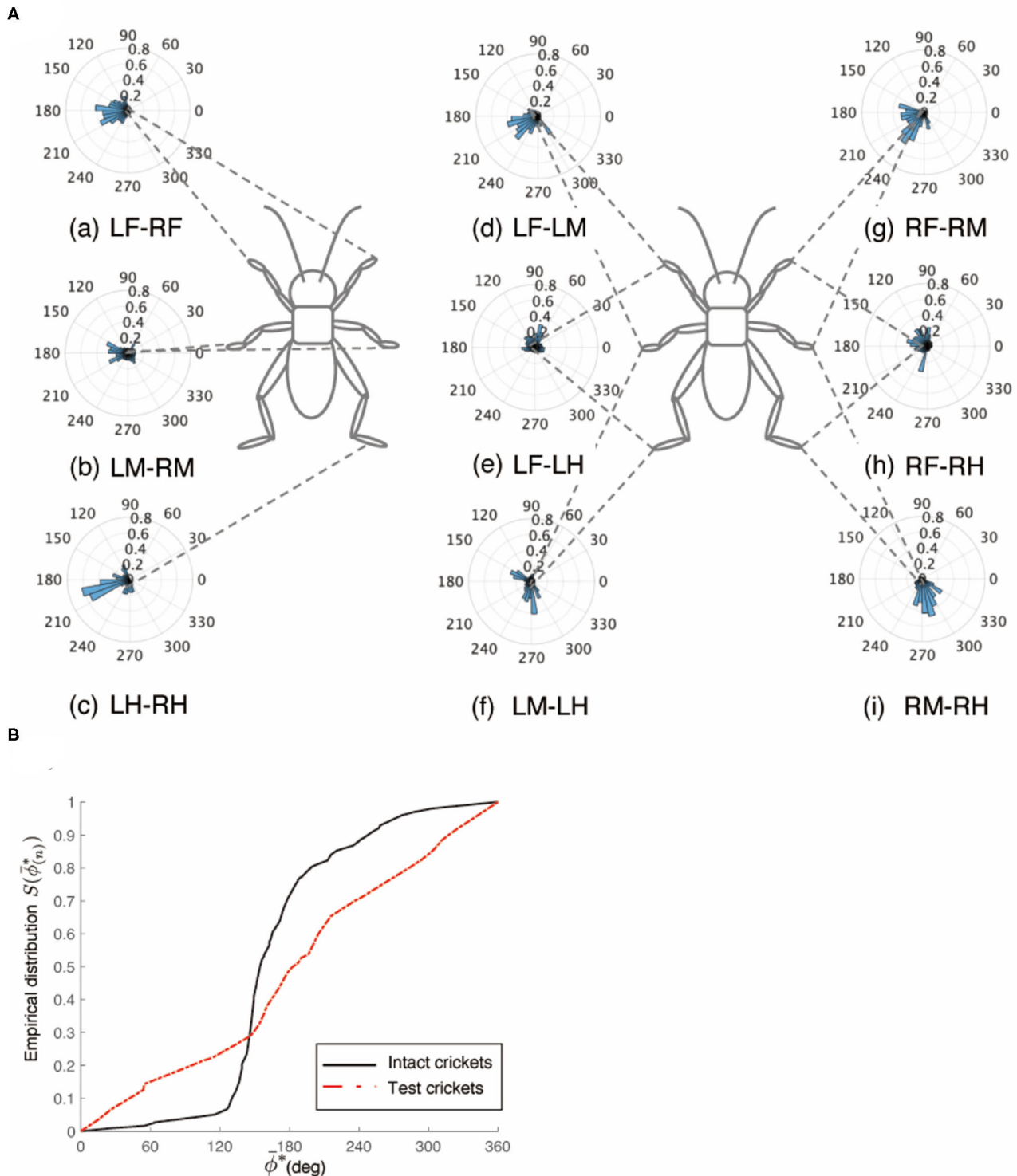


FIGURE 8 | Walking gait patterns of crickets in which paired nerve connectives between metathoracic ganglion and abdominal ganglia were cut. **(A)** Polar histograms indicate phase differences between two legs in test crickets ($N = 5$). The polar histograms demonstrate that the test crickets did not exhibit a tripod gait pattern on the floating ball of the treadmill. (a–i) Phase differences between pairs of legs. **(B)** Comparison of the empirical distribution function of phase differences between left and right legs ϕ_{LM-RM} . The black line indicates the empirical distribution function of the intact crickets and the red line indicates that of the crickets in which the paired nerve connectives between the metathoracic ganglion and abdominal ganglia were cut. LF, left foreleg; RF, right foreleg; LM, left midleg; RM, right midleg; LH, left hind leg; RH, right hind leg.

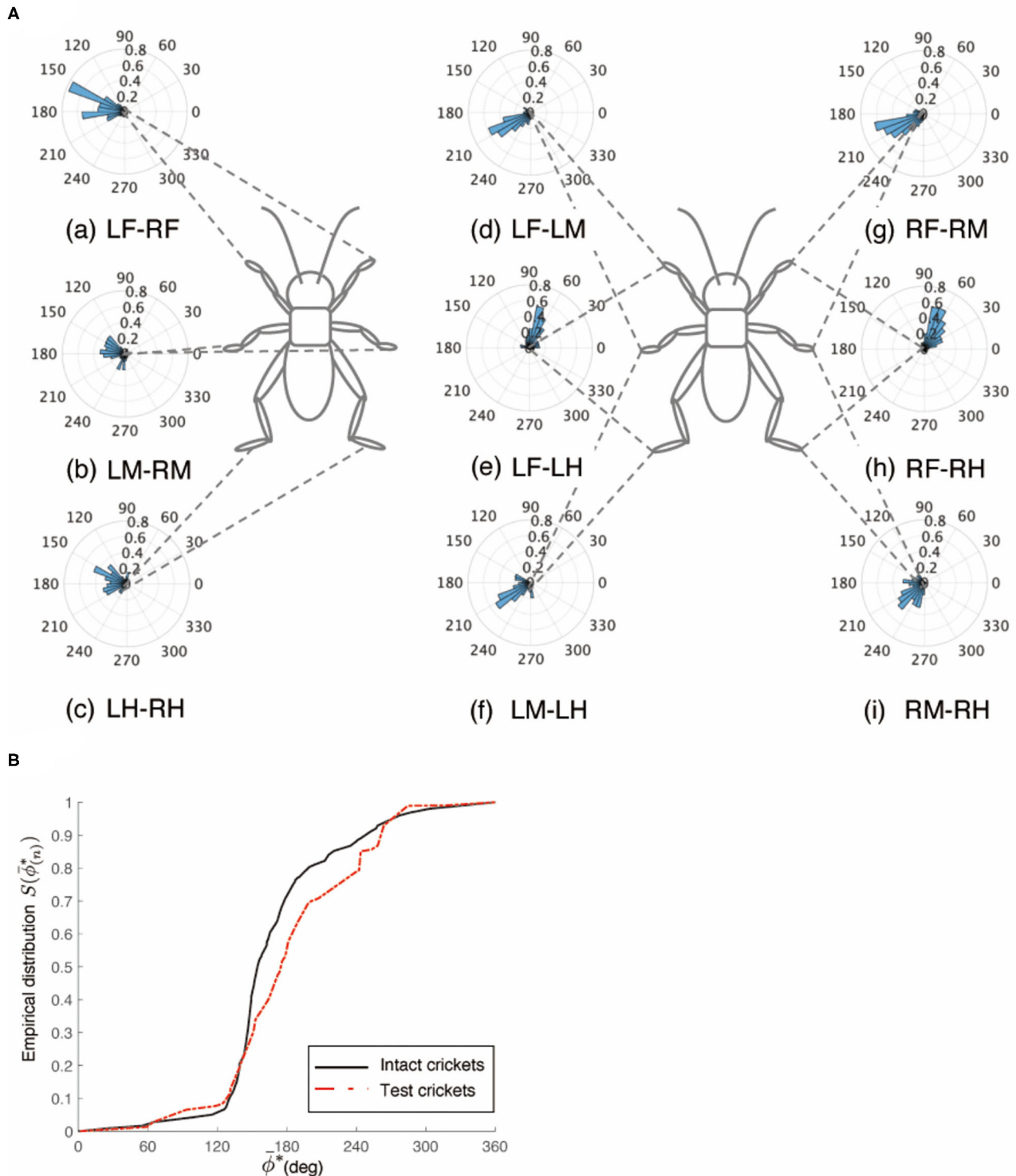


FIGURE 9 | Walking gait patterns of crickets in which left side of nerve connectives between metathoracic ganglion and abdominal ganglia was cut. **(A)** Polar histograms indicate phase differences between two legs in test crickets ($N = 5$). The polar histograms demonstrate that the test crickets exhibited a tripod gait pattern on the floating ball of the treadmill. (a–i) Phase differences between pairs of legs. **(B)** Comparison of the empirical distribution function of phase differences between left and right legs ϕ_{LM-RM}^* . The black line indicates the empirical distribution function of the intact crickets and the red line indicates that of the crickets in which the left side of the nerve connectives between the metathoracic ganglion and abdominal ganglia was cut. LF, left foreleg; RF, right foreleg; LM, left midleg; RM, right midleg; LH, left hind leg; RH, right hind leg.

after-defecation walking (Naniwa et al., 2019). Thus, certain types of internal or external stimuli contribute to the initiation of walking in brainless crickets. It has been reported that the brain inhibits all reflex activities (Bethe, 1898). Neuronal signals for coordinating the leg movements are generated in the thoracic ganglia of insects. A decrease in the inhibition from the brain may have contributed to the treated crickets walking straight forward in this study.

One of the remarkable findings of this study is that the crickets in which one side of the circumesophageal connectives was cut exhibited walking, while it continued to turn in the opposite direction to that of the surgical cut of the connective (**Figure 3**). The disconnection of the connective induces loss of frequency entrainment, which in turn causes loss of phase entrainment. This phenomenon appeared as though the inhibition from the brain to the cut-side pathway was abolished. The legs on the side of the connective cut moved more (**Supplementary Figures 1C–F**), which in turn pushed the body to the opposite side to continue turning. Movements of the opposite side could be introduced when they were bent. Therefore, the movements of the opposite side legs appeared to be caused by the local reflex. Movements of the legs in insects are detected by proprioceptive receptors (Tuthill and Wilson, 2016) such as the chordotonal organs (Hofmann et al., 1985; Büschges, 1994), campaniform sensilla (Bässler, 1977), and hair plate (Pearson et al., 1976; Wong and Pearson, 1976). Moreover, sensory afferents directly activate the extensor motor neurons of the trochanter and directly inhibit the flexor motor neurons in the cockroach (Pearson et al., 1976). The leg reflection initiated by a tactile stimulus was suppressed by the inhibitory descending signals from the brain, whereas the reflection occurs without brain signals in cockroach (Mu and Ritzmann, 2008). Thus, bending the leg joints could activate the directory extensor motor neurons to extend the legs of the crickets. Therefore, our results suggest that inhibition of the brain contributes to the regulation of coordinated walking in crickets.

The descending signals from the SEG into the thoracic ganglia are important for initiating walking. Inhibiting or blocking descending signals from SEG reduces the induction and maintenance of walking (Gal and Libersat, 2006, 2008). The crickets in which the paired connectives between the SEG and prothoracic ganglion were cut did not walk, except after defecation, as reported for the behavior of the headless cricket (Naniwa et al., 2019). The motor neurons that activate the leg muscles originate in the thoracic ganglia. The rhythmic activities of neurons, known as CPGs, in the thoracic ganglia are thought to be closely linked to coordinated leg movements (Büschges et al., 1995; Büschges, 1998; Ritzmann and Büschges, 2007). The CPGs are modulated by the descending signals from the brain that initiate, maintain, modify, and stop the motor outputs for walking (Bidaye et al., 2017). The roles of the SEG are believed to modulate the interactions between the sensory inputs from the legs and motor output (Knebel et al., 2018, 2019). It has also been reported that descending signals from the SEG can exhibit pattern generators in the chest and abdomen (Kien, 1990). It has been reported that the SEG plays an important role in the initiation, maintenance, and coordination of walking in the locust (Kien and Altman, 1984). Our behavior

experiments confirmed the important role of the SEG in initiating walking.

Another significant finding in this study is that the crickets in which one side of the paired connective between the SEG and prothoracic ganglion was cut walked like the intact crickets (**Figures 5, 9**). Furthermore, the crickets in which one side of the circumesophageal connectives and one side of the connectives between either the ipsilateral or contralateral side of the SEG and prothoracic ganglion were cut continued to turn in the opposite side to that of the circumesophageal connective cut (**Figures 6, 7**). This suggests that the descending signals from the SEG converge and are processed in the thoracic ganglia and that the leg movements are regulated by the information from the SEG, even if it is only passed through one side of the connectives. Therefore, neurons may exist that integrate the information passed through the left and right pathways. Bilaterally symmetrical dorsal unpaired median (DUM) neurons have been identified in insects [locust: (Plotnikova, 1969); cockroach: (Crossman et al., 1971); and crickets (Clark, 1976)]. Certain DUM neurons terminate in the leg muscles of cockroaches (Denburg and Barker, 1982; Tanaka and Washio, 1988). Moreover, the DUM neurons in the prothoracic ganglion contribute to walking regulation in crickets (Gras et al., 1990). In the case of locusts, the effect of the neural network comprising the brain, subesophageal ganglion, and thoracic ganglion on locomotion patterns has been investigated (Kien, 1983; Kien and Williams, 1983). Further investigation is required to clarify which neurons contribute to interlimb coordination in crickets.

Effect of Ascending Signals From Abdominal Nervous System on Walking

In insects, the abdominal nervous system serves as the center for controlling avoidance behavior (Mendenhall and Murphey, 1974; Tauber and Camhi, 1995; Card, 2012), mating behavior (Killian et al., 2006), egg-laying behavior (Sugawara and Loher, 1986), and defecation walking (Naniwa et al., 2019). These behaviors are closely linked to walking. Therefore, ascending signals from the abdominal ganglia into the thoracic ganglia may contribute to initiating and regulating walking in crickets. Furthermore, the descending signals that are modulated by the sensory feedback signals from the legs contribute to the modulation of the coordinated walking gait (Bidaye et al., 2017; Knebel et al., 2018). Thoracic ganglia form a network as CPGs that are spontaneously excited by SEG to establish a constant rhythm, while also coordinating leg motor patterns based on ascending signals from the lower ganglia (Bässler et al., 1985; Kien and Altman, 1992; Knebel et al., 2019). The coordinated rhythmic leg motor pattern is modulated by sensory signals acquired by mechanoreceptive organs of the legs (Owaki et al., 2021). These studies indicate the activities of the CPGs in the thoracic ganglia are modulated by multi kinds of signals, e.g., descending signals, sensory feedback, and so on. Our results add ascending signals as other signals to modulate CPG activities in the thoracic ganglia. Activation of the giant interneurons originated in the terminal abdominal ganglion elicit avoidance walking in the crickets (e.g., Jacobs and Murphey, 1987; Yono and Aonuma, 2008). Some of the giant neurons innervate axons into the thoracic ganglia and extend neuronal branches (Hirota

et al., 1993). The neuronal branches of the ascending neurons in the anterior ganglia have outputs to motor control (Aonuma et al., 1994). Therefore, ascending signals from the abdominal nervous systems could modulate motor control in the thoracic ganglia. Ascending signals from the abdominal nervous systems and the descending signals from the brain and SEG could converge in the thoracic ganglia to coordinate walking gait patterns in crickets. The disconnection of the paired connectives between the metathoracic ganglion and first free abdominal ganglion prevented tripod gait walking in the crickets. However, the disconnection of one side of the connectives between the metathoracic ganglion and first free abdominal ganglion did not affect the expression of the tripod gait. Therefore, similar to the descending signals from the SEG into the thoracic ganglia, the ascending signals may be transferred into the bilateral neurons to be integrated and processed in the thoracic ganglia. Coordinated walking gait patterns are thought to be produced by the CPGs, descending central commands, and sensory feedback loops. This study demonstrated that the ascending signals from the abdominal nervous system also contribute to the generation of coordinated walking gait patterns in insects. It is technically difficult to cut the metathoracic ganglion and to fuse the first and second abdominal ganglia to examine how these ganglia contribute to the coordinated gait pattern. In contrast, cutting between the terminal abdominal ganglion and the sixth abdominal ganglion did not affect the expression of the tripod gait pattern (Supplementary Video 11). This suggests that the sensory signals from cercus may not mainly contribute to the expression of the tripod pattern. Thus, it is necessary to investigate which ganglion or which group of ganglia interact with SEG to coordinate the tripod gait and to investigate which types of neurons contribute to regulating the leg movements in crickets.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author/s.

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AUTHOR CONTRIBUTIONS

KN and HA conceived and designed the experiment, performed the experiment, analyzed the data, and wrote the manuscript.

FUNDING

This work was supported by JSPS KAKENHI (Grant-in-Aid for Scientific Research (S), Grant No. 17H06150), Japan.

ACKNOWLEDGMENTS

We thank Professors K. Osuka and Y. Sugimoto (Osaka University) and Dr. K. Kagaya (University of Tokyo) for their comments on this study.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frobt.2021.625094/full#supplementary-material>

Supplementary Figure 1 | Mean and standard deviation of the frequency of movement of each leg and the movement amplitude of the midleg. The black letters indicate the frequencies of the leg movements. The red letters indicate the stroke angle of the midleg. A comparison test between intact cricket and experimental crickets was performed. A comparison test between the right and left middle leg in the experimental cricket was performed. Mann–Whitney *U*-test was used for the comparison test of the leg frequency and the movement amplitude. Significance level $\alpha = 0.01$. **(A)** Intact crickets exhibited a tripod gait. **(B)** Disconnection of the paired circumesophageal exhibited a tripod gait. **(C)** Disconnection of the left-side of the circumesophageal connective exhibited a turn clockwise. **(D)** Disconnection of the left-side connective between the SEG and prothoracic ganglion exhibited a tripod gait. **(E)** Disconnection of the left-side of the circumesophageal connective and the left-side connective between the SEG and prothoracic ganglion (cutting ipsilateral side) exhibited a turn clockwise. **(F)** Disconnection of the left-side of the circumesophageal connective and the right-side connective between the SEG and prothoracic ganglion exhibited a turn clockwise. **(G)** Disconnection of the paired connectives between the metathoracic ganglion and first free abdominal ganglion exhibited an uncoordinated gait. **(H)** Disconnection of the left-side connective between the metathoracic ganglion and first free abdominal ganglion exhibited a tripod gait.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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A Reciprocal Excitatory Reflex Between Extensors Reproduces the Prolongation of Stance Phase in Walking Cats: Analysis on a Robotic Platform

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OPEN ACCESS

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Received: 04 December 2020

Accepted: 15 March 2021

Published: 08 April 2021

Citation:

Tanikawa T, Masuda Y and Ishikawa M
(2021) A Reciprocal Excitatory Reflex
Between Extensors Reproduces the
Prolongation of Stance Phase in
Walking Cats: Analysis on a Robotic
Platform.
Front. Neurobot. 15:636864.
doi: 10.3389/fnbot.2021.636864

Spinal reflex is essential to the robust locomotion of quadruped animals. To investigate the reflex mechanisms, we developed a quadruped robot platform that emulates the neuromuscular dynamics of animals. The leg is designed to be highly back-drivable, and four Hill-type muscles and neuronal pathways are simulated on each leg using software. By searching for the reflex circuit that contributes to the generation of steady gait in cats through robotic experiments, we found a simple reflex circuit that could produce leg trajectories and a steady gait. In addition, this circuit can reproduce the experimental behavior observed in cats. As a major contribution of this study, we show that the underlying structure of the reflex circuit is the reciprocal coupling between extensor muscles via excitatory neural pathways. In the walking experiments on the robot, a steady gait and experimental behaviors of walking cats emerged from the reflex circuit without any central pattern generators. Furthermore, to take advantage of walking experiments using a neurophysiological robotic platform, we conducted experiments in which a part of the proposed reflex circuit was disconnected for a certain period of time during walking. The results showed that the prolongation of the stance phase caused by the reciprocal excitatory reflex contributed greatly to the generation of a steady gait.

Keywords: spinal reflex, neurophysiology, bio-inspired robot, quadruped, walking, gait generation, hill-type muscle, autonomous decentralized control

1. INTRODUCTION

Quadruped animals can immediately respond to various environmental disturbances and achieve steady locomotion. Many experiments have been conducted to reveal the mechanism of motion generation in quadrupeds. Grillner (1975) reported that the central pattern generator (CPG) in the spinal cord generates a rhythmic gait pattern, even when the nerves from the brain and proprioceptors are suspended. However, sensory feedback from receptors contributes significantly to the motion generation of animals. Pearson (2004) demonstrated that sensory feedback through reflex pathways determines the timing of phase transitions in a step cycle and shapes the characteristics of movement patterns, which contributes significantly to extensor activation in walking cats.

Functions of the motor coordination of reflexes in walking quadrupeds have been investigated in animal experiments. In experiments by Whelan et al. (1995), electrical stimulation on the afferent nerves from ankle extensor muscles prolonged the stance phase in walking cats. This result suggests that the unloading of the ankle extensor muscles initiates the stance-to-swing transition. In experiments by McVea et al. (2005), assisting the flexor muscle movement in walking cats during the swing phase accelerated the activation timing of the ankle extensor muscles. This result suggests that the angle of the hip joint initiates the swing-to-stance transition. These studies highlight individual reflex mechanisms in stance and swing phases; however, the entire reflex circuit that generates the walking motion has not yet been identified.

In recent years, the constructivist approach has been employed to investigate the locomotion mechanism of animals by reproducing motor control of animals using robots and computer simulations. Habu et al. (2018) has proposed a neuromuscular model that reproduces the musculoskeletal system and detailed neural pathways of cats. In the walking simulation, they designed a CPG network to generate a trot gait, and when they introduced feedback of ground reaction forces into the CPG, the model changed the gait from trot to walk and gallop. As a simpler model to understand the locomotion mechanism of animals, Maufroy et al. (2010), Aoi et al. (2013), and Owaki and Ishiguro (2017) proposed an oscillator model that adjusts leg phase based on the ground contact information. In a walking experiment, their robots can produce multiple animal-like gait patterns depending on the speed.

Several studies have shown a crucial result in this research field that the leg trajectories and steady gait can be achieved by the interaction between spinal reflexes, body dynamics, and environment, without using oscillator models or complex CPG models. A human musculoskeletal model of Geyer and Herr (2010) produced steady alternating gait using only reflex rules. A cat hind leg model of Ekeberg and Pearson (2005) also showed alternative gait only with the reflex rules, and Rosendo et al. (2014) investigated this idea in real-world experiments using a musculoskeletal robot. However, in these studies, the designers divided the walking motion into multiple phases (ex. stance, liftoff, swing, and touchdown phase) and designed a separate reflex rule for each phase. Therefore, it is not clear how these many reflex rules are integrated in the animal body, i.e., the overall structure of the reflex circuit that produces a steady gait and leg trajectory.

In order to clarify the structure of the reflex circuit that generates the steady locomotion of cats, we explored the reflex circuit using a quadruped robot platform that emulates the neuromuscular dynamics of animals.

As a result, we found a simple reflex circuit that could produce a steady gait and leg trajectories and also reproduce the experimental behavior of cats. The major contribution of this study is clarifying the essential structure of the reflex circuit to produce a steady gait, which is the reciprocal excitatory reflex between hip and knee–ankle extensor muscles. To evaluate the proposed reflex circuit, we conducted walking experiments and reproduced a neurophysiological experiment based on cats on

a quadruped robot. In the walking experiments, the quadruped robot did not have a central pattern generator; however, it produced a gait pattern and leg trajectories autonomously. In the reproduction experiment of cats' walking behaviors, the robot reproduces the swing-to-stance transition based on the hip angle in McVea et al. (2005) and a prolongation function of the stance phase, with stimulation on the ankle extensor nerves, as in Whelan et al. (1995). Moreover, utilizing a robot with a reprogrammable reflex law in real time, we conducted an experiment to remove the reciprocal excitatory pathway between the extensors (the prolongation function of the stance phase) during walking. The absence of the reciprocal excitatory pathway reduced the gait stability of the robot. This result suggests that the prolongation function provided by the reciprocal excitatory pathway between the hip and knee–ankle extensors stabilizes the gait pattern.

In section 2, we explain the mechanical design and control system of the quadruped robot platform. Sections 3 and 4 describe muscle and reflex model and their implementation to the robot. Section 5 presents the result of walking experiments, and the gait emergence mechanism and a comparison with a previous study are discussed in section 6. Section 7 summarizes the effect of proposed reflex circuit and addresses about future work.

2. QUADRUPED ROBOT THAT REPRODUCES MUSCULAR PROPERTIES AND REFLEXES

To reproduce and understand the reflex mechanism of animals, we construct a quadruped robotic platform, shown in **Figure 1**, that can reproduce muscle characteristics and reflexes like those in Zhao et al. (2020). This quadruped robot comprises highly back-drivable legs to reproduce the flexibility of animals and torque-controllable motors that enable the robot to emulate the muscle characteristics virtually.

First, we explain the mechanical design of the quadruped robot platform. As shown in **Figure 2**, each leg consists of two links, and the legs can move freely in the sagittal plane by driving the upper and lower rotational joints. The leg module can also rotate in the roll direction as adduction and abduction motion; thus, the legs have three degrees of freedom. Each joint is driven by a brushless direct current (BLDC) motor (MN6007 KV160, T-Motor, China). The torque is transmitted by gears and timing belts in the lower rotational joints and by only gears in the other two joints. We embed the motors inside the hip part of the leg module to reduce the moment of leg inertia. The reduction ratio is as low as 1:7 so that all joints achieve high back-drivability, and the measurement of motor current enables torque control. A rotary encoder (ATM102-V, CUI Devices, USA) is installed on the back of each motor to measure the rotation angle. The body length, distance between the hips, link length of the legs, and weight are 470 mm, 289 mm, 152 mm, and 7.6 kg, respectively.

Next, we describe the control system of the quadruped robot. This control system comprises a low-level controller for the BLDC motor and a high-level controller that reproduces

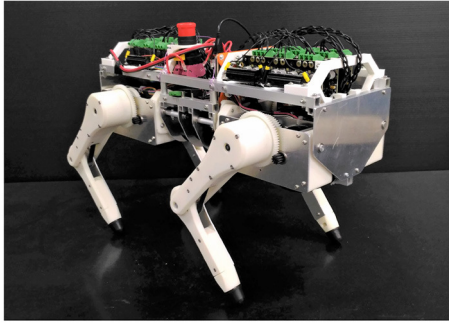


FIGURE 1 | Snapshot of a quadruped robotic platform that can reproduce muscle characteristics and reflexes.

the muscle characteristics and reflexes. The motor driver (v3.6 24V, ODrive) provides low-level control for the motor torque with current feedback and measures the angle using the rotary encoder at a frequency of 8 kHz. A microcontroller (Teensy 3.6) provides high-level control. It emulates virtual muscles and reflex circuits based on the angle information received from the motor driver and commands the target torques to reproduce their characteristics to the motor driver. The communication frequency between the controllers is 1 kHz.

3. REPRODUCTION OF MUSCLE PROPERTIES

To reproduce and understand the reflex mechanisms of animals, we emulate muscles and neural models using a quadruped robot software.

3.1. Muscle Model

We introduce a Hill-type muscle model developed by Geyer and Herr (2010), which is shown in **Figure 3A**. The Hill-type muscle model consists of a contractile element (CE) that exerts tension according to the muscle activation, a parallel-connected elastic element (PE), and a series-connected elastic element (SE). The CE has a length-dependent property, wherein the contraction force is maximized at an optimal length, and a velocity-dependent property. The contraction force becomes relatively small and large during contraction and extension, respectively. The elastic elements, PE and SE, have non-linear elastic properties that produce tension when they exceed a particular length.

Next, we formulate the details of the Hill-type muscle model developed by Geyer and Herr (2010). Using muscle activity $A \in [0, 1]$, we express the generated CE force, F_{ce} , as

$$F_{ce} = AF_{\max} f_l(l_{ce}) f_v(v_{ce}), \quad (1)$$

where $F_{\max}$ is the maximum isometric force, and l_{ce} and v_{ce} are the length and velocity of the CE, respectively. The force-length and force-velocity characteristics, $f_l(l_{ce})$ and $f_v(v_{ce})$, respectively,

are represented as

$$f_l(l_{ce}) = \exp \left(c \left| \frac{l_{ce} - l_{\text{opt}}}{l_{\text{opt}} \omega} \right|^3 \right) \quad (2)$$

$$f_v(v_{ce}) = \begin{cases} \frac{v_{\max} - v_{ce}}{v_{\max} + K v_{ce}} & v_{ce} < 0 \\ \frac{v_{\max} + v_{ce}}{N + (N - 1) \frac{v_{\max} + v_{ce}}{7.56 K v_{ce} - v_{\max}}} & v_{ce} \geq 0 \end{cases}, \quad (3)$$

where l_{opt} is the length of $f_l(l_{\text{opt}}) = 1$, and c , ω , $v_{\max}$, K , and N are parameters that are used to determine the muscle characteristics. The graphs of functions $f_l(l_{ce})$ and $f_v(v_{ce})$ are presented in **Figure 3B**. The PE force, F_{pe} , and SE force, F_{se} , are expressed as

$$F_{pe}(l_{ce}) = \begin{cases} F_{\max} \left(\frac{l_{ce} - l_{\text{opt}}}{l_{\text{opt}} \epsilon_{pe}} \right)^2 & l_{ce} > l_{\text{opt}} \\ 0 & l_{ce} \leq l_{\text{opt}} \end{cases} \quad (4)$$

$$F_{se}(l_{se}) = \begin{cases} F_{\max} \left(\frac{l_{se} - l_{\text{slack}}}{l_{\text{slack}} \epsilon_{ref}} \right)^2 & l_{se} > l_{\text{slack}} \\ 0 & l_{se} \leq l_{\text{slack}} \end{cases}, \quad (5)$$

where l_{se} is the SE length, l_{slack} is the rest length of SE, and ϵ_{pe} and ϵ_{ref} are the reference strains of PE and SE, respectively.

3.2. Implementation of Muscle Models to the Robot

In this subsection, we discuss the muscle placement on the quadruped robot. Although quadruped animals have numerous muscles in their legs, we classify them into radial and angular muscles based on the direction of force generation to improve our understanding of the walking phenomena. According to the muscle classification, the two-link legs of the quadruped robot are considered to possess virtual rotational hip joints and linear joints between the hips and toes, as shown in **Figure 4**. The extensors and flexors are placed on each virtual joint. The muscles of virtual rotational and linear joints approximately correspond to the hip muscles and knee-ankle muscles in animals, respectively.

We reproduce the muscle characteristics in the quadruped robot using the following method developed by van Soest and Bobbert (1993):

- 1) Compute muscle length l_{mtu} from the measured leg joint angles.
- 2) Update CE length l_{ce} . Because the SE is connected in series to the CE and the PE, the muscle force, F_{mtu} , is expressed as

$$F_{mtu} = F_{se} = F_{ce} + F_{pe}. \quad (6)$$

Using Equations (1) and (6), the velocity of the CE is deformed as

$$v_{ce} = \frac{dl_{ce}}{dt} = f_v^{-1} \left[\frac{F_{se}(l_{se}) - F_{pe}(l_{ce})}{AF_{\max} f_l(l_{ce})} \right], \quad (7)$$

and l_{ce} is computable by integrating Equation (7).

- 3) The muscle force, F_{mtu} , is obtained by calculating F_{se} in Equation (5) using $l_{se} = l_{mtu} - l_{ce}$. The muscle characteristics are reproduced by generating motor torques that correspond to the muscle forces.

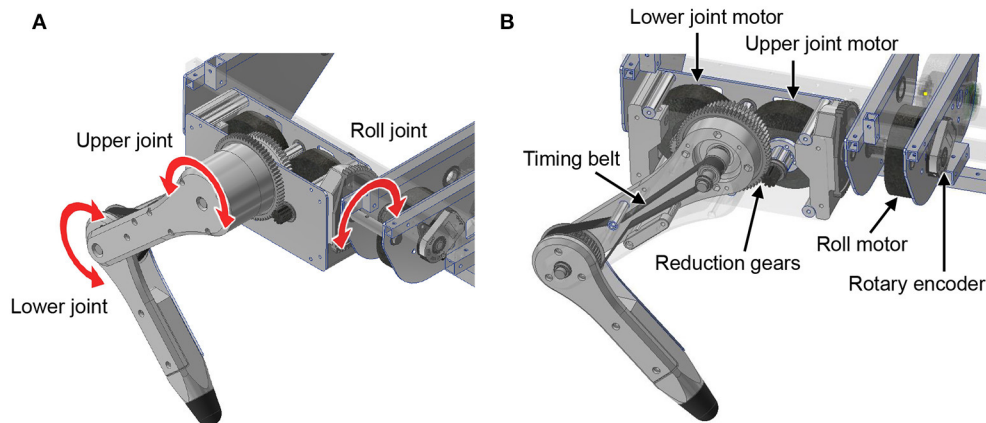


FIGURE 2 | Leg design of the quadruped robot. **(A)** Degree of freedom for the legs. **(B)** Detailed mechanism of the legs.

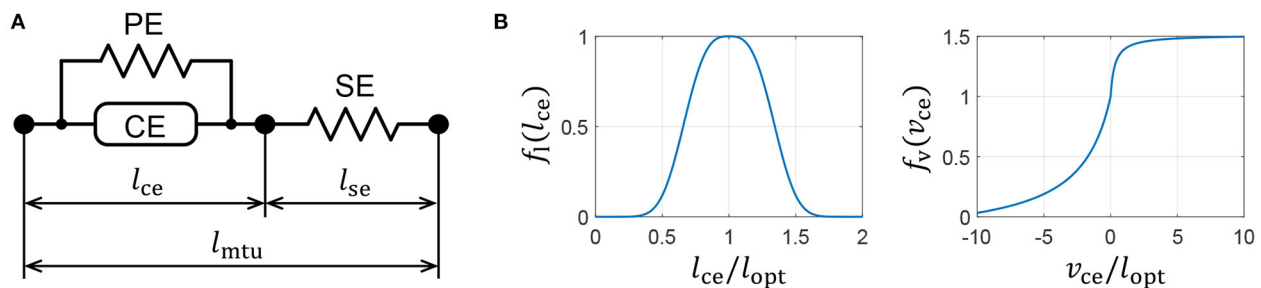


FIGURE 3 | Muscle properties reproduced on a quadruped robot. **(A)** Hill-type muscle model. **(B)** Force-length and force-velocity characteristics of the contractile element (CE).

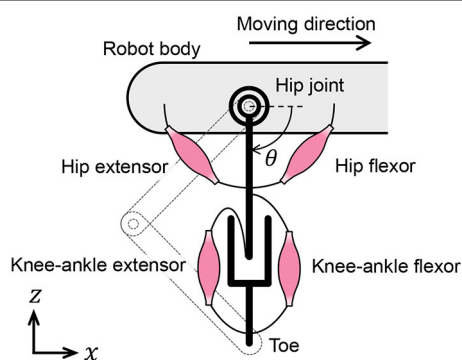


FIGURE 4 | Placement of muscle models on the quadruped robot.

Please see Geyer and Herr (2010) for more detail.

4. IMPLEMENTATION OF THE REFLEX CIRCUIT

To reproduce and understand the reflex mechanism in animal walking, we construct a reflex circuit that can reproduce the

walking functions of cats. In this section, we propose a simple reflex circuit based on the results of previous experiments on walking cats.

4.1. Design of the Reflex Pathway

We describe two results from previous experiments on walking cats to construct a reflex pathway for the quadruped robot. In experiments by Whelan et al. (1995), electric stimulation on afferent nerves from ankle extensor muscles prolonged the stance phase. This result suggests that the unloading of ankle extensor muscles initiates the stance-to-swing transition. In experiments by McVea et al. (2005), assisting the flexor muscle movement during the swing phase accelerated the activation timing of the ankle extensor muscles. This suggests that the angle of the hip joint initiates the swing-to-stance transition.

We designed the reflex pathways, shown in **Figure 5**, using these results. From the first experiment, we embedded excitatory reflex pathways from the force receptors of the knee-ankle extensors to the hip and knee-ankle extensor muscles. These pathways provide a function; if the knee-ankle receptors continue to sense the ground reaction force, the muscles continue to extend the knee-ankle and hip joints. From the second experiment, we embedded an excitatory reflex pathway from the force receptors of the hip extensors to the knee-ankle extensor

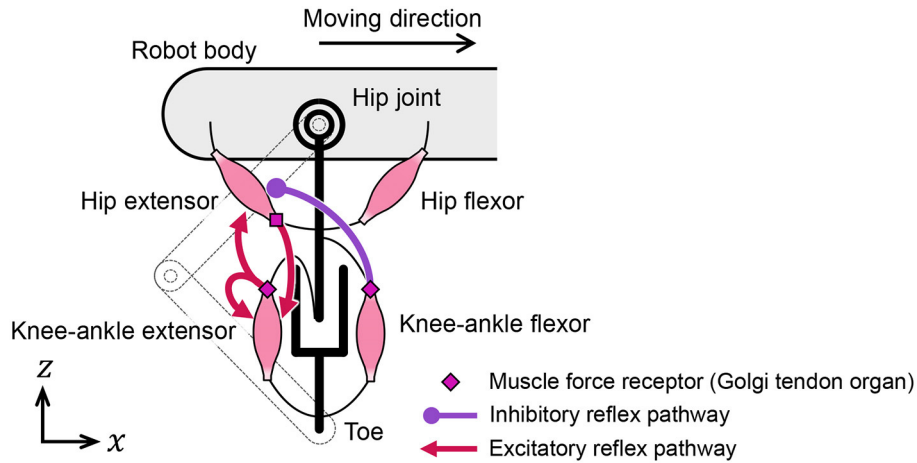


FIGURE 5 | Reflex pathways embedded in the quadruped robot.

muscles. With this pathway, if the hip extensor muscles are fully stretched and generate tension, the sensory signal initiates the swing-to-stance transition. It is important to note that to suppress excessive excitation of the hip extensor at the end of the swing phase, we embedded an inhibitory reflex pathway from the force receptors of knee-ankle flexors to hip extensors through trial and error.

4.2. Modeling of the Reflex Circuit

This subsection introduces a model of the spinal reflex that can generate walking motions with the quadruped robot. We implemented a simple reflex circuit, shown in **Figure 6A**, which is part of the neural circuit model proposed by Rybak et al. (2006).

We formulate a model of the reflex circuit. In the following equations, the superscript set of the leg muscles is denoted as $\mathcal{M} = \{\text{HE, HF, KE, KF}\}$, where HE, HF, KE, and KF denote the hip extensors, hip flexors, knee-ankle extensors, and knee-ankle flexors, respectively. For the state of a muscle, $i \in \mathcal{M}$, at time t , we denote the muscle activation as $A^i(t)$, the muscle force scaled by $F_{\max}$ as $F^i(t)$, and the excitation of the interneuron as $S^i(t)$.

The implementation model of the reflex circuit is shown in **Figure 6B**. The behavior of a motor neuron that determines muscle activity $A^i(t)$ is expressed by Geyer et al. (2003) as

$$\tau_{mn} \frac{dA^i(t)}{dt} + A^i(t) = S^i(t), \quad (8)$$

where τ_{mn} is a time constant of the excitation-contraction coupling. The excitation of the interneuron, $S^i(t)$, is given by

$$\tau_{in} \frac{dS^i(t)}{dt} + S^i(t) = s_0^i + \sum_{j \in \mathcal{M}} G_{Fj}^i F^j(t - \Delta_f) - G_m^i S^{\bar{j}}(t) \quad (9)$$

$$S^i(t) = \begin{cases} 0 & s^i(t) < 0 \\ s^i(t) & 0 \leq s^i(t) \leq 1 \\ 1 & s^i(t) > 1 \end{cases}, \quad (10)$$

where $s^i(t)$ is the internal state of the interneuron. The second term on the right-hand side of Equation (9) expresses the reflex

pathways that feedback muscle force to the interneurons, and the third term expresses the reciprocal inhibition pathways of the interneurons. In Equation (9), superscript $\bar{i} \in \mathcal{M}$ is the antagonist muscle of muscle i , and $\bar{i}$ represents HF, HE, KF, and KE, when i is HE, HF, KE, and KF, respectively. Moreover, s_0^i is the bias of the neural input, τ_{in} is the time constant of the interneurons, G_{Fj}^i is the gain of the muscle force feedback, G_m^i is the gain of the reciprocal inhibition, and Δ_f is the time delay of the signal propagation.

5. WALKING EXPERIMENTS USING THE QUADRUPEL ROBOT WITH REFLEX AND MUSCLE CHARACTERISTICS

To evaluate the proposed reflex circuit based on cat walking behaviors, we conducted walking experiments and reproduced a physiological experiment based on cats on the quadruped robot. In addition, by utilizing a robot with a reprogrammable reflex law in real time, we conducted an experiment to remove the reciprocal excitatory pathway between the extensors (the prolongation function of the stance phase) during walking.

5.1. Experimental Conditions

The parameters for the hip muscles were set as $l_{opt} = \pi/6$ rad, $l_{slack} = \pi/6$ rad, and $F_{\max} = 5$ N·m, and those for the knee-ankle muscles were set as $l_{opt} = 80$ mm, $l_{slack} = 80$ mm, and $F_{\max} = 80$ N. Additionally, we positioned the muscles to satisfy $l_{ce} = 0.9l_{opt}$ for the hip muscles and $l_{ce} = 0.8l_{opt}$ for the knee-ankle muscles when the toe coordinates with respect to the hip joint are $(x, z) = (0 \text{ m}, -0.21 \text{ m})$. Other muscle parameters were obtained from Geyer and Herr (2010).

We applied a virtual spring-damper characteristic to the roll joint of the leg module with a natural angle in the downward direction. The spring constant was set to 100 N·m/rad, and the damping factor was set to 1 N·m/s/rad.

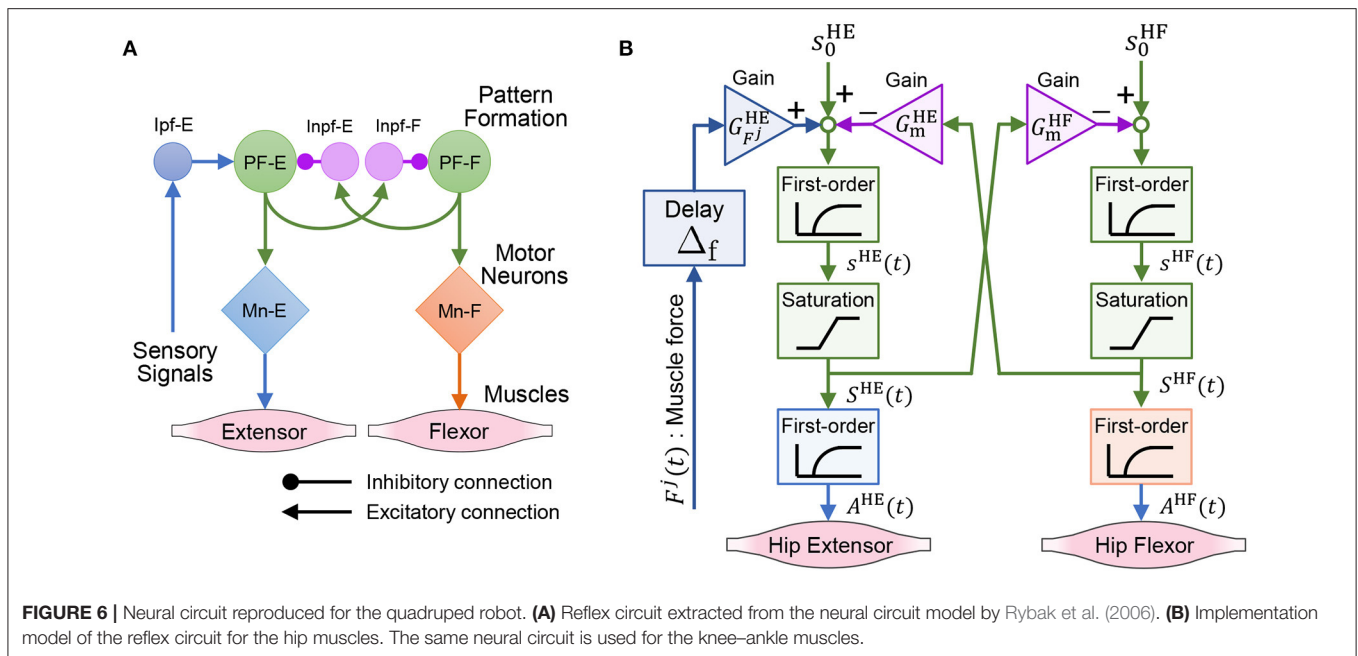


TABLE 1 | Values of the reflex circuit parameters in Equation (9).

i	s_0^i	G_{FHE}^i	G_{FHF}^i	G_{FKE}^i	G_{FKF}^i	G_m^i
HE	0	0	0	1.2	-1	0.15
HF	1	0	0	0	0	10
KE	-0.1	4	0	1.5	0	0
KF	1	0	0	0	0	10

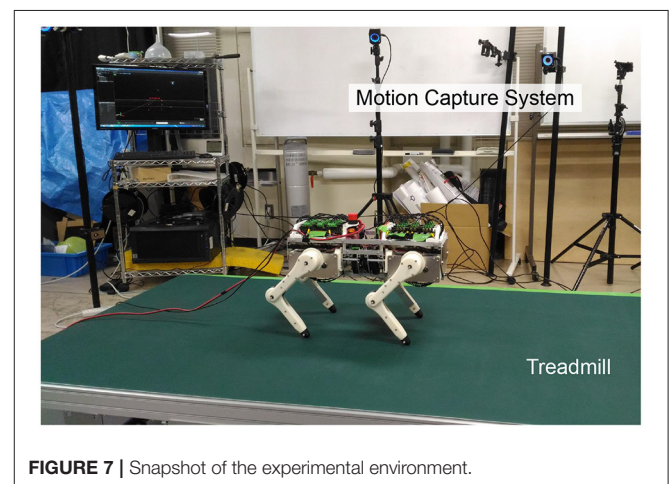
The parameters of the reflex circuit in Equation (9) are presented in **Table 1**. In **Table 1**, G_{FKE}^{HE} , G_{FKF}^{HE} , G_{FHE}^{KE} , and G_{FKE}^{KE} represent the gains for the excitatory feedback from the knee-ankle extensor to the hip extensor, the inhibitory feedback from the knee-ankle flexor to the hip extensor, the excitatory feedback from the hip extensor to the knee-ankle extensor, and the self-excitatory feedback of the knee-ankle extensor, respectively. The parameters of the reflex circuit were adjusted to generate a walking motion. The delay time of the muscle information, Δ_f , was set to 15 ms, and the time constants of the motor neurons, τ_{mn} , and interneurons, τ_{in} , were set to 10 and 5 ms, respectively.

Figure 7 depicts the experimental environment. The quadruped robot walked on a treadmill, and a motion capture system measured its movements.

5.2. Walking Experiment on a Treadmill

First, we conducted a walking experiment using the proposed reflex circuit¹. The periodic motion of the legs did not appear in the air because this robot, which has a reflex circuit, generates

¹For the video of walking experiments, please refer to the following link: <https://youtu.be/kxsAbZCh5KY>.



motion via its interaction with the environment. At the beginning of the walking experiment, we held the robot with each leg at rest and placed it on a treadmill to activate the reflex circuit.

The quadruped robot generated a steady gait, even though it did not contain a central rhythm generator or pattern generator. **Figure 8** presents the gait diagram of the robot. RF, LF, RH, and LH in **Figure 8** represent the right-fore leg, left-fore leg, right-hind leg, and left-hind leg, respectively, and the colored regions indicate ground contact. The result reveals that the ground contact timing of each leg is gradually adjusted with time. After 4 s, the timing of the stance phases between RF–RH and LF–LH were the same, and each of them was in antiphase; thus, a pace gait emerged.

Figure 9 depicts the toe position of the RH leg with respect to the hip joint (in the x-axis) and the ground (in the z-axis)

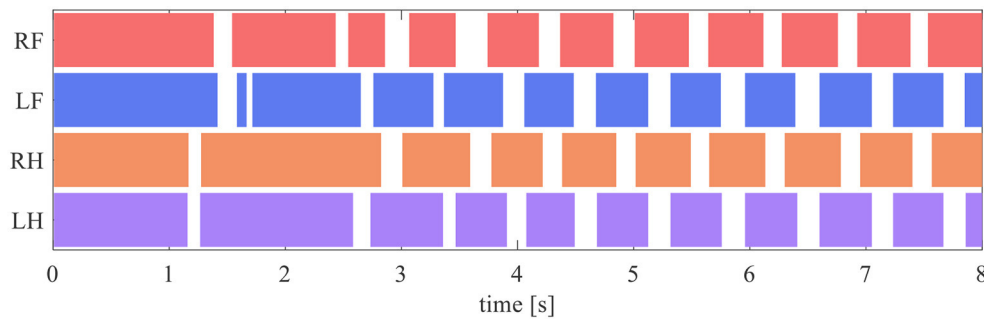


FIGURE 8 | Gait diagram. RF, LF, RH, and LH represent the right-fore leg, left-fore leg, right-hind leg, and left-hind leg, respectively, and the colored regions indicate ground contact.

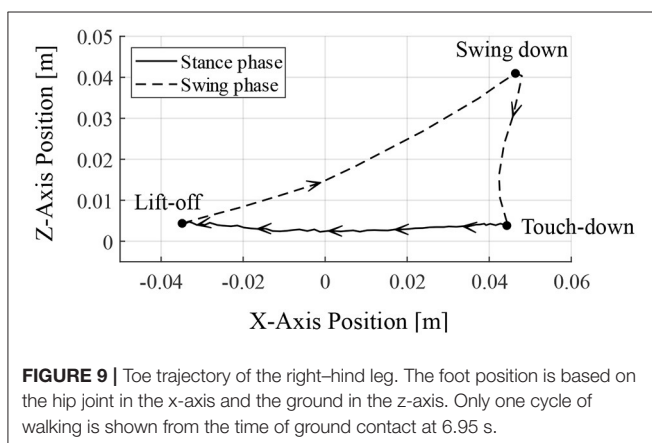


FIGURE 9 | Toe trajectory of the right-hind leg. The foot position is based on the hip joint in the x-axis and the ground in the z-axis. Only one cycle of walking is shown from the time of ground contact at 6.95 s.

for one cycle of walking from 6.95 s, when the leg contacted the ground. The arrows in **Figure 9** indicate the direction of the toe movement. The result indicates that the proposed reflex circuit produces a walking trajectory autonomously, without a pre-designed trajectory.

Moreover, we investigated the mechanism of the motion generation phenomenon using the proposed reflex circuit. **Figure 10** presents the values of each term on the right-hand side of Equation (9) for the hip and knee-ankle extensors, displaying the neural input from each feedback pathway and the total neural input to the interneurons². In **Figure 10**, before the touch-down, the hip extensor is inactive, the knee-ankle extensor is activated, and the leg is located down the front. After the touch-down, tension is generated in the hip and knee-ankle extensors, and the terms of muscle force feedback, F^{HE} and F^{KE} , became larger, resulting in the activation of both hip and knee-ankle extensors. At the time of the stance-to-swing transition, the terms of F^{HE} and F^{KE} become smaller, owing to the unloading of the weight on the leg; the hip and knee-ankle extensor muscles

become inactive. At that time, the hip and knee-ankle flexors are activated, owing to the reduced inhibitory effect from the extensor interneurons, which produces a swing motion. At the timing of the leg swinging down, when the leg is moved forward, the term of F^{HE} on the knee-ankle extensor becomes larger. This implies that the hip extensor muscle is fully stretched, and it generates tension in the late swing phase. This activates the knee-ankle extensor muscle, which results in the swinging down of the leg. Subsequently, the swing-to-stance transition occurs at the timing of touch-down, and the walking motion is generated by repeating these sequences.

5.3. Walking Experiment With Different Initial States

In order to investigate the convergence property of the gait emerging from the reflex circuit, we conduct walking experiments from different initial conditions. When using the reflex parameters in **Table 1**, all the legs remain forward and stationary in the air. Therefore, to prepare the different initial conditions, we set the input bias s_0^{HE} of the hip extensors to different values until just before the start of the walking experiment. The different bias values for s_0^{HE} force the hip extensors to be activated or deactivated, as a result, we prepare two initial positions, one with the leg forward ($s_0^{\text{HE}} = -1$) and one with the leg backward ($s_0^{\text{HE}} = 1$). By combining the two initial positions of each leg, we prepared the initial state of **Table 2**.

Note that we fixed the initial state of the right hind leg to $s_0^{\text{HE}} = -1$ to evaluate the stability of the gait by the phase difference between each leg and the right hind leg.

The phase difference of the leg $k \in \{\text{RF, LF, LH}\}$ to the right hind leg, Φ_k , was calculated by the following equation based on Rosendo et al. (2014) using the ground contact time;

$$\Phi_k = 2\pi \frac{T_{k(\text{actual})} - T_{\text{RH}(\text{previous})}}{T_{\text{RH}(\text{next})} - T_{\text{RH}(\text{previous})}}, \quad (11)$$

where $T_{k(\text{actual})}$ is the contact time of each leg k , $T_{\text{RH}(\text{previous})}$ and $T_{\text{RH}(\text{next})}$ is the previous and next contact time of the right hind leg respectively. In Equation (11), since the phase difference between leg k and the right hind leg is calculated in the range

²The neural input of flexor interneurons is not displayed in **Figure 10**; however, the flexor muscle becomes inactive when the extensor is activated for each joint. In contrast, the flexor is activated when the extensor is inactive, owing to the reciprocal inhibition of interneurons.

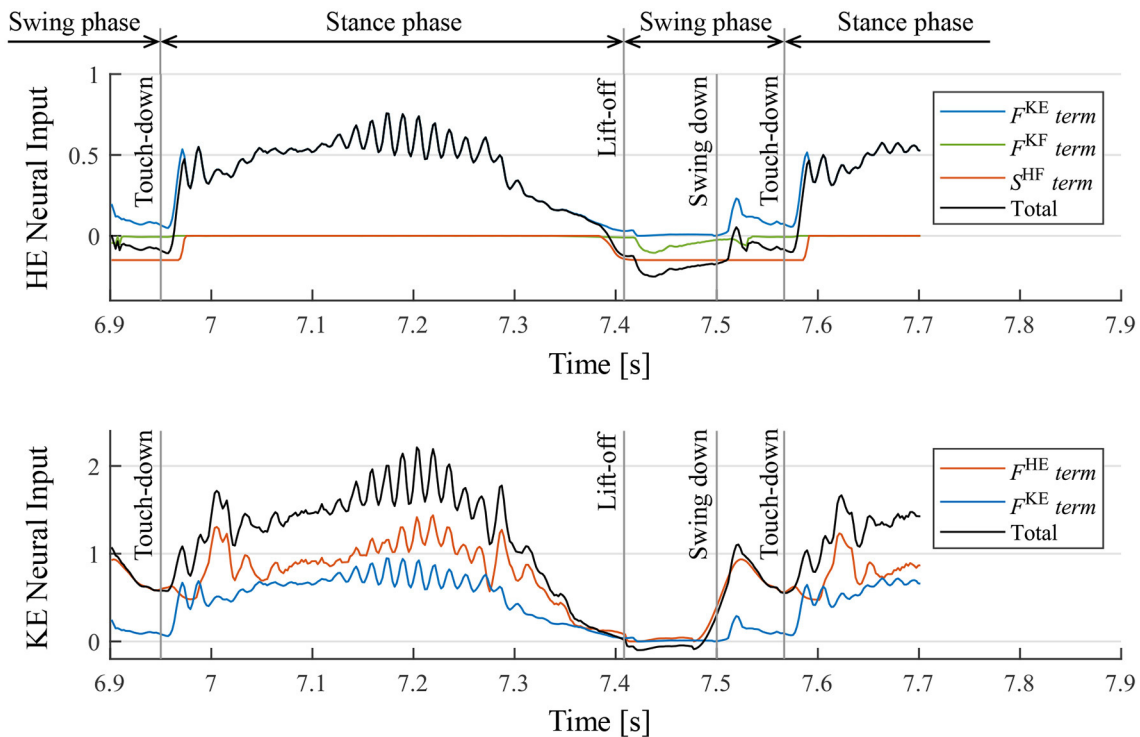


FIGURE 10 | Neural input to interneurons of the hip extensor (HE) and knee-ankle extensor (KE) and the breakdowns. F^{KE} , F^{KF} , and F^{HE} are the magnitude of the muscle force feedback, and S^{HF} is the inhibitory neural input from the interneuron of the antagonist muscle. It should be noted that the sum of the knee-ankle extensor neural inputs includes an offset of -0.1 .

of $[0, 2\pi)$, the value of Φ_k changes drastically around 0 and 2π , e.g., it becomes 0 when exceeding 2π and 2π when falling below 0. Therefore, in order to prevent this drastic change in value, when the phase difference Φ_k converges around the 0 or 2π , we calculate the phase difference within the range of $[-\pi, \pi)$ using the following equation;

$$\Phi_{0k} = \begin{cases} \Phi_k & \Phi_k < \pi \\ \Phi_k - 2\pi & \Phi_k \geq \pi \end{cases} \quad (12)$$

Figure 11 illustrates the experimental results from the initial state in **Table 2**. In the results from all initial conditions, the RF–RH phase difference Φ_{RF} converges near 0 rad, and the RF–RH phase difference Φ_{LF} and LH–RH phase difference Φ_{LH} converges near π rad. The results indicate that the front–hind legs are in the in-phase, and the left–right legs are in anti-phases, thus the robot produced a steady pace gait in all experiments.

5.4. Reproduction Experiment of Prolongation of Stance Phase via Nerve Stimulation

In the experiments by Whelan et al. (1995), electrical stimulation of the afferent nerves from the ankle extensor muscles prolonged the stance phase in walking cats. In this section, we conduct a robotic experiment using a similar condition as that in the cat experiment to evaluate the proposed reflex circuit.

TABLE 2 | List of initial conditions (value of s_0^{HE}) at the beginning of the walking experiment.

Initial state	Values of s_0^{HE}			
	RF	LF	LH	RH
A	−1	−1	−1	−1
B	1	−1	−1	−1
C	−1	1	−1	−1
D	1	1	−1	−1
E	−1	−1	1	−1
F	1	−1	1	−1
G	−1	1	1	−1
H	1	1	1	−1

In the experiment, the muscle force feedback pathway was stimulated after the quadruped robot produced a steady gait under the same conditions as those detailed in section 5.2. To reproduce the stimulation of afferent nerve which is considered to carry muscle force information of the ankle, the value of the afferent force feedback from the knee-ankle extensor was set as $F^{KE} = 0.5$ on the quadruped robot. The timing of the stimulation is 200 ms after the activation of the knee-ankle extensors as with the cat experiment. **Figure 12** depicts the ground contact of each leg during the walking experiment. We stimulated the knee-ankle extensor afferent of the RH leg from

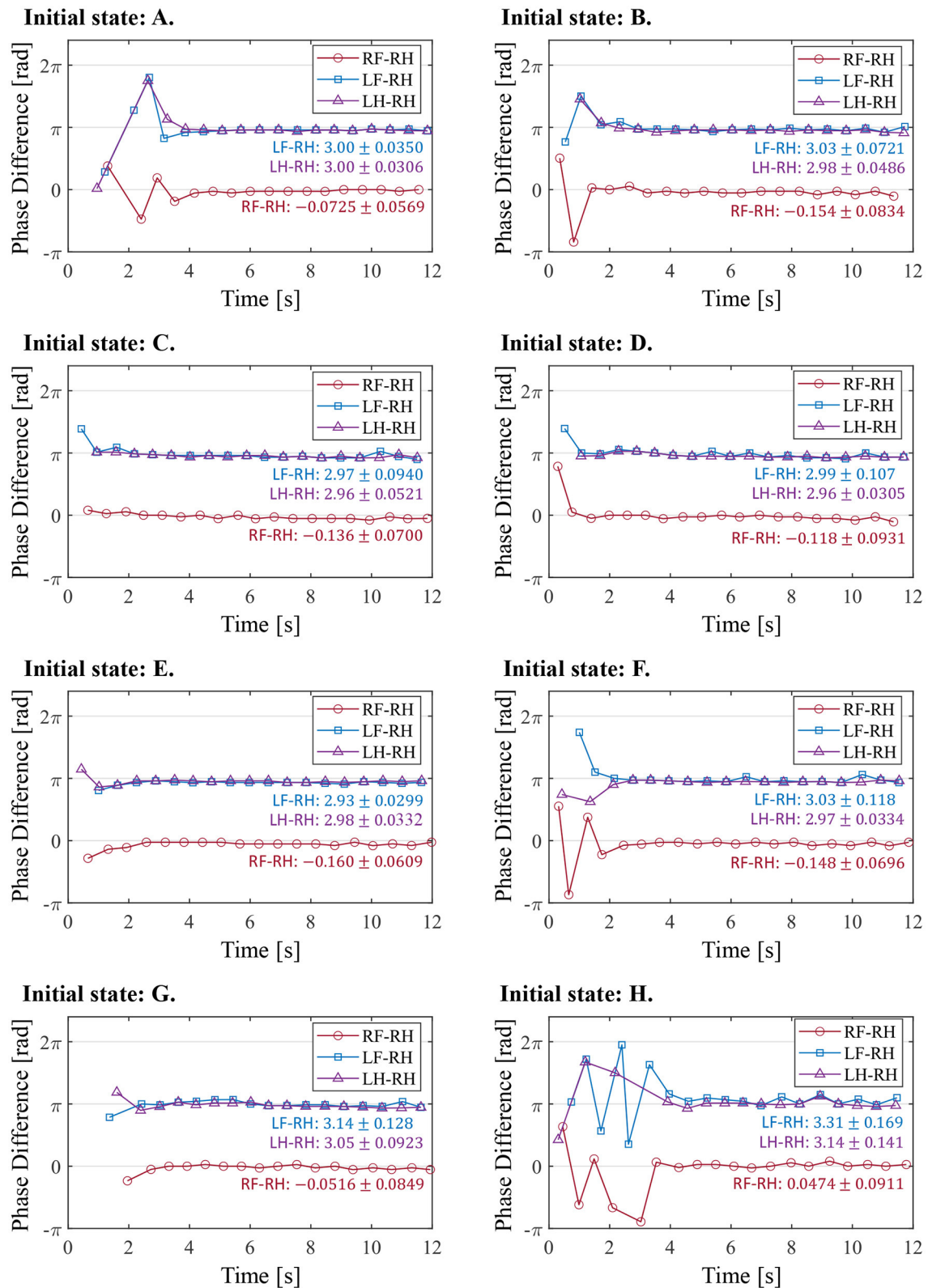


FIGURE 11 | The phase difference between each leg and the right hind leg in the experiment from the different initial conditions. The initial states (A–H) correspond with those in Table 2. The figure also shows the mean and standard deviation of each phase difference after 4 s, when the gait was stabilized.

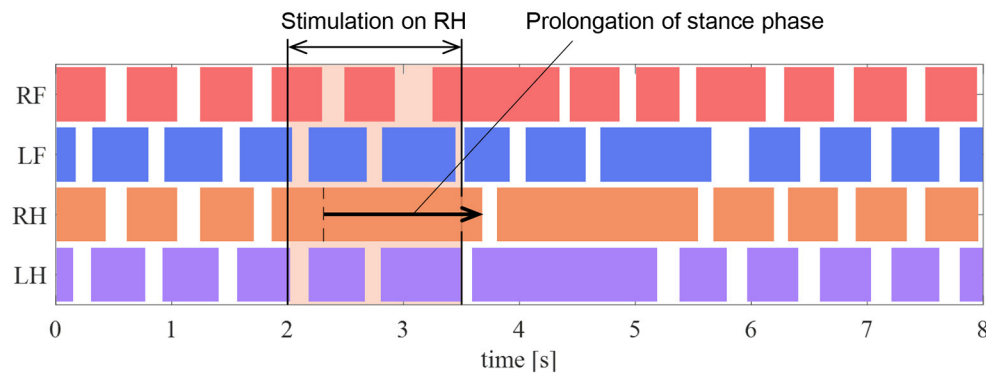


FIGURE 12 | Gait chart in the stimulation experiment of the reflex pathway. The colored regions indicate ground contact.

2 to 3.5 s. The contact time of the RH leg in **Figure 12** during stimulation increased by 1.37 s compared with the normal gait. This indicates that the stance phase was prolonged. Thus, the proposed circuit with the reciprocal excitatory reflex reproduces the prolongation function of the stance phase observed in the walking cat experiments.

5.5. Experiment to Disable the Prolongation Function of the Stance Phase

In section 5.4, we demonstrated that the proposed circuit reproduced the prolongation function of the stance phase observed in the cat walking experiments by Whelan et al. (1995). This section investigates the effects of the proposed reflex pathway that provides the stance phase prolongation function for walking.

We investigated the effects of removing the reciprocal excitatory pathway in all the legs after the quadruped robot produced a steady gait under the same conditions as those in section 5.2. In the experiment, we set $F^{KE} = 0$ to disable the afferent feedbacks from the knee–ankle extensor to the hip and knee–ankle extensors when the angle of the hip joint was greater than 1.68 rad, thereby forcing the stance-to-swing transition. This corresponds to the temporary disconnection of the afferent nerve from the ankle extensor muscle in walking cats.

Figure 13A presents the ground contact for each leg during the walking experiment, and **Figure 13B** depicts the phase difference of each leg relative to the right hind leg. As shown in **Figure 13**, when the afferent feedback from the knee–ankle extensors was disabled after 2 s, the resulting gait was unsteady. This result indicates that the reciprocal excitatory reflex with a prolongation function of the stance phase stabilizes the gait pattern.

6. DISCUSSION

6.1. Gait Emergence Mechanism With the Proposed Reflex Circuit

To reveal the reflex mechanism in animal walking, we proposed the simple reflex circuit based on walking cat experiments and evaluated it using the quadruped robot. In the walking

experiment, the robot does not have CPGs or neural connections between its legs; however, the proposed reflex circuit exhibited rhythm generation and gait pattern adjustment, as shown in **Figure 8**. In this subsection, we discuss the mechanism of rhythm and gait emergence.

In the proposed reflex circuit, the rhythm generation function is considered a result of the self-excitatory force feedback of the knee–ankle extensor and the reciprocal inhibition of knee–ankle interneurons. These circuits activate the knee–ankle extensor to kick the ground when the reaction force is applied to the leg. Additionally, they activate the knee–ankle flexor to lift the leg when the leg is unloaded.

There are two possible reasons for the gait pattern adjustment. The first is the force–velocity characteristics of the muscle. Previous research by Masuda et al. (2017) has demonstrated that a quadruped robot without any closed loop controllers can lead to the emergence of some gaits depending on the applied voltage. This gait emergence phenomenon was caused by the characteristics of the DC motors that adjust the leg phases by slowing down the rotational speed when subject to the ground reaction force. The Hill-type muscle model used in this study also exhibits the force–velocity characteristics, which causes the contraction speed to slow down when a reaction force is applied. This is shown in **Figure 3B** and is similar to the DC motor's characteristics. Therefore, the contraction speed of the hip extensor muscles was adjusted by the muscle property during the support phase, in response to the ground reaction force, and it may have caused the gait emergence.

The second reason for the gait pattern adjustment is the prolongation function of the stance phase, owing to the muscle force feedback. Support legs continue to prolong the stance phase when the other legs are in the swing phase, owing to load concentration on the support legs. They shift to the swing phase immediately after the load is distributed when the other legs come into contact with the ground, thereby controlling the phase difference among legs. The studies (Ekeberg and Pearson, 2005; Maufroy et al., 2010; Rosendo et al., 2014; Habu et al., 2018) focusing the prolongation function also showed the similar phenomenon of gait stabilization.

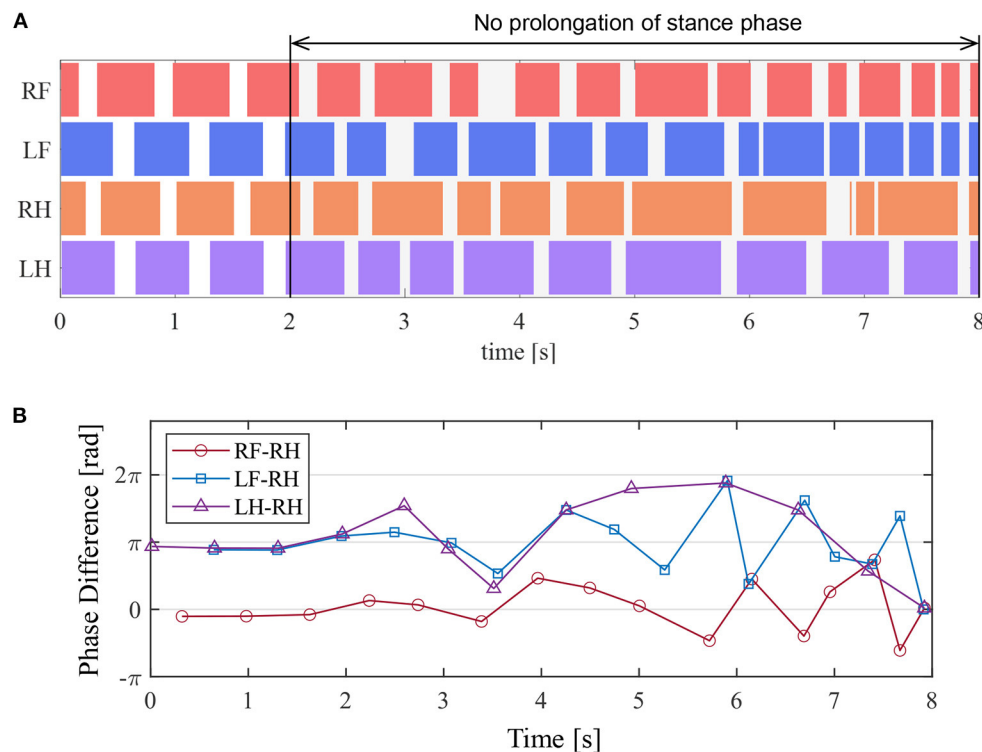


FIGURE 13 | Experimental result to disable the prolongation function of the stance phase. **(A)** Gait chart. The colored regions indicate ground contact. **(B)** The phase difference between each leg and the right hind leg.

6.2. Major Reflex Pathways Contributing to the Walking Motion Generation and Reproduction of Cat Behavior

This study presented a simple reflex circuit that generated leg trajectories and a steady gait and also reproduced the behavior of cats. This reflex circuit consists of reciprocal excitatory reflex between hip and knee-ankle extensors, self-excitatory reflex of knee-ankle extensors, and inhibitory reflex from knee-ankle flexors to hip extensors. In this section, we discuss that the reciprocal excitatory reflex between extensor muscles are particularly important in the generation of walking motions.

First, there are two major motor functions provided by the reciprocal excitatory reflex between extensors. The first is the knee extension associated with hip flexion at the end of the swing phase. When the hip extensor is fully stretched by the leg inertia at the end of the swing phase, the reflex from the hip extensor to the knee-ankle extensor is activated. As a result, the robot swing down the limb. The second is propulsion associated with leg loading during the stance phase. When an external force is applied to the knee-ankle extensor due to leg load in the early stage of the stance phase, the reflex from the knee-ankle extensor to the hip extensor is activated, resulting in a hip extension. Thanks to the reflex pathways, the hip extensor is activated according to ground reaction force on the knee-ankle extensor, as a result, the hip extensor produces

forward propulsion when ground reaction forces and frictional forces increase.

Next, we explain how the reciprocal excitatory reflex between the extensor muscles affects the reproduction of cat behavior. The experiment by McVea et al. (2005) shows that assisting the flexor muscle movement during the swing phase accelerated the activation timing of the ankle extensor muscles. In the reciprocal excitatory reflex between extensor muscles we proposed, when the leg swing is accelerated by assisting the hip flexion, the activation of the knee-ankle extensors is advanced according to the hip flexion, thus reproducing the same phenomenon as in the walking cat. Moreover in an experiment of walking cats, Whelan et al. (1995) showed that electric stimulation on afferent nerves from ankle extensor muscles prolonged the stance phase. The same phenomenon was observed in the reciprocal excitatory reflex as shown in the section 5.4. Therefore, the reciprocal excitatory reflex between extensor muscles contribute to the generation of leg trajectories and the reproduction of behavior in cats, and may be a promising candidate for the structure of reflex pathways in animals.

6.3. Comparison With Previous Studies

As a closely related study to our result, a phase oscillator model of Maufroy et al. (2010) focusing on the prolongation of the stance phase in cats generated a steady gait in robot experiments.

On the contrary, in order to clarify the structure of the reflex circuit that generates the steady locomotion of cats, we implemented the reflex circuit model instead of a phase oscillator. reciprocal excitation we proposed agree with the previous models already know. In spite of the different implementations, since the result of this study is similar to those of previous studies, the reciprocal excitatory reflex between extensors we proposed has similar functions as the previous model of Maufroy et al. (2010).

In researches without using oscillator models or complex CPG models, a human model of Geyer and Herr (2010), cat model of Ekeberg and Pearson (2005), and cheetah model of Rosendo et al. (2014) produced leg trajectories and steady gait by the interaction between spinal reflexes, body dynamics, and environment. However, in these studies, the designers divided the walking motion into multiple phases (ex. stance, liftoff, swing, and touchdown phase) and designed a separate reflex rule for each phase. Therefore, it is not clear how these many reflex rules are integrated in the animal body, i.e., the overall structure of the reflex circuit that produces a steady gait and leg trajectory.

On the other hand, the major contribution of this study is clarifying the essential structure of the reflex circuit to produce a steady gait, which is the reciprocal excitatory reflex between hip and knee–ankle extensor muscles. This reciprocal excitatory reflex between extensors, which activates the hip extensor as the knee extensor is loaded, is a mechanically reasonable structure to produce forward propulsion when ground reaction force and frictional force increase. To the best of our knowledge, there are no existing examples of such a simple reflex circuit that generates the leg trajectory and steady gait autonomously. The proposed reflex circuit may be the current minimum sufficient structure for reflex circuits that reproduce animal gait.

In the simulation of a walking cat's hind legs by Ekeberg and Pearson (2005), the hip angle and the force of the ankle extensors were considered sensory candidates to initiate the stance-to-swing transition; a walking simulation was performed for these two candidates. As a result, the quadruped fell down in the case of the phase transition using the hip angle, and it walked with a steady gait in the case of the phase transition using the unloading of the ankle extensor. On the other hand, the experiment that disabled the prolongation function of the stance phase using the hip angle in section 5.5 demonstrated that the prolongation function based on the knee–ankle extensor force was more important for a steady gait than the phase transition based on the hip angle. Therefore, the results of this study support the hypothesis of Ekeberg and Pearson (2005) that ankle extensor unloading is the dominant factor in the stance-to-swing transition, instead of the hip angle.

6.4. Study Limitations

In this study, we showed that a reflex circuit with reciprocal excitation between extensor muscles produced leg trajectories and a steady gait, but the only gait observed within the parameters studied by the authors was the pace gait. It is not clear why the quadruped robot produced the pace gait, which is not a typical gait in cats. However, the models of Owaki and Ishiguro (2017) and Habu et al. (2018), which focused on the prolongation of the stance phase, produced multiple gait

patterns such as walking, trotting, and galloping. Therefore, as in the previous studies, our model may also generate other gaits than pace by changing the body parameters, neuronal parameters, or adding reflex pathways. For example, the robot by Owaki et al. (2013) changed its gait from trot to pace by adding a mass to the robot and raising its center of gravity. Since our robot may also have a higher center of gravity than other robots in previous studies, we expect that our robot generates other gaits by changing the body parameters related to the center of gravity. In addition, there are 10 adjustable parameters in the reflex circuit. It is difficult to investigate the influence of all these parameters on the gait, so it is a future task to investigate it.

7. CONCLUSION

In this study, to clarify the structure of the reflex circuit that generates the steady locomotion of cats, we explored the reflex circuit using a quadruped robot platform that emulates the neuromuscular dynamics of animals. This circuit consists of a reciprocal excitatory muscle force feedback between the hip and knee–ankle extensors, a self-excitatory muscle force feedback in the knee–ankle extensors, and an inhibitory muscle force feedback from the knee–ankle flexor to the hip extensor, which is designed based on the results of walking cat experiments.

The major contribution of this study is clarifying the essential structure of the reflex circuit to produce a steady gait, which is the reciprocal excitatory reflex between hip and knee–ankle extensor muscles. In the walking experiments conducted on a quadruped robot with virtual muscles and a reflex circuit, a leg trajectory and gait pattern emerged, even though there were no CPGs or neural connections among the legs. Additionally, the robot reproduced the prolongation function of the stance phase using the stimulation of the ankle extensor nerves, which has been observed in walking cat experiments. Moreover, utilizing a robot with a reprogrammable reflex law in real time, we conducted an experiment to remove the reciprocal excitatory pathway between the extensors (the prolongation function of the stance phase) during walking. The absence of the reciprocal excitatory pathway reduced the gait stability of the robot. The results show that the reciprocal excitatory reflex between extensor muscles contribute to the generation of leg trajectories and the reproduction of behavior in cats. Therefore we believe that it may be a promising candidate for a key structure for generating the animal walking.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

TT developed the robot, conducted the experiments and analysis, and wrote the draft of the manuscript. YM designed the study,

contributed to the experiments and the interpretation of data, and assisted in preparing the manuscript. MI contributed to the interpretation of data and assisted in the preparation of the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

This research was partially supported by JSPS KAKENHI [Grant-in-Aid for Scientific Research (S)] Grant Number JP17H06150,

JSPS KAKENHI (Grant-in-Aid for Challenging Exploratory Research) Grant Number JP19K21974, JSPS KAKENHI (Grant-in-Aid for Young Scientists) Grant Number JP20K14695, and The Kyoto Technoscience Center Research and Development Grant.

ACKNOWLEDGMENTS

We would like to thank Editage (www.editage.com) for English language editing.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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A Comparative Study of Adaptive Interlimb Coordination Mechanisms for Self-Organized Robot Locomotion

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OPEN ACCESS

Edited by:

Claudius Gros,
Goethe University Frankfurt, Germany

Reviewed by:

Bulcsú Sándor,
Babeş-Bolyai University, Romania
Soichiro Fujiki,
Dokkyo Medical University, Japan

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Specialty section:

This article was submitted to
Computational Intelligence in
Robotics,
a section of the journal
Frontiers in Robotics and AI

Received: 07 December 2020

Accepted: 16 March 2021

Published: 12 April 2021

Citation:

Sun T, Xiong X, Dai Z, Owaki D and
Manoonpong P (2021) A Comparative
Study of Adaptive Interlimb
Coordination Mechanisms for
Self-Organized Robot Locomotion.
Front. Robot. AI 8:638684.
doi: 10.3389/frobt.2021.638684

Walking animals demonstrate impressive self-organized locomotion and adaptation to body property changes by skillfully manipulating their complicated and redundant musculoskeletal systems. Adaptive interlimb coordination plays a crucial role in this achievement. It has been identified that interlimb coordination is generated through dynamical interactions between the neural system, musculoskeletal system, and environment. Based on this principle, two classical interlimb coordination mechanisms (continuous phase modulation and phase resetting) have been proposed independently. These mechanisms use decoupled central pattern generators (CPGs) with sensory feedback, such as ground reaction forces (GRFs), to generate robot locomotion autonomously without predefining it (i.e., self-organized locomotion). A comparative study was conducted on the two mechanisms under decoupled CPG-based control implemented on a quadruped robot in simulation. Their characteristics were compared by observing their CPG phase convergence processes at different control parameter values. Additionally, the mechanisms were investigated when the robot faced various unexpected situations, such as noisy feedback, leg motor damage, and carrying a load. The comparative study reveals that the phase modulation and resetting mechanisms demonstrate satisfactory performance when they are subjected to symmetric and asymmetric GRF distributions, respectively. This work also suggests a strategy for the appropriate selection of adaptive interlimb coordination mechanisms under different conditions and for the optimal setting of their control parameter values to enhance their control performance.

Keywords: adaptive interlimb coordination, phase resetting, phase modulation, decoupled CPGs, sensory feedback, self-organized locomotion

1. INTRODUCTION

Walking animals demonstrate impressive self-organized locomotion and adaptation to body property changes by skillfully manipulating their complicated and redundant musculoskeletal systems (Taga et al., 1991; Dickinson et al., 2000; Der and Martius, 2012; Grabowska et al., 2012). Many studies have clarified that adaptive interlimb coordination plays a crucial role in this

achievement (Aoi et al., 2017; Mantziaris et al., 2017). Investigations of various aspects of adaptive interlimb coordination mechanisms have attracted significant attention in various research fields.

To demonstrate these mechanisms, biologists have proposed some neurological principles, such as central pattern generators (CPGs) (Marder and Bucher, 2001), reflex chains (Grillner, 1975), and sensory feedback (Grillner, 2003; Rossignol et al., 2006), through biological experiments. In addition, roboticists have developed many bio-inspired neural control schemes for legged robots to emulate animal-like self-organized locomotion (Kimura et al., 2007; Owaki et al., 2013; Barikhan et al., 2014; Ambe et al., 2018; Fukui et al., 2019; Miguel-Blanco and Manoonpong, 2020). To realize self-organized locomotion and adaptation on artificial legged systems, many adaptive robot control schemes based on distributed abstract CPGs incorporating ground reaction force (GRF) feedback have been proposed (Kimura et al., 2007; Owaki et al., 2013; Barikhan et al., 2014; Ambe et al., 2018; Fukui et al., 2019). Specifically, the GRF feedback is exploited to modulate the phase relationships of the CPGs under two main strategies: (continuous) phase modulation (PM) and (discrete) phase resetting (PR).

PM typically uses continuous GRFs to modulate CPG phases continuously (Kimura et al., 2007; Owaki et al., 2013, 2017; Barikhan et al., 2014; Fukuhara et al., 2018; Miguel-Blanco and Manoonpong, 2020). In contrast, the PR uses discrete GRFs to reset the CPG phases intermittently (Tsujita et al., 2001; Aoi and Tsuchiya, 2007; Nomura et al., 2009; Aoi et al., 2010, 2012; Ambe et al., 2018). While both mechanisms have proved their effectiveness in their own right and have been widely used in various fashions, they have not been systematically analyzed and compared to identify their characteristics in detail. For instance, how the control parameter values of the mechanisms influence the phase convergence process and whether the mechanisms show different performances in different situations. It is necessary to consider in which situations the PM (PR) works better.

From this point of view, a comparative study of the PM and PR for self-organized locomotion was conducted. They were used to modulate four decoupled neural SO (2)-based CPGs¹ (Pasemann et al., 2003) relying on local GRF information. The modulated CPGs, acting as an adaptive neural controller, were implemented on a quadruped robot in simulation, as shown in **Figures 1A,B**. The CPG outputs were utilized to drive the robot joint movements such that the robot could autonomously perform self-organized locomotion, as shown in **Figure 1C**. The study focused on: (1) the parameter characteristics of the PM and PR and (2) their adaptations to unexpected robot situations (e.g., noisy feedback, leg motor damage, and carrying a load). The validation of the study was quantified by three metrics including: phase convergence time, phase deviation, and cost of transport (COT). Consequently, this work provides suggestions on how to choose adaptive interlimb coordination mechanisms properly in different situations and set their control parameter values optimally to enhance their control performance.

The rest of this article is structured as follows. Details of the materials and methods are provided in section 2. The experimental results are presented in section 3. A discussion of the experimental results and the conclusions are provided in section 4.

2. MATERIALS AND METHODS

In this section, the adaptive neural controller for studying the PM and PR is elucidated. It is composed of four identical and decoupled neural SO (2)-based CPGs (Pasemann et al., 2003; Sun et al., 2018) modulated by the PM or PR. Subsequently, a simulation environment with a quadruped robot (called “Lilibot”) is introduced. It is an experimental platform for assessing the PM and PR by implementing the adaptive neural controller on the robot to generate self-organized locomotion. In addition, certain variables and metrics for analyzing and assessing the CPG phase convergence and self-organized locomotion are introduced.

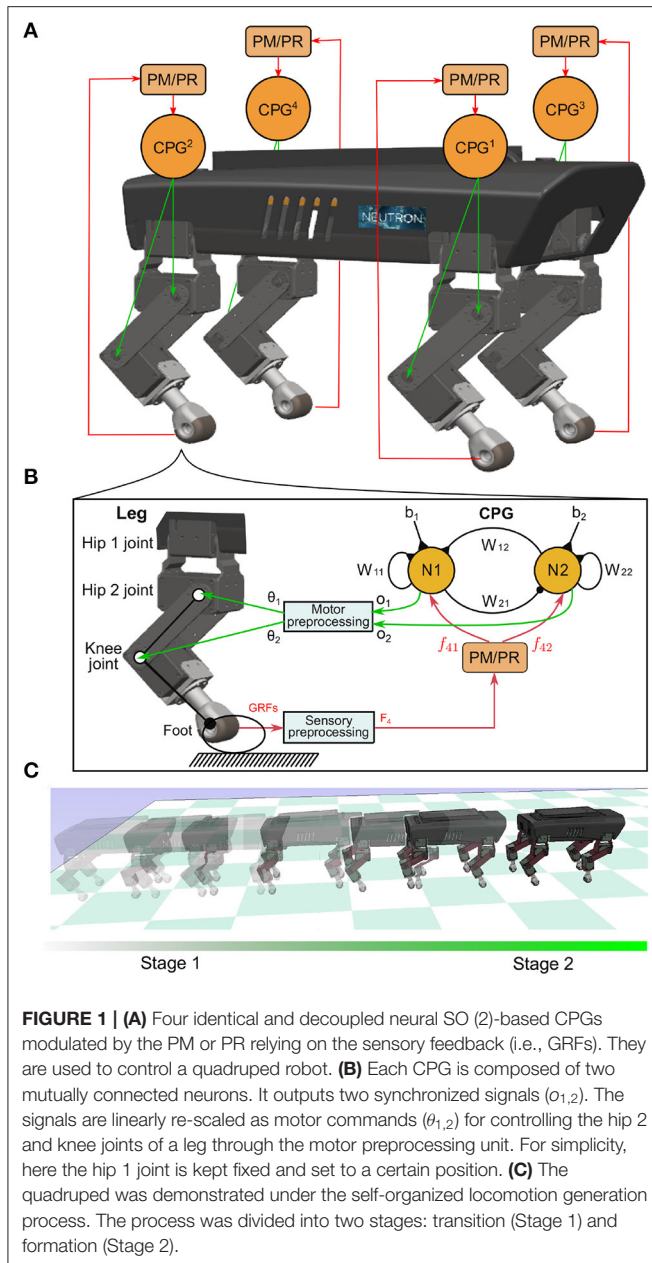
2.1. Adaptive Neural Controller

The adaptive neural controller integrates the four CPGs with either PM or PR. The controller was proposed for easily demonstrating the PM and PR in an integrative manner. The PM and PR have numerous forms that comply with different CPG models and robots (Kimura et al., 2007; Owaki et al., 2013; Barikhan et al., 2014; Sun et al., 2020). To compare the PM and PR conveniently and consistently, four neural SO (2) oscillators are used as four decoupled CPGs. The SO (2)-based CPG has a simple neural network topology with analyzable neural dynamics (Pasemann et al., 2003). Thus, it can easily integrate either the PM or the PR for straightforwardly modulating or resetting the CPG’ phase. Detailed descriptions are provided in the following.

2.1.1. Decoupled Neural SO (2)-Based CPGs

Four decoupled neural SO (2)-based CPGs were used to produce multiple periodic signals for driving the quadruped robot (see **Figure 1**). Each neural SO (2)-based CPG consists of two connected neurons, where their neural activities are later adjusted by the PM or PR. It outputs two periodic signals that are transferred by a motor preprocessing unit to drive the hip 2 and knee joints of a leg. As a result, the leg’s foot can trace a proper ellipse-like trajectory with swing forward and stance backward. The foot movement status detected by the GRF is transferred to the PM or PR through a sensory preprocessing unit. Based on the GRF feedback, the PM or PR generates modulation signals to its corresponding CPG. In the single closed-loop CPG-based control, the outputs of the CPG coordinate the two joint movements of the leg (i.e., intralimb coordination), while the interlimb coordination among legs is realized only by the interactions between the robot body dynamics and the environment (i.e., physical communications) through the PM (Owaki et al., 2013) or PR (Aoi et al., 2012) with GRF feedback of each leg. This is because the four CPGs are decoupled and have no direct neural communication between them. The four CPGs can

¹Note that an SO (2)-based CPG is a special type of 2-neuron network where the weight matrix of the network is an element in the special orthogonal group SO(2).



be described using a matrix in discrete time equations as follows:

$$\mathbf{a}(n+1) = \mathbf{w} \cdot \mathbf{o}(n) + \mathbf{b} + \mathbf{f}(n) \quad (1)$$

$$\mathbf{o} = \tanh(\mathbf{a}), \quad (2)$$

where $\mathbf{a} = (a_{ik})$, $\mathbf{o} = (o_{ik})$, and $\mathbf{b} = (b_{ik}) \in \mathbb{R}^{2 \times 4}$ represent the activations, outputs and biases of the CPG neurons, respectively. Each column of the three matrix variables (i.e., $\mathbf{a}$, $\mathbf{o}$, and $\mathbf{b}$) represents the values of a CPG. Moreover, n indicates the time of the discrete-time equations, where the update frequency is 60 Hz in the following investigations. $\mathbf{w} \in \mathbb{R}^{2 \times 2}$ is the synaptic weights of a CPG (see Equation 4). $\mathbf{f} = (f_{ik}) \in \mathbb{R}^{2 \times 4}$ represents the

modulation term of the PM or PR (see Equations 6–8). f_{ik} is the PM or PR term projecting to the i th neuron of the k th CPG. The projection can adjust the CPG neuron activities online, thereby resulting in the CPG phase adaptation.

The CPG outputs ($\mathbf{o}$) are used to drive the joint movements through a linear transformation of the motor preprocessing unit (see Figure 1). It is given by the following equation:

$$\boldsymbol{\theta} = \boldsymbol{\alpha} \mathbf{o} + \boldsymbol{\beta}, \quad (3)$$

where $\boldsymbol{\theta}$ and $\boldsymbol{\beta} \in \mathbb{R}^{2 \times 4}$ represent the desired joint angles and their biases, respectively.

Based on previous work (Manoonpong et al., 2013), each SO (2)-based CPG can generate periodic coordinated signals for intralimb and interlimb coordination by setting its weights and biases as follows:

$$\mathbf{w} = \begin{pmatrix} 1.4 & 2.6 \\ -2.6 & 1.4 \end{pmatrix}, \quad (4)$$

$$\mathbf{b} = \begin{pmatrix} 0.01 & 0.01 & 0.01 & 0.01 \\ 0.01 & 0.01 & 0.01 & 0.01 \end{pmatrix}. \quad (5)$$

The CPGs' parameter setup is used for the following investigations.

2.1.2. Phase Modulation (PM) Mechanism

The fundamental principle of the PM is to modulate the CPG phase continuously by relying on the continuous GRF signal. Based on the model of the neural SO (2)-based CPG with sensory feedback introduced by (Barikhan et al., 2014), a modified version of the sensory feedback is proposed. It is formulated as the PM modulation term in the following equations:

$$f_{ik}(n) = \begin{cases} -\gamma \frac{F_k(n)}{mg} \cos(o_{ik}(n)), & i = 1, \\ -\gamma \frac{F_k(n)}{mg} \sin(o_{ik}(n)), & i = 2, \end{cases} \quad (6)$$

where o_{ik} is the output of the i th neuron in the k th CPG, γ is a positive constant that represents the sensory feedback gain, and F_k is the GRF value whose range depends on the specific robot weight. Here, mg represents the weight of the robot. It is 2.5 kg for the robot used in the investigations. The robot weight is introduced to normalize the sensory feedback gain for generalization. In addition, γ is a dimensionless parameter that is independent of the robot.

From Equation (6), one can find that the greater the $F_k(n)$ a leg perceives, the higher the inhibition [if $f_{ik}(n) < 0$] or excitation [if $f_{ik}(n) > 0$] the corresponding leg's PM makes. More specifically, when the robot is on the ground, its four legs support and promote the robot body together. Thus, there is an approximately equal distribution among the GRFs of the four legs during locomotion. This means that, when the GRF of a stance leg decreases, the GRFs of other stance legs must increase. Therefore, the four CPGs have different modulation strengths. This results in phase differences among the four CPGs. Once the CPG phase differences converge to a proper status, adaptive interlimb coordination (i.e., self-organized locomotion) emerges (Owaki et al., 2013; Sun et al., 2018).

2.1.3. Phase Resetting (PR) Mechanism

The fundamental principle of the PR is to reset the CPG phase intermittently by relying on the discrete GRF signal. For neural SO (2)-based CPG, the PR functionality is realized by resetting the CPG neuron activities to specific values when the GRF value increases over a threshold. Thus, the PR modulation term can be described as follows:

$$f_{ik}(n) = \begin{cases} (1 - (w_{11}o_{1k}(n) + w_{12}o_{2k}(n) + b_{1k}))\kappa, & i = 1, \\ -(w_{21}o_{1k}(n) + w_{22}o_{2k}(n) + b_{2k})\kappa, & i = 2, \end{cases} \quad (7)$$

$$\kappa = \begin{cases} 1.0, & F_k(n) > F_t \frac{mg}{4}, \quad F_k(n-1) \leq F_t \frac{mg}{4}, \\ 0.0, & \text{otherwise} \end{cases} \quad (8)$$

where o_{ik} is the activity/output of the i th neuron in the k th CPG, mg is the weight of the robot, and F_t is a positive value representing GRF threshold factor that influences the timing of the PR. Here, $\frac{mg}{4}$ is regarded as a reference GRF value given that the four legs share the support of the robot weight. Once the GRF $[F_k(n)]$ of a leg becomes more than $\frac{mg}{4}$, the leg is indicated to be in the stance phase, thereby triggering the PR. Thus, to realize proper phase resetting, F_t value can be easily set in a small range ~ 1.0 . Moreover, F_t is a dimensionless parameter that is independent of the robot.

More specifically, the condition in Equation (8) indicates that once the GRF value of a leg increases over $F_t \frac{mg}{4}$, then κ of the leg (e.g., the k th leg) is equal to 1.0. As a result,

$$f_{ik}(n) = \begin{cases} 1 - (w_{11}o_{1k}(n) + w_{12}o_{2k}(n) + 0.01), & i = 1, \\ -(w_{21}o_{1k}(n) + w_{22}o_{2k}(n) + 0.01), & i = 2, \end{cases} \quad (9)$$

Replacing them into Equations (1) and (2), the k th neural SO(2)-based CPG outputs at the next step are approximately reset to:

$$\begin{aligned} o_{ik}(n+1) &= \tanh(a_{ik}(n+1)) \\ &= \begin{cases} \tanh(w_{11}o_{1k}(n) + w_{12}o_{2k}(n) + 0.01 + 1 - (w_{11}o_{1k}(n) + w_{12}o_{2k}(n) + 0.01)), & i = 1, \\ \tanh(w_{21}o_{1k}(n) + w_{22}o_{2k}(n) + 0.01 - (w_{21}o_{1k}(n) + w_{22}o_{2k}(n) + 0.01)), & i = 2, \end{cases} \\ &= \begin{cases} \tanh(1), & i = 1, \\ \tanh(0), & i = 2, \end{cases} \\ &\approx \begin{cases} 0.76, & i = 1, \\ 0, & i = 2, \end{cases} \end{aligned} \quad (10)$$

The CPG outputs are reset to the approximation from its limit cycle when a phase-resetting event occurs, followed by the CPG outputs returning to its limit cycle (see **Figure 3A**). Owing to the differences among the four GRFs, the phases of the CPGs are reset at different moments, thereby having phase differences. For example, when the robot wriggles with four legs supporting it on the ground, the GRFs of the four legs are close to $F_t \frac{mg}{4}$. In this case, the robot torso twisting back and forth leads to the GRFs with different change tendencies (e.g., front leg GRFs increase while hind leg GRFs decrease), which results in the GRFs of the legs meeting the PR condition at different moments. When the CPG phase differences converge to a proper status, adaptive interlimb coordination (i.e., self-organized locomotion) emerges (Aoi et al., 2010, 2012). More detailed information on the locomotion generation process can be found in the following experiments and corresponding videos.

2.2. Experimental Platform

The experimental platform for studying the PM and PR is a quadruped robot in the simulation. The simulated robot is based on a small-size quadruped robot with multiple sensory feedback (Lilibot) which was developed in our previous works (Sun et al., 2020). The simulation environment was built using CoppeliaSim² with physical engine Vortex³. The framework for connecting the robot with the adaptive neural controller (including the PM or PR) is based on the robot operation system (ROS)⁴ (see **Figure 2**). The robot and controller are regarded as two ROS nodes and communicate with each other through two ROS topics. A motor topic is used to transfer commands from the controller node to the robot node, while a sensory topic is used to acquire GRF signals from the robot node and then send them to the controller node. The update frequency of the two ROS nodes is 60 Hz, the CoppeliaSim calculation time step is 50 ms (20 Hz) during which main script of the simulated models is executed once. The simulation runs on a laptop (Thinkpad E470C) setup with an Intel Core i5-7200U and 8GB DDR4. The detailed information and source of the robotic platform can be found at <https://gitlab.com/neutron-nuaa/lilibot>. The launch sequence of the modules in the simulation is the CoppeliaSim initially and the two ROS nodes after 60 steps (3 s in CoppeliaSim).

2.3. Measurement of CPG Phase Convergence and Self-Organized Locomotion

In this study, we focused on the autonomous phase regulation of decoupled CPGs modulated by the PM and PR, resulting in quadruped self-organized locomotion. Here, we consider a neural SO(2)-based CPG with specific dynamical properties in which the

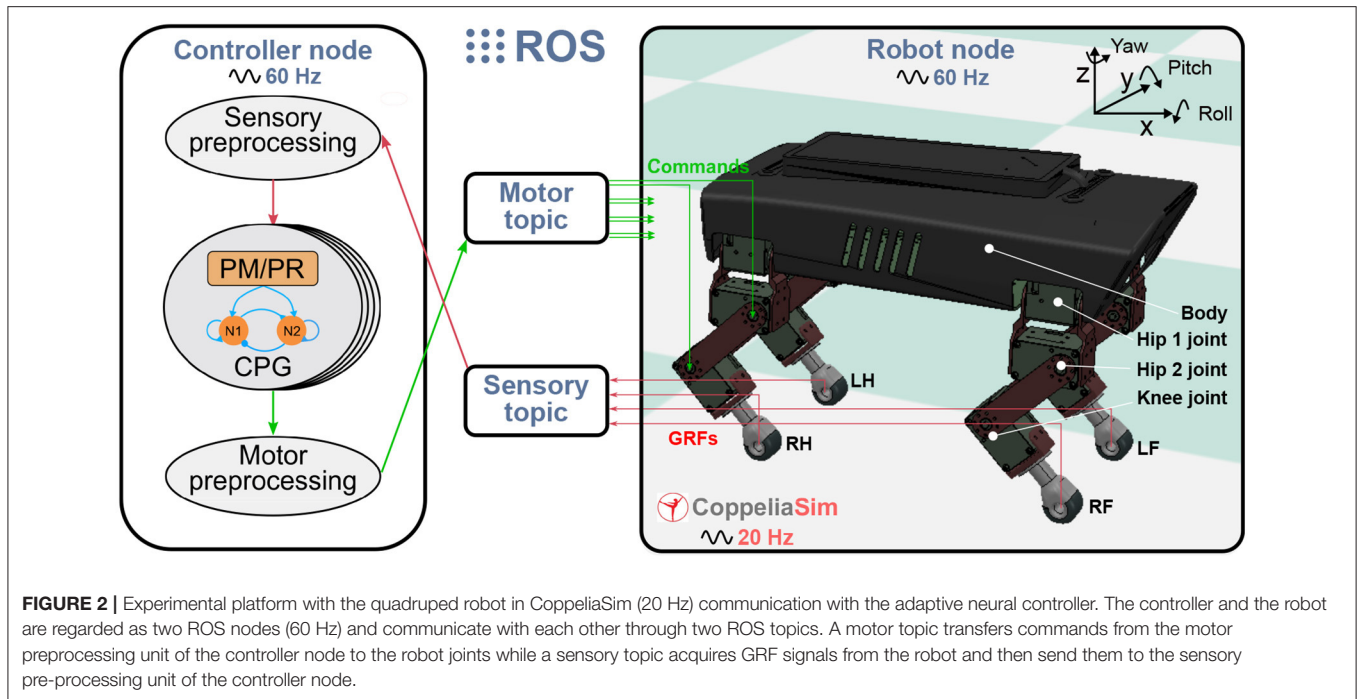
CPG with a certain frequency exhibits a limit cycle similar to a unit circle in phase space, as shown in **Figure 3A**. In other words, the PM and PR are used to modulate the CPG phase rather than adapting to other properties (for example, amplitudes, offsets, and frequency). As a result, under the CPG parameter setup in Equations (4) and (5), the phase relationship of the decoupled CPGs converges to a certain state where the quadruped robot can form a specific gait (i.e., trot-like gait).

To clearly analyze and assess the characteristics of the PM and PR for the CPG phase regulation, several variables and metrics (see **Table 1**) were introduced to measure their CPG phase convergence process and resulting self-organized locomotion

²<https://www.coppeliarobotics.com/>

³<https://www.cm-labs.com/vortex-studio/>

⁴<https://www.ros.org/>



(see **Figure 3**). The metrics were used to assess the PM and PR in the experiments. Because the variables are the basis of the metric definitions, the variables are here introduced in the following subsection first. They include the phase difference and its mean and standard deviation.

2.3.1. Variables

A phase difference between two CPGs can identify the phase relationship of the two CPGs as well as the movement relationship between the two limbs/legs controlled by the two CPGs. The outputs of a CPG (e.g., o_{k1} and o_{k2}) at a moment can be illustrated as a point (P^k) in a phase diagram (see **Figure 3A**). The two axes of the phase diagram represent the CPG outputs $o_{1,2}$. When the CPGs produce periodic signals (see **Figure 3B**), their outputs follow their limit cycle to move. The limit cycle of a neural SO (2)-based CPG is similar to a circle whose origin is at the center of the coordinate. In the adaptive neural controller, the four neural SO (2)-based CPGs are identical with the same parameter values, so their limit cycles are the same in the phase diagram. Therefore, a phase difference (e.g., ϕ_{kl}) between two CPGs (i.e., the k th and l th CPGs) can be represented by the angle between the two points (i.e., P^k and P^l). Its mathematical description is as follows:

$$\phi_{kl} = \arccos\left(\frac{P_k \cdot P_l}{\|P_k\| \|P_l\|}\right), \quad (11)$$

where P_k and P_l represent the vectors of the k th and l th CPGs in the phase diagram, respectively (**Figure 3A**). $\phi_{kl} \in [0, \pi]$ represents the magnitude of their (relative) phase difference. Based on this definition (ϕ_{kl}), when the adaptive neural controller is implemented on the quadruped robot to generate self-organized locomotion (**Figure 3D**), one can find the phase

differences (i.e., ϕ_{12} and ϕ_{13}) change from in phase to stable phase relationships (**Figure 3B**). As a result, the phase differences among the CPGs can display their phase relationship online (see **Figure 3C**). A video to show the phase difference convergences of the four decoupled CPGs modulated by the PM and PR can be seen in <http://www.manoonpong.com/AICM/video1.mp4>.

The phase differences undulate during the phase convergence process. To monitor the undulation, the mean and standard deviation of the phase differences are introduced. Because $\phi_{kl} \in [0, \pi]$ changes in a linear manner, it can be regarded as linear data rather than circular data when calculating its statistical variables. Thus, the mean and standard deviation are described as follows:

$$\phi_{kl}^{mean}(n) = \begin{cases} \frac{1}{N} \sum_{i=n-N}^n \phi_{kl}(i), & n > N \\ \frac{1}{n} \sum_{i=0}^n \phi_{kl}(i), & n \leq N \end{cases}, \quad (12)$$

$$\phi_{kl}^{std}(n) = \begin{cases} \frac{1}{N} \sqrt{\sum_{i=n-N}^n (\phi_{kl}(i) - \phi_{kl}^{mean}(n))^2}, & n > N \\ \frac{1}{n} \sqrt{\sum_{i=1}^n (\phi_{kl}(i) - \phi_{kl}^{mean}(n))^2}, & n \leq N \end{cases}, \quad (13)$$

$$\phi^{std}(n) = \sum_{l=2}^4 \phi_{1l}^{std}(n), \quad (14)$$

where $\phi_{kl}^{mean}(n)$ and $\phi_{kl}^{std}(n)$ are the mean and standard deviation of the phase difference ϕ_{kl} at current step n , respectively. N is

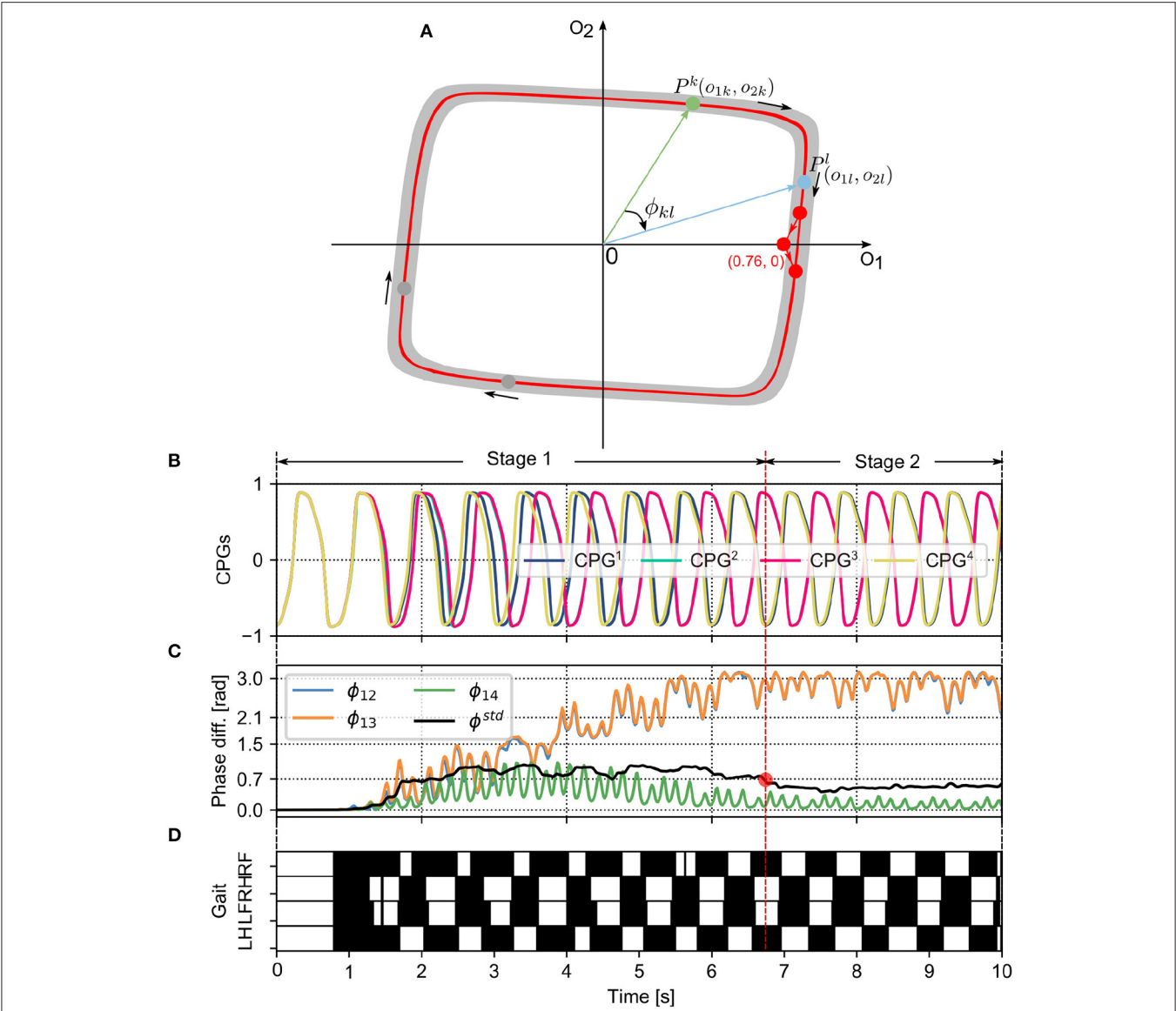


FIGURE 3 | (A) The limit cycle of the SO(2)-based CPGs that was used to investigate the autonomous phase regulation. The coordinates (0.76, 0) represent the phase-reset point realized by the PR. A phase difference (e.g., ϕ_{kl}) between two CPGs (i.e., the k th and l th CPGs) is defined as the angle between the two points (i.e., P^k and P^l). (B) The first neuron outputs (o_{1k} with $k=1, 2, 3$, and 4) of the four CPGs that are used to control the four legs, respectively (see Figure 1). (C) The CPG phase differences (i.e., ϕ_{12} , ϕ_{13} , ϕ_{14}) and their standard deviation (ϕ^{std}). ϕ^{std} can indirectly reflect the phase deviation. Empirically, once the value of ϕ^{std} reduces to < 0.7 (see the red point), the CPG outputs and phase differences become more stable. The CPG phase convergence process can be divided into two stages (Stage 1 and Stage 2) determined by the point. (D) In the corresponding gait diagram, the black areas indicate stance phases while the white areas indicate swing phases. Note that, ϕ_{12} , ϕ_{13} , and ϕ_{14} are the phase differences of the CPG^2 , CPG^3 , and CPG^4 with respect to the CPG^1 , respectively. RF, RH, LF, and LH are the right front, right hind, left front, and left hind legs, respectively.

TABLE 1 | List of the variables and defined metrics.

Variables	Symbols	Metrics	Symbols
Phase difference	$\phi_{kl}(n)$	Phase convergence time	T
Mean of phase difference	$\phi_{kl}^{mean}(n)$	phase deviation	ϕ^s
Standard deviation of phase difference	$\phi_{kl}^{std}(n)$	Cost of transport	COT
Sum of standard deviation of phase differences	$\phi^{std}(n)$		

the number of steps in a period from the current to a previous step. It is empirically set to 50 in the following experiments. Here, $\phi^{std}(n)$ is the sum of $\phi_{12}^{std}(n)$, $\phi_{13}^{std}(n)$, and $\phi_{14}^{std}(n)$ at the n th step. This can reflect the instantaneous/current deviation of the phase differences in overall. The less $\phi^{std}(n)$, the higher the phase deviation at the n th step.

To identify whether the CPG phase relationships are so stable that self-organized locomotion is recognized to be formed, according to the instantaneous indication of the phase deviation [$\phi^{std}(n)$], a constant ϕ_t^{std} is introduced as a threshold for distinguishing the phase convergence process. It is empirically set to 0.7 in the following experiments.

2.3.2. Metrics

Based on the proposed variables (see **Table 1**), the first metric is phase convergence time, which indicates how long the CPG phase relationship takes to converge and the robot takes to generate self-organized locomotion under the restrict conditions. The state transition of the decoupled CPGs with the PM/PR from the initial fixpoint (0, 0, 0) to the desired fixpoint (π , π , 0) is accompanied by a process in which ϕ^{std} first increases and then decreases. Based on many experiments, we realize that if ϕ^{std} first reduces to less than a threshold ($\phi_t^{std} = 0.75$) from a high value, the dynamical system will converge, and the quadruped robot can form a trot-like gait. Thus, the phase convergence time (T) is described as:

$$T = \frac{\min(n_i)}{H}, \quad \phi^{std}(n_i - 1) \geq \phi_t^{std}, \phi^{std}(n_i) < \phi_t^{std}, \quad (15)$$

where ϕ_t^{std} is the threshold. n_i is the step when ϕ^{std} is reduced to less than ϕ_t^{std} in a trial, whereas $\min(n_i)$ is the minimal value of n_i and represents the step when ϕ^{std} first reduces to less than the threshold. H is the update frequency of the control node (i.e., 60 Hz).

The second metric is *phase deviation*, which estimates the deviation of the phase differences. It can reflect the extent to which the converged CPG phase relationships are sustained during a self-organized locomotion period. It is defined using the reciprocal of the mean of $\phi^{std}(n)$ as follows:

$$\phi^s = \frac{1}{\text{mean}(\phi^{std}(n))}, \quad \text{mean}(\phi^{std}(n)) \neq 0, \quad (16)$$

where $\text{mean}(\phi^{std}(n))$ represents the mean of ϕ^{std} in the period (e.g., with M steps). The greater ϕ^s , the higher the phase deviation of the formed self-organized locomotion over the period.

The last metric is the *cost of transport (COT)*. It is used to measure the energy efficiency of the formed self-organized locomotion over a period. The COT is described as follows:

$$\left\{ \begin{array}{l} COT = \frac{E}{mgd}, \\ E = \sum_{j=1}^{12} \sum_{n=1}^M \frac{I_j(n)V_j(n)}{H}, \end{array} \right. \quad (17)$$

where E is the energy consumption when the robot with weight mg travels with a distance d . The energy is calculated using the robot joint motor current $I_j(n)$ and voltage $V_j(n)$. M indicates the number of steps over the period. H is the update frequency of the experimental system.

3. EXPERIMENTAL RESULTS

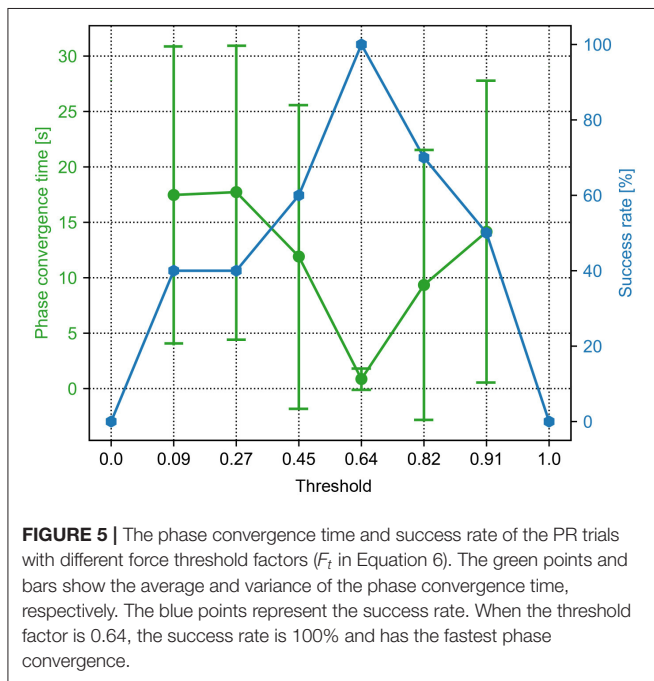
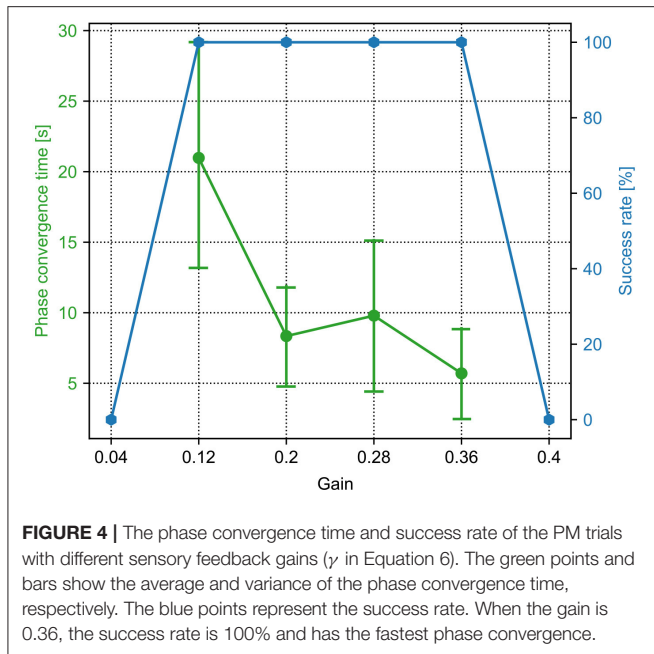
To systematically analyze and compare the characteristics of the PM and PR for self-organized locomotion, three robot experiments were conducted to measure the proposed metrics. First, the phase convergence time (see Equation 15) of the PM and PR under different parameter values was investigated. Subsequently, the phase convergence time of the PM and PR under different robot situations (i.e., a normal situation as a baseline, noisy feedback, leg damage, and carrying a load) were compared. Finally, the phase deviation (see Equation 16) and COT (see Equation 17) under the robot situations were also studied. More than 15 trials were conducted for each experiment under each mechanism (i.e., the PM or PR). Each trial was performed for more than 35 s.

At the beginning of each trial, an identical initialization procedure was conducted to maintain all experimental trials with the same initial conditions when the PM/PR was activated (initial state). The initialization required 270 time steps of 13.5 s, from the start of the simulation ($n = 0$) to the moment of dropping the robot on the ground ($n = n_0$, where $n_0 = 270$ in the following experiments). This initialization duration was selected to provide sufficient time to fulfill three settings: (1) setting/initializing the GRFs [$F_k(n_0)$] to zero by holding the robot in the air; (2) setting the joints of the four legs to the initial positions [$\theta_{ik}(n_0)$] at the beginning of the simulation in all trials, so that the four legs had the same initial movement when the robot was dropped on the ground; (3) setting the CPG weights and biases to the initial values shown in Equations (4) and (5). The four neural SO(2)-based CPGs had the same parameter values and performed as the quasi-periodic attractors (see **Figure 3A**). As a result, the four CPGs generated stable periodic signals [$o_{ik}(n_0)$] in phase to control leg movement in the initial state (see **Figure 3B**).

3.1. Phase Convergence Time Under Different Parameter Values

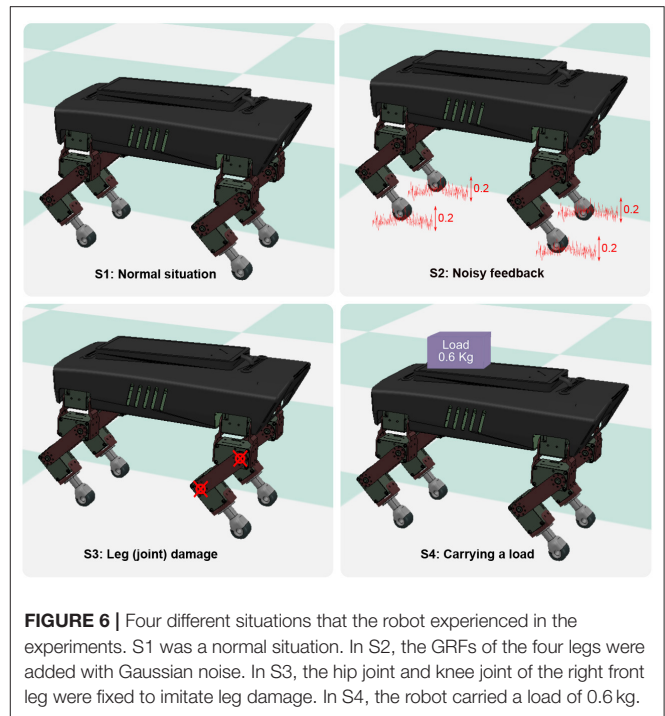
From Equations (6) and (8), it is known that the PM and PR parameters (i.e., sensory feedback gain γ and force threshold factor F_t) play a key role in the CPG phase convergence. Therefore, this experiment investigated the optimal parameter values for fast CPG phase convergence through massive trials. To do that, the proposed adaptive neural controller with the PM or PR was applied to the robot. After initialization, the robot was placed on the ground, and it started to interact with the environment to form self-organized locomotion. The experimental results are depicted in **Figures 4, 5**.

For the PM, a sequence of the sensory feedback gains from 0.0 to 1.0 was tested. The range of the gain (i.e., 0.04, 0.12, 0.2, 0.28, 0.36, and 0.4) is shown in **Figure 4**. The other parameter values are not shown because they cannot enable the CPG phase differences to converge in all 15 trials. In the figure, the phase convergence time and success rate within 15 trials were recorded. Obviously, when the gain is in the range of [0.12, 0.36], the success rate is 100%. This means that the PM with these parameter values enables the robot to generate self-organized gait robustly in all 15 trials. One can also find that the best value of the gain is 0.36, by which the average phase convergence time is ~ 6 s.



Consequently, the fastest phase convergence speed of the PM can be realized by setting γ to 0.36. This value was used for the PM in the following experiments.

For the PR, a sequence of the force threshold factor from 0.0 to 1.5 was tested. The range of the threshold (i.e., 0.0, 0.09, 0.27, 0.45, 0.64, 0.82, 0.91, and 1.0) is shown in **Figure 5**. The other parameter values are not shown because they cannot enable the CPG phase differences to converge in all 15 trials. In the figure, the phase convergence time and success rate



within 15 trials were recorded. Obviously, when the threshold factor is in the range of [0.09, 0.91], the success rate is $\geq 40\%$. Especially, when the threshold factor is 0.64, the success rate is 100%. This means that the PR with the parameter value enables the robot to generate self-organized gait robustly in all 15 trials. In addition, the corresponding average phase convergence time is just approximately a second with a small derivation. Consequently, 0.64 is the optimal parameter value of the PR for the fastest phase convergence speed. This value was also used for the PR in the following experiments.

A success rate of 0 and 100% implies that the robot could not and could perform self-organized locomotion in all 15 trials. The basis for determining whether the robot forms self-organized locomotion (walking pattern) is that the phase differences (ϕ_{12} , ϕ_{13} , ϕ_{14}) among the four CPGs converge to particular states around the desired fixpoint ($\pi, \pi, 0$) or the sum of their standard deviation (ϕ_{std}) first reduces to less than a threshold (i.e., 0.7). For example, if the robot can perform a trot-like gait, the phase differences (ϕ_{12} , ϕ_{13} , ϕ_{14}) should converge to approximately ($\pi, \pi, 0$) (see **Supplementary Figures 1, 2**).

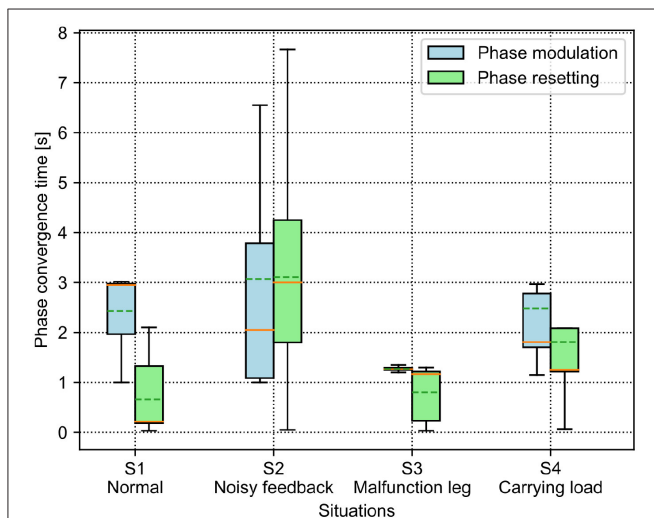
3.2. Phase Convergence Time in Different Situations

The sensory feedback, GRF information, plays an essential role in the function of the PM and PR. To observe the adaptation of the PM and PR with respect to the GRFs, the PM and PR were examined in different robot situations, in which the robot might perceive different GRFs. The situations are illustrated in **Figure 6**. Their description can be seen in **Table 2**.

The abnormal situations (S2, S3, and S4) were used to compare the functional properties of the PM and PR. The

TABLE 2 | The description of the four different situations that the robot experienced in the experiments.

Situations	Description
S1 (normal situation)	This was a normal situation. It served as a baseline for comparison with other unexpected situations.
S2 (noisy feedback)	The GRFs of four legs were added with Gaussian noise with an amplitude of 20% of the maximum value of the GRFs.
S3 (leg damage)	The hip and knee joints of the right front leg were fixed, so the right front leg was unable to move during the experiments.
S4 (carrying a load)	The experiment robot (Lilibot) carried a 0.6 kg load, and the load was near its hind legs.

**FIGURE 7 |** Phase convergence time of the PM and PR in four different situations. The solid and dashed lines in the boxes indicate the median and mean values of the phase convergence time, respectively.

parameter settings of the abnormal situations were determined empirically to distinguish them from the normal situation (S1). In the S2 situation, Gaussian-distributed noise was empirically determined based on a trade-off between significant noise effects and the undisturbed phase regulation function of the PM and PR. Consequently, we used Gaussian distributed noise with a standard deviation of 20% of the GRFs. In the S4 situation, the weight of the payload was selected based on a trade-off between obviously distinct GRFs of the legs and the robot load capability.

The experiments were also performed by implementing the adaptive neural controller with the PM or PR on the quadruped robot but in the four situations. A video to show the robot generating self-organized locomotion under the PM and PR in the four situations are shown in <http://www.manoonpong.com/AICM/video2.mp4>. The experimental results can be seen in **Figure 7**.

For the PM, the average phase convergence time is <3 s in all situations. The best performance is in the S3 situation with the lowest average and variance of the phase convergence time,

while the worst is in the S2 situation with the largest variance. Moreover, some trials in the S2 situation require more than 6 s to realize phase convergence. Overall, the unexpected situations (i.e., S2, S3, and S4) have faster phase convergence than that of the normal situation (S1). This is because the unexpected situations induced significant differentiation among the GRFs which can speed up the phase difference convergence.

For the PR, the phase convergence time of every situation in some trails is less than a second. Moreover, the average phase convergence time is <2 s, except for in the S2 situation, which exhibits the worst performance with the largest average and variance of the phase convergence time. Some trails cost more than 7 s to realize phase convergence in the S2 situation. This is because the added sensory noise made the GRFs randomly cross the force threshold so that the regular phase resetting process was destroyed. In the worst case, the CPG phase would never be reset.

To compare the results, the PR shows faster phase convergence than the PM on average, except for the trials in the S2 situation. This is because the PR rapidly reset the CPG phases once the GRFs increased over the threshold (i.e., 0.64) while the PM utilized the continuous GRFs with the gain (i.e., 0.36) to adjust the CPG phases smoothly. Consequently, the continuous phase modulation of the PM can cause slower but stable phase convergence. The rapid but intermittent phase resetting of the PR can cause faster phase convergence but with random success.

3.3. Phase Deviation and COT in Different Situations

After the CPG phase differences (ϕ_{kl}) converge, the robot exhibits self-organized locomotion. It is also important to study how the phase differences and the formed locomotion are maintained. Therefore, this experiment exploited the deviation of the converged phase differences and used energy efficiency to assess the self-organized locomotion in the various situations.

The results of the phase deviation are shown in **Figure 8**. For the PM, the S1 situation has the greatest average phase deviation among the four situations. Specifically, the average phase deviation in the S1 and S2 situations is >1.5 , while it is <1.5 in the other two situations. For the PR, the S2 situation has a large drop in the average phase deviation compared with the other situations. Specifically, the average phase deviation in the S1 and S2 situations is <1.75 , while it is >1.75 in the other two situations. Comparatively, the average phase deviation of the PM is higher than that of the PR in the S1 and S2 situations, but lower than that of the PR in the S3 and S4 situations.

The results of the energy efficiency (measured by COT) are shown in **Figure 9**. For the PM, the lowest and the highest average COT are in the S1 and S3 situations, respectively. Specifically, the average COT in the S1 and S2 situations is <0.9 , while it is >0.9 in the S3 and S4 situations. For the PR, the S2 situation has the highest COT in the four situations. Comparatively, the average COT of the PM is less than that of the PR in the S1 and S2 situations, but higher than that of the PR in the S3 and S4 situations.

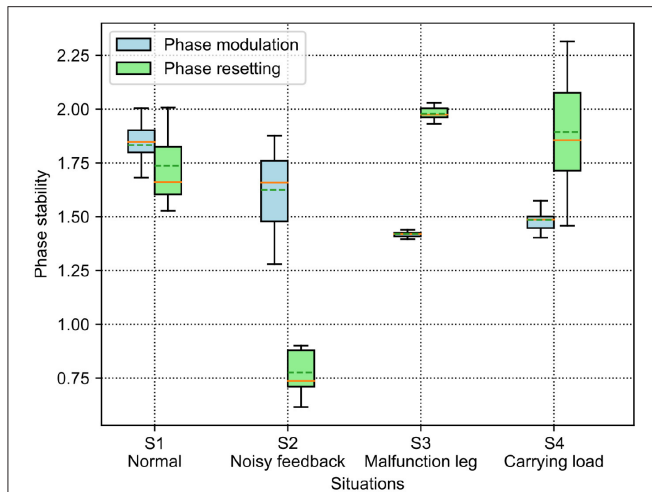


FIGURE 8 | Phase deviation of the self-organized robot locomotion under the PM and PR in the four situations. The solid and dashed lines in the boxes indicate the median and mean values of the phase deviation, respectively.

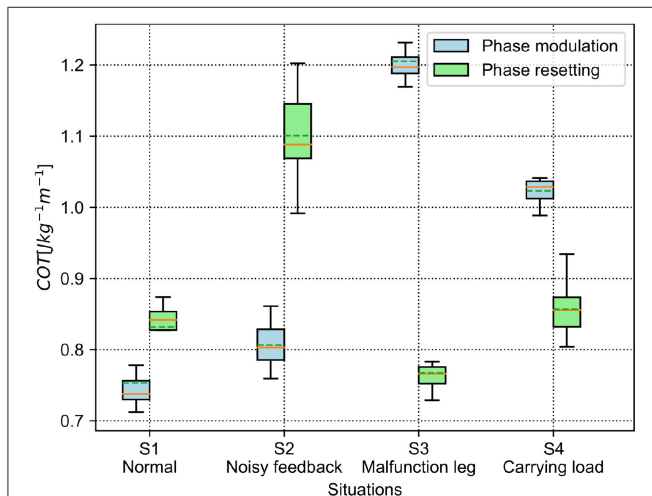


FIGURE 9 | COT of the self-organized robot locomotion under the PM and PR in the four situations. The solid and dashed lines in the boxes indicate the median and mean values of the COT, respectively.

According to the results shown in **Figures 8, 9**, the statistical analysis reveals that the PM has higher phase deviation and energy efficiency (lower COT value) than those of the PR in the S1 and S2 situations, while this result is reversed in the S3 and S4 situations.

Both the PM and PR have different performances (i.e., phase deviation and COT) in these situations. This results from the situations causing the robot to perceive different GRF distributions. The statistical GRFs under the PM and PR in the experiments are shown in **Figures 10, 11**, respectively.

In **Figure 10**, under the PM, the four legs (i.e., the RF, RH, LF, and LH legs) show more similar GRFs values in the S1 and S2 situations than in S3 and S4 situations. This phenomenon can

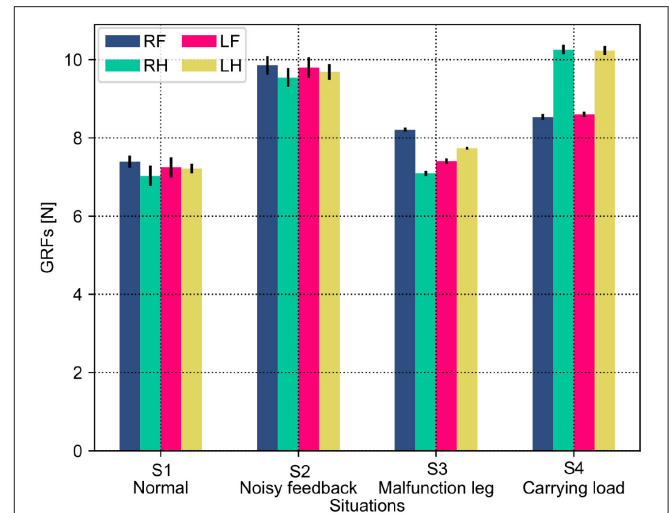


FIGURE 10 | GRF distribution of the self-organized robot locomotion under the PM in four situations. Note that RF, RH, LF, and LH indicate the right front, right hind, left front, and left hind legs, respectively.

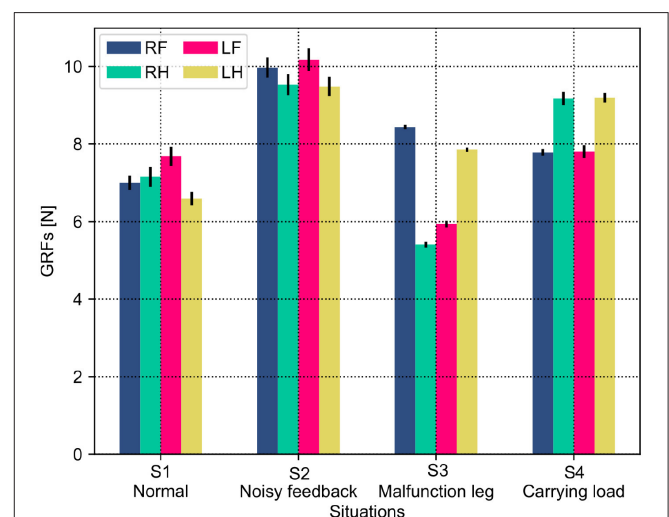


FIGURE 11 | GRF distribution of the self-organized robot locomotion under the PR in the four situations. Note that RF, RH, LF, and LH indicate the right front, right hind, left front, and left hind legs, respectively.

also be seen in **Figure 11** under the PR. The GRF distributions of the four legs in the S1 and S2 situations are symmetric, while, in the S3 and S4 situations, the GRFs show relative asymmetry. Taken together, the PM shows higher phase deviation and energy efficiency when facing a symmetric GRF distribution, while the PR shows higher performance when facing an asymmetric GRF distribution.

4. DISCUSSION AND CONCLUSION

The aim of this study was to comparatively analyze the characteristics of the two classical adaptive interlimb

coordination mechanisms, the PM (see Equation 6) and PR (see Equation 7), for autonomous CPG phase regulation and resulting self-organized locomotion and adaptation. The essential functions of the PM and PR represent two different ways to regulate the phase relationships among decoupled CPGs. Typically, the PM uses continuous GRFs to modulate CPG phases gradually while the PR uses discrete GRFs to reset the CPG phases intermittently. In this study, the two mechanisms were separately applied to the adaptive neural controller with four decoupled SO (2)-based CPGs (see Figure 1). They were implemented on the quadruped robot to experimentally assess the PM's and PR's parameters and adaptability to unexpected robot situations (see Figure 6). The experimental results indicate that (1) the PM and PR parameter values significantly influence the success rate and speed of the CPG phase convergences; (2) overall, the PM exhibits slower but more stable phase convergence while the PR exhibits faster but less stable phase convergence (see Figures 4, 5); (3) the CPG phase convergence time varies in different situations (see Figure 7); and (4) the PM and PR perform better when the robot is subjected to symmetrical and asymmetrical GRF distributions, respectively (see Figures 8–11).

The decoupled CPGs with the PM/PR form a complex dynamical system that comprises three sublevels. Its difference equations can be seen in Equations (1), (6), and (7). (1) The top sublevel dynamical system comprises four identical and decoupled CPGs with the PM or PR, the state variables of which are the CPG phase differences (i.e., ϕ_{12} , ϕ_{13} , and ϕ_{14}). (2) The middle sublevel dynamical system is a CPG with the PM or PR. The PM or PR term can be regarded as external adjustments on the CPG (basis sublevel dynamical system) when the robot interacts with the ground. (3) The basis sublevel dynamical system is a neural SO(2)-based CPG. Its state variables are the CPG outputs (o_{ik} , $i = 1, 2$). Here, it is an oscillatory system under the proper parameter configuration (see Equations 4 and 5). Its dynamics is a limit cycle in the phase space (see Figure 3A). The initial conditions of a multiple-coupling CPG system strongly influence the convergence results (Dénes et al., 2019). In this work, the initial condition of the top sublevel dynamical system is the CPG coordination [$o_{1k}(n_0)$, $o_{2k}(n_0)$] at the CPG limit cycle when the robot lands on the ground ($n = n_0$). Thus, the ensemble of the initial conditions of the top dynamical system is the entire CPG limit cycle. In all experiments, we considered the initial condition of the time 270 steps ($n_0 = 270$) where $o_{1k}(n_0) \approx 0.836$ and $o_{2k}(n_0) \approx 0.067$.

The convergence results (e.g., success rate) of the top sublevel dynamical system depend on the initial condition as well as the PM and PR parameter values [sensory feedback gain (γ) and GRF threshold (F_t)]. When the PM and PR parameter values are outside their effective range (e.g., $\gamma \notin [0.12, 0.6]$ and $F_t \notin [0.09, 0.91]$, see Figures 4, 5), the robot cannot achieve self-organized locomotion (success rate is 0%) regardless of any initial condition. In this case, the top sublevel dynamical system always stays at an initial fixpoint (0,0,0) (see Supplementary Figures 1, 2). This is because the PM and PR with inappropriate parameter values cannot drive the system dynamics from the initial fixpoint to the desired fixpoint ($\pi, \pi, 0$)

where a gait can be formed. More specifically, for the PM, if $\gamma < 0.12$ (e.g., $\gamma = 0$, Supplementary Figure 3), the sensory feedback strength is extremely weak to modulate the CPG phase; if $\gamma > 0.6$ (e.g., $\gamma = 1$, Supplementary Figure 5), the sensory feedback modulation is extremely strong, thereby significantly changing the CPG properties (e.g., output amplitudes and offsets). For the PR, if $F_t < 0.09$ (e.g., $F_t = 0$, Supplementary Figure 6), the four CPG phases are reset at the same time so that their phase differences are zero; if $F_t > 0.91$ (e.g., $F_t = 1.5$, Supplementary Figure 8), the four CPG phases never reset because the sensory feedback cannot meet the phase-resetting condition.

The statistical results (success rate) of the self-organized locomotion are related to the initial condition and parameter values. For the PM, if the parameter value (γ) is in the range of [0.12, 0.6], the PM-based control enables the robot to generate self-organized locomotion with a 100% success rate. The experimental real-time data of the case (e.g., $\gamma = 0.36$) are shown in Supplementary Figure 4. The dynamical system converges to the desired fixpoint ($\pi, \pi, 0$) in the phase space (see Supplementary Figure 1). For the PR, if the parameter value (F_t) is in the range of [0.09, 0.91], the PR-based control enables the robot to generate self-organized locomotion (e.g., $F_t = 0.64$, Supplementary Figure 7) with some uncertainties. The dynamical system can converge to the desired fixpoint ($\pi, \pi, 0$) in the phase space (Supplementary Figure 2). A slight difference in the initial condition may cause distinct convergence results. For example, when F_t is 0.45, in one trial (Supplementary Figure 9), the robot can perform self-organized locomotion; in another trial using the same parameter value and the same initial procedure, the robot cannot generate self-organized locomotion (see Supplementary Figure 10). This is because, in the success case, the GRFs of the four legs can cross the GRF threshold at slightly different times owing to slightly different dynamics among the four legs at the touch moment, even when the four legs touch the ground at the same time. This is because the GRFs of the four legs approached the GRF threshold with a slightly different increase rate when the robot touched the ground (see Supplementary Figure 9). According to this, the results based on the PR are more sensitive to the initial condition than those based on the PM.

The cases with a 0% success rate in Figures 4, 5 result from the inappropriate “physical coupling strength” of the CPGs. In this work, the adaptive synchronizations/coordination among the decoupled CPGs is realized via sensory feedback in the form of the PM or PR, which provides physical communication/coupling effects on the CPGs. The PM and PR parameter values (γ of the PM and F_t of the PR) determine the “physical coupling strength.” When the parameter values are extremely small or large, the “physical coupling strength” also becomes extremely small or large such that synchronization will not be achieved. As a result, the CPG phase relationships (ϕ_{12} , ϕ_{13} , and ϕ_{14}) of the decoupled CPGs are not appropriate for forming a stable gait.

The PM and PR have been analyzed from various aspects in different ways in other works (Aoi et al., 2012; Owaki et al., 2013, 2017; Ambe et al., 2018). For instance, Owaki et al. (2013) have summarized the spontaneous phase shift of the decoupled

CPGs, which are regulated by local force feedback in the form of the PM, as follows: (i) a phase delay is introduced in the CPG of each leg owing to the physical effect of the local force feedback; (ii) this phase delay, which is introduced when the leg is in a stance phase, allows time for other legs to enter the stance phase; (iii) as more legs begin to support the body, the load on the support leg decreases; consequently, the feedback effect on the support leg decreases, allowing it to enter the swing phase. The mechanism reveals how the phases of the CPG are appropriately modified by local sensory feedback, resulting in the generation of the self-organized locomotion. Ambe et al. (2018) analyzed the phase evolution of (no direct interaction) ipsilateral oscillators, which are regulated by local force feedback in the form of the phase resetting. In this case, the CPG phases are shifted and converge to the final state when the legs touch the ground at proper moment. This is because the force feedback can regulate the leg retraction timings by resetting the CPG phase.

However, in the above-mentioned studies the characteristics of the PM and PR models' parameters seem to receive less attention and have not been reported in detail. In this work, the effects of the parameters of the PM and PR on the CPG phase convergences were systematically investigated. As a result, their optimal normalized parameter values were found (see **Figures 4, 5**). This increases the practicality of the two mechanisms for obtaining fast phase convergence in the normal situation (i.e., the S1 situation) by reducing the manual parameter tuning. However, the phase convergence times vary in different robot situations (see **Figure 7**). This suggests that adaptive parameter values of the PM and PR are necessary in various situations. Recently, some studies have implemented learning techniques to obtain adaptive sensory feedback gains of the PM mechanisms (Sun et al., 2018; Dujany et al., 2020; Miguel-Blanco and Manoonpong, 2020).

Another important property of the PM and PR is their adaptability to changes in body properties. It has been reported in many works (Owaki et al., 2013, 2017; Ambe et al., 2018), in which researchers have reproduced certain impressive animal-like movements on legged robots, such as self-organized gaits and autonomous gait transition in response to changes in body properties (e.g., leg amputations and weight redistribution) and environments. These works viewed the adaptability in terms of adaptive walking patterns. In this work, the phase deviation (Equation 16) and energy efficiency (i.e., COT, see Equation 17) were exploited in four elaborated robot situations (see **Figure 6**).

The four situations varied the four legs' GRF amplitudes and exhibited two different GRF distributions: symmetrical GRFs (in the S1 and S2 situations) and asymmetrical GRFs (in the S3 and S4 situations). The experimental results show that the higher phase deviation of the CPGs corresponds to the higher energy efficiency of the self-organized locomotion. This reflects a straightforward relationship of the control metric to locomotion performance. The relationship maybe attributed to the higher phase deviation with fewer unpredictable joint movement changes, thereby saving energy cost. Moreover, the PM and PR exhibited good performance when they were subjected to symmetric and asymmetric GRF distributions,

respectively. This indicates that the two mechanisms should be selected in different situations in the self-organized robot locomotion.

Taken together, the comparative study of the PM and PR in this work reveals not only the relationship between their parameter values and the speed of the self-organized locomotion generation, but also the preferred situations for high phase deviation and energy efficiency in locomotion. Based on this study, it suggests that the PM and PR are effective in different situations. However, these conclusions are based on the robot experiments with the specific neural SO(2)-based CPG setup and the simulated quadruped robot platform. This limits the generality of the conclusions in general CPG and legged robots. In addition, the definition of the phase convergence time depends on empirically tuned parameters (i.e., ϕ_i^{std} in Equation 15 and N in Equation 12), which were determined by observing the experiments implemented in our specific robotic platform. As a result, the statistical results of the phase convergence time, phase deviation (**Figures 4, 5, 7, 8**) could be affected by the experimental platform. Moreover, the metric ϕ_i^{std} is not monotonic and could crossover the threshold more than once, for example, in the S2 situation where the GRFs have additional noise (see **Supplementary Figure 16**). Thus, to obtain the same experimental conclusion on other experimental platforms, the empirical parameters should be adjusted manually according to a specific experimental platform. Thus, in future work, we will further theoretically investigate the two mechanisms based on a dynamical system perspective (Sándor et al., 2015; Aguilar et al., 2016; Martin et al., 2016; Dénes et al., 2019) to further analyze the properties of the mechanisms (e.g., using Poincaré map Owaki and Ishiguro, 2017) and structural stability and to verify the experimental results on other robotic systems, such as hexapod robots.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

TS implemented the control methods, analyzed the data, and wrote the original manuscript. XX guided the experimental design and the research direction, as well as reviewed the manuscript. ZD supervised the study. DO supervised the study and reviewed the manuscript. PM fully supervised this study (including the research idea, experimental design, experimental data analysis) and wrote the manuscript. All authors contributed to the article and approved the submitted version.

ACKNOWLEDGMENTS

We gratefully acknowledged the financial support of NSFC-DfG Collaborative Research Program (Grant no. 51861135306, PM, project Co-PI), the NUAA research fund (Grant no.

1005-YQRO7001, PM, Project PI), the National Natural Science Foundation of China (Grant no. 51435008 to ZD), and Chinese Government Scholarship (Grant no. CSC201906830012 to TS). The authors would like to also thank Weijia Zong, Yan Li, and Potiwat Ngamkajornwiwat for their comments.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frobt.2021.638684/full#supplementary-material>

Conference on Intelligent Robots and Systems. Expanding the Societal Role of Robotics in the Next Millennium (Cat. No. 01CH37180), Vol. 4 (Maui, HI: IEEE), 2318–2325.

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Corrigendum: [A Comparative Study of Adaptive Interlimb Coordination Mechanisms for Self-Organized Robot Locomotion]

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Keywords: adaptive interlimb coordination, phase resetting, phase modulation, decoupled CPGs, sensory feedback, self-organized locomotion

OPEN ACCESS

Approved by:

Frontiers in Robotics and AI Editorial Office, Frontiers Media SA, Switzerland

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Specialty section:

This article was submitted to Computational Intelligence in Robotics, a section of the journal Frontiers in Robotics and AI

Received: 29 April 2021

Accepted: 10 May 2021

Published: 02 June 2021

Citation:

Sun T, Xiong X, Dai Z, Owaki D and Manoonpong P (2021) Corrigendum: [A Comparative Study of Adaptive Interlimb Coordination Mechanisms for Self-Organized Robot Locomotion]. Front. Robot. AI 8:702167. doi: 10.3389/frobt.2021.702167

A corrigendum on

A Comparative Study of Adaptive Interlimb Coordination Mechanisms for Self-Organized Robot Locomotion

by Sun T, Xiong X, Dai Z, Owaki D and Manoonpong P (2021) A Comparative Study of Adaptive Interlimb Coordination Mechanisms for Self-Organized Robot Locomotion. Front. Robot. AI 8:638684. doi:10.3389/frobt.2021.638684

In the original article, there were errors.

In the published article, there was an error in affiliation 1. Instead of “College of Mechanical and Electrical Engineering, Institute of Bio-inspired Structure and Surface Engineering, Nanjing University of Aeronautics and Astronautics, Nanjing, China”, it should be “Institute of Bio-inspired Structure and Surface Engineering, College of Mechanical and Electrical Engineering, Nanjing University of Aeronautics and Astronautics, Nanjing, China”.

In the published article, there was an error in affiliation 2. Instead of “Embodied Artificial Intelligence and Neurobotics Lab, University of Southern Denmark Biorobotics, Mærsk Mc-Kinney Møller Institute, University of Southern Denmark, Odense, Denmark”, it should be “Embodied Artificial Intelligence and Neurorobotics Laboratory, SDU Biorobotics, The Mærsk Mc-Kinney Møller Institute, University of Southern Denmark, Odense, Denmark”.

The authors apologize for this error and state that this does not change the scientific conclusions of the article in any way. The original article has been updated.

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AQuRo: A Cat-like Adaptive Quadruped Robot With Novel Bio-Inspired Capabilities

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OPEN ACCESS

Edited by:

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Reviewed by:

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Specialty section:

This article was submitted to
Computational Intelligence in Robotics,
a section of the journal
Frontiers in Robotics and AI

Received: 15 May 2020

Accepted: 28 January 2021

Published: 12 April 2021

Citation:

Saputra AA, Takesue N, Wada K,
Ijspeert AJ and Kubota N (2021)
AQuRo: A Cat-like Adaptive
Quadruped Robot With Novel Bio-
Inspired Capabilities.
Front. Robot. AI 8:562524.
doi: 10.3389/frobt.2021.562524

There are currently many quadruped robots suited to a wide range of applications, but traversing some terrains, such as vertical ladders, remains an open challenge. There is still a need to develop adaptive robots that can walk and climb efficiently. This paper presents an adaptive quadruped robot that, by mimicking feline structure, supports several novel capabilities. We design a novel paw structure and several point-cloud-based sensory structures incorporating a quad-composite time-of-flight sensor and a dual-laser range finder. The proposed robot is equipped with physical and cognitive capabilities which include: 1) a dynamic-density topological map building with attention model, 2) affordance perception using the topological map, and 3) a neural-based locomotion model. The novel capabilities show strong integration between locomotion and internal-external sensory information, enabling short-term adaptations in response to environmental changes. The robot performed well in several situations: walking on natural terrain, walking with a leg malfunction, avoiding a sudden obstacle, climbing a vertical ladder. Further, we consider current problems and future development.

Keywords: quadruped robot, bio-inspired model, neural-based locomotion, internal-external sensory information, novel capabilities

INTRODUCTION

Robots have become necessary to ease human tasks in many contexts such as industrial, military, entertainment, and disaster settings. Robots have different structures for different purposes. Arm-like robots feature in industrial contexts for performing hand-like functions. Humanoid robots with a wheeled base are often used in social and entertainment contexts. Likewise, robots with legs have an advantage on rough terrain, making them suitable for military and disaster contexts. From a broader perspective, legged robots are more versatile than wheeled robots simply because less than half of the world's terrain can be accessed on wheels.

There are currently many varieties of legged robot exhibiting inspired designs and performance. Boston Dynamics has built many quadruped robots that have excellent capability on rough terrain (Ackerman, 2016). Quadruped robots developed at Waseda University have also demonstrated performance on rough terrain and in ladder-climbing (Hashimoto et al., 2019). Their movement, however, seems slow compared with existing quadruped robots. Most legged robot researchers implement biological structures of quadruped animals to benefit from the animal's performance. MIT, for example, has built

a Cheetah-like robot that moves at high speed (Hyun et al., 2014). BigDog (Raibert et al., 2008), Spotmini (Ackerman, 2016), HyQ (Semini et al., 2011), and Laikago (Spectrum, 2019) are inspired by dogs. They show flexibility of omnidirectional movement on natural terrain. Ijspeert's group took their inspiration from salamanders (Crespi et al., 2013). Animal-inspired robots, however, draw their mobility capabilities from the animals that they are designed after. In contrast to dogs and salamanders, cats are able to climb as well as walk, run and leap over rough terrain. Their claws allow agile climbing behaviors. We have therefore proposed a quadruped robot inspired by feline morphology. We propose a unique paw structure with a gripping mechanism.

The proposed robot is equipped with physical and cognitive capabilities, which include: 1) affordance perception for movement behavior, 2) path planning, 3) a dynamic locomotion generator, 4) stabilization behavior.

For the movement-related perception process, researchers have used different sensors and different strategies. LittleDog (Kolter et al., 2009) used stereo-vision to build the terrain model for the space in front of the robot. Then, it performs footstep planning for the next stepping movement (Kolter et al., 2008). Other researchers have done similar work in perception strategy (Diebel et al., 2004)(Gao et al., 2007). Havoutis *et al.* used an RGBD camera to perceive environmental conditions. Their robot then generates a motion pattern and undertakes foothold planning (Havoutis et al., 2013). Their subsequent work continues on to advanced implementation, such as stair-climbing (Winkler et al., 2015). The MIT Cheetah robot performs impressively while running and jumping to avoid an obstacle (Park et al., 2015). This robot uses LRF (laser range finder) sensors to detect upcoming obstacles, and identifies them using an iterative end-point fitting (IEPF) algorithm. Once an obstacle is perceived, the robot prepares the jump by controlling speed.

Manchester *et al.*, used more complex external sensors such as vision, laser, and radar sensors. Their robot builds a terrain map model and then generates a sequence of footstep locations and associated joint trajectories. The perception is only effective on slow timescales. The footstep planning is updated in every footstep (Manchester et al., 2011). The high-rate timescale is used only for internal sensory response. Many researchers also conducted footstep planning, updated at every footstep, in both bipedal (Deits and Tedrake, 2014) (Maier et al., 2013) (Kuindersma et al., 2016) and hexapodal robots (Belter and Skrzypczyński, 2011). Taking a different approach, Hoffmann *et al.* use a closed-loop strategy for perception and action. They developed interaction between the robot's embodiment and its environmental context. The robot adjusts its gait or speed when environmental changes are detected (Hoffmann et al., 2011). In this work, the robot reconstructs its map before generating motion plans that address only high-level motion (speed, step length, step height). Next, the stability model controls the low-level

motion. The external sensory information is hence not directly used in low-level motion planning. In our proposal, the cognitive model plays a role in the lower-level locomotion model. Using external sensory information and a laser sensor costs less in computational processing to detect object shapes, than using a vision sensor.

The locomotion generator, as its name suggests, generates the movement behavior appropriate to particular conditions. There are many models for legged-robot locomotion. Most researchers implement trajectory-based locomotion for its simplicity; this has been done in bipedal (Manchester et al., 2011)(Zhang et al., 2014b)(Nandi et al., 2016)(Saputra et al., 2015a)(Khusainov et al., 2016)(Saputra et al., 2015c), quadrupedal (Winkler et al., 2015)(Kolter et al., 2008)(Mastalli et al., 2017)(Zhang et al., 2016)(Matsuzawa et al., 2016), and hexapodal robots (Qian and Goldman, 2015) (Zhu et al., 2016). Trajectory-based models control the motion planning in Cartesian coordinates using polynomial equations or Bézier curves (Manchester et al., 2011). Other researchers use center-of-gravity-based trajectory generation for quadrupedal robots (Winkler et al., 2015)(Mastalli et al., 2017). These center-of-gravity trajectory models have been successfully implemented for complex terrain. However, this approach has proven lacking on dynamic locomotion behavior. The trajectory-based approach needs to plan scenario motion planning in advance, and requires extensive parameter-tuning.

On the other hand, some researchers have tried other ways to develop dynamic locomotion patterns that can synchronize automatically with sensory feedback. They consider natural processes to develop locomotion models from human and animal gaits. Quadrupedal animals can generate gait patterns (walk, pace, amble, trot, gallop) automatically, depending on the animal's intentions and environmental conditions. The animal's body structure also regulates the gait pattern, which means every kind of animal has different gait efficiencies. Nakada *et al.* propose a neuromorphic locomotion model with a CMOS (Complementary Metal Oxide Semiconductor) controller for inter-limb coordination in quadrupedal robots (Nakada et al., 2003), while other researchers propose central pattern generation (CPG) for quadrupedal robot locomotion (Ijspeert and Cabelguen, 2006)(Asadi et al., 2015)(Maufray et al., 2008)(Zhang et al., 2014a)(Sun et al., 2018)(Liu et al., 2018). Ijspeert's group proposed CPG-based control of their salamander robot (Ijspeert and Cabelguen, 2006), which can transition dynamically from walking to swimming. Transitional movements in quadruped robot have also been proposed using CPG model by several researchers (Maufray et al., 2010; Fukuoka et al., 2015; Owaki and Ishiguro, 2017). Other researchers have developed integration between CPG and ground reaction feedback to synchronize the gait with terrain conditions (Maufray et al., 2008). Zhang *et al.*, for example, designed a CPG-based controller for trotting (Zhang et al., 2014a). CPG gait generators can be implemented using a spiking neural

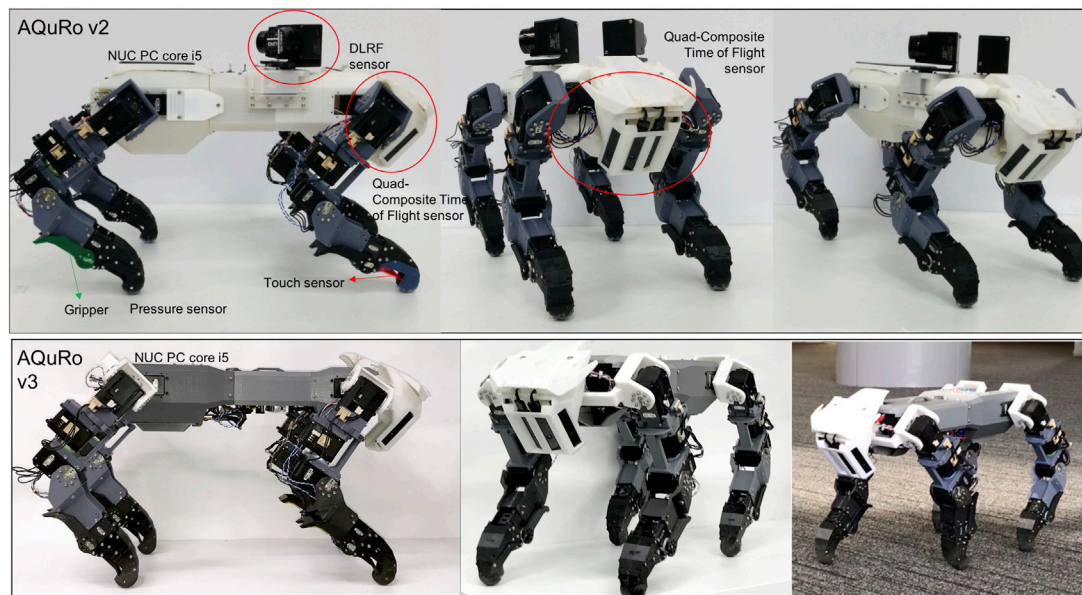


FIGURE 1 | The quadruped robot. AQuRo v2 is attached with DLRF sensor and AQuRo v3 has slimmer body without DLRF sensor.

network (Espinal et al., 2016) or a recurrent neural network (Tran et al., 2014). Sun *et al.* used a decoupled neural CPG circuit for adaptive locomotion (Sun et al., 2018). In our previous model, we combined the CPG with a Bézier curve model for efficiency. We implemented our ideas in a small quadrupedal robot, but it showed limitations on handling variant gait (Saputra et al., 2016)(Saputra et al., 2015b). The quadrupedal robot proposed in the present paper will be implemented as an efficient neural-based locomotion model using a single-rhythm generator-based CPG model, and will include a reflex system for synchronizing with locomotion events. Here, the reflex system is composed as the muscle reflex system explained in (Saputra et al., 2020b) and sensory afferent from force sensor in each leg explained in *Affordance Detection for Grasping*.

Our robot is equipped with external and internal sensors. We use point-cloud data information generated by a laser depth sensor as external sensory information. There are many robots that effectively detect and recognize obstacles using depth sensors (Park et al., 2015)(Hashimoto et al., 2019)(Camurri et al., 2015). The WAREC robot, for example, has a rotating laser range-finder array for scanning the surrounding environment (Hashimoto et al., 2019). Since depth sensors are limited in frequency rate, size, weight, and range, we propose a light-weight array of time-of-flight sensors which alleviates these limitations. To provide internal sensory information, we use an inertial measuring unit (IMU), four force sensors, and four grip-touch sensors.

This paper is organized as follows: In *Design of Robot's Hardware*, we describe the robot's mechanical and hardware design. *Movement-Related Capabilities* examines the robot's

unique capabilities. *Robot Implementation* shows the implementation of the robot and demonstrates its effectiveness. Finally, in *Conclusions and Future Plans*, we conclude the paper.

DESIGN OF ROBOT'S HARDWARE

As stated in the Council on Competitiveness—Nippon (COCN) report, robots suitable for use in disaster situations must be able to move over all of rough, sloped and natural terrain (grass, uneven soil), through narrow spaces, and be able to climb stairs and vertical ladders (Council on Competitiveness Nippon (COCN), 2013). When we seek inspiration from the animal kingdom, the cat family (Felidae) stands out as able to do all of these things. Cats can handle many complex environmental conditions. They can swim, are agile, and can climb trees. The cat offers a most appropriate archetype to imitate in agile quadrupedal robots. The feline robot that we developed is shown in **Figure 1**.

Mechanical Design

Our proposed quadrupedal robot is similar in size to a mature domestic cat: 25 cm (width) × 60 cm (length) × 30 cm (height). The robot has around 7 kg of weight. **Figure 2** The robot's foreleg imitates the cat's forelimb structure minus the wrist joint. It has only two joints, the shoulder and elbow. There are three actuators associated with the ball joint structure of the shoulder, and one actuator associated with the hinge joint structure of the elbow. To design the

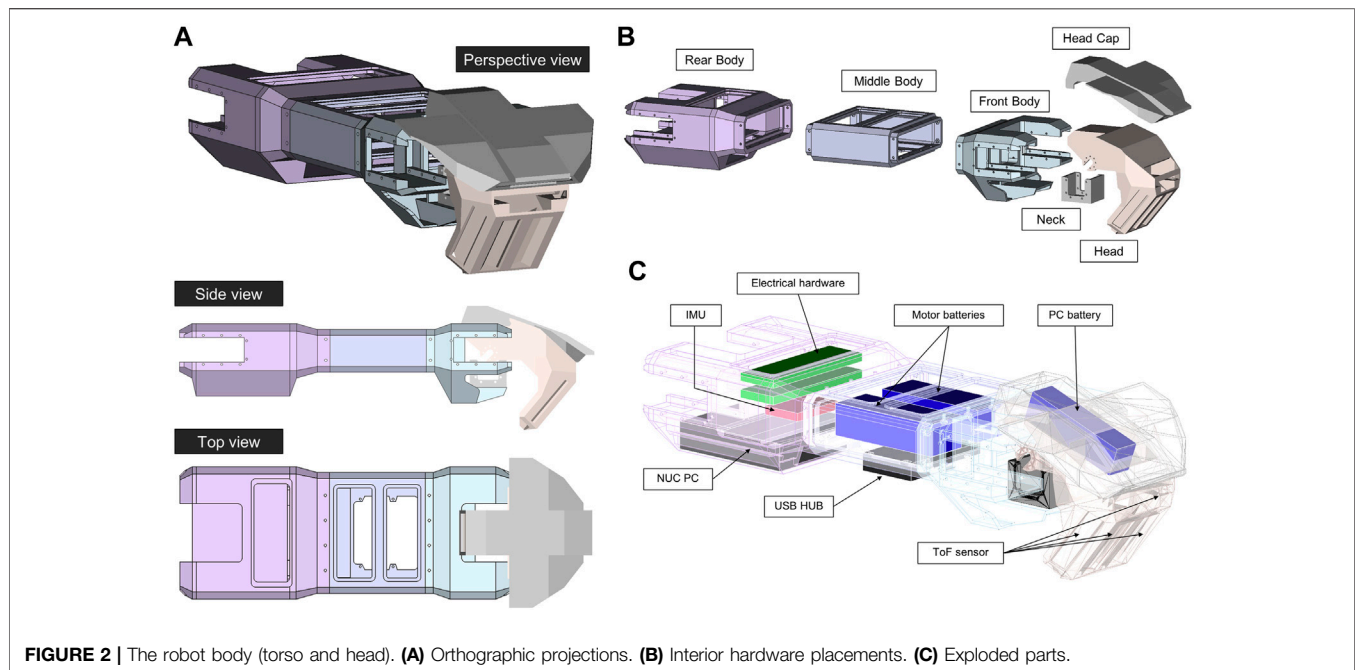


FIGURE 2 | The robot body (torso and head). **(A)** Orthographic projections. **(B)** Interior hardware placements. **(C)** Exploded parts.

robot's hindleg, we considered the cat's rhythmic motion, in which the proximal and distal leg segments maintain their relative angular orientation during most of the cycle, the deviation of angular joints differing only at the onset of toe-off (Witte et al., 2001). In the hindlegs, therefore, we simplified by eliminating the knee joint so the ankle and hip joints could be directly integrated. The leg can be seen in **Figure 3**. There are five degrees of freedom in each leg, one of which is used as the gripper joint. The tibia is 175 mm long, and the femur is 145 mm long. The robot's Denavit-Hartenberg parameters are summarized in **Table 1**.

Robot Body

The robot's overall body shape can be seen in **Figure 1**. The shell was 3D-printed in poly-(lactic acid) (PLA). The robot body comprises three parts: rear, middle, and front. The rear legs are attached to the rear part, which also holds the NUC PC, IMU sensor, and electrical hardware. The middle part holds two batteries for the motors and a USB Hub. The front part provides an attachment point for the neck and head. The head holds a battery for the PC.

End Effector

We designed the end effector to support agile movements such as walking on rough terrain and climbing vertical ladders. The end effectors must also measure the ground reaction force, and must satisfy size constraints. When climbing, cats use claws to grasp rocky walls, trees, poles, etc. Shiquan et al. developed an end effector with a dense array of micro-spines (Wang et al., 2016) for rock climbing. It needs a larger space, however, than is appropriate for our proposed robot. Furthermore, cats grasp by using two limbs in concert. Cats also find it difficult to climb vertical ladders.

In contrast, humans and monkeys have hands to hold and hang from ladder rungs. However, the hand mechanism for such hanging behavior needs a huge torque, which would require a correspondingly bigger servomotor. We simplified using a hook-shaped end effector that requires no actuator. The design can be seen in **Figure 4**. The end is rounded to simplify footing, eliminating the need for an actuator. Furthermore, in the sensory design, we put a force-sensitive resistor (FSR) between the upper and lower parts of the paw. A switch inside the hook cavity serves as a sensor to detect whether the paw is hooked over a rung. Behind the paw is a moveable claw for grasping and for supporting the hindleg to stand on a rung. The claw, moved by a low-torque servomotor, helps to avoid slippage.

Sensory System

We provided the cat robot with several sensors representing exteroceptors and interoceptors. To represent the exteroceptors, we built a quad-composite time-of-flight sensor for detecting the surroundings in front the robot, and a dual-laser range-finder for observing more widely. To represent interoceptors, we installed force sensors (force-sensitive resistors) and touch sensors (microswitches) in each leg, and an inertial measurement unit (IMU) inside the body. We use IMU module NG-IMU, as specified in **Table 2**.

Quad-Composite Time of Flight Sensor

This sensor will be installed in the head of the robot. It combines four CamBoard pico flexx ToF sensors made by pmd, as specified in **Table 3**. The composite sensor structure is depicted in **Figure 5**. This design, combined with the

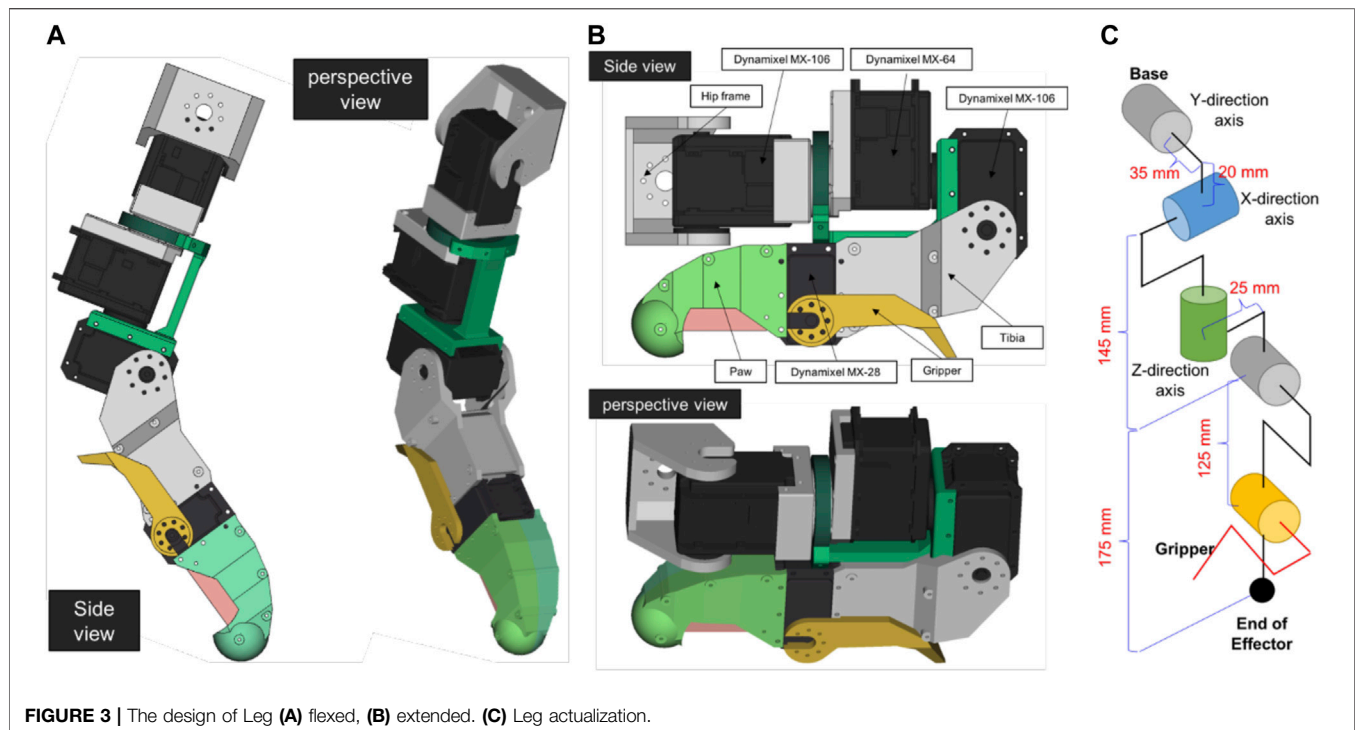


FIGURE 3 | The design of Leg (A) flexed, (B) extended. (C) Leg actualization.

TABLE 1 | DH Table of the joint leg structure.

Joint	Hip-y (mm)	Hip-x	Hip-z (mm)	Knee
α_i	$\pi/2$	$-\pi/2$	$-\pi/2$	0
a_i	20	0	25	172 mm
d_i	35	0	145	0
$\theta_{0,i}$	$\pi/2$	$-\pi/2$	$-\pi/2$	$-\pi/2$
θ_i	$\theta_{0,1} + \theta_1$	$\theta_{0,1} + \theta_2$	$\theta_{0,1} + \theta_3$	$\theta_{0,1} + \theta_4$

robot's head shape, provides a wide field of view in order to minimize the number of actuators needed in the robot's neck. The neck hence contains only one actuator, rotating in the sagittal plane. The CAD design drawings and photographs can be seen in **Figure 6**.

Dual-Laser Range Finder Sensor (DLRF)

The DLRF is composed of two LRF sensors, with each LRF is attached to a Dynamixel MX-28 servomotor. This mechanism allows the sensors to measure distances. The design can be seen in **Figure 7**. **Table 4** shows the specifications of the LRF sensor used. In **Figure 7C** we can see the moving mechanism of the sensors. The sensors will move symmetrically, where if the left sensor moving clockwise then the opposite sensor will move counterclockwise. Each sensor will move 240 [degree] of range. After reaching the limit degree, then the sensor will move the opposite direction.

Electrical Hardware

The robot has been equipped with a hardware configuration to handle both the internal and the external sensory information.

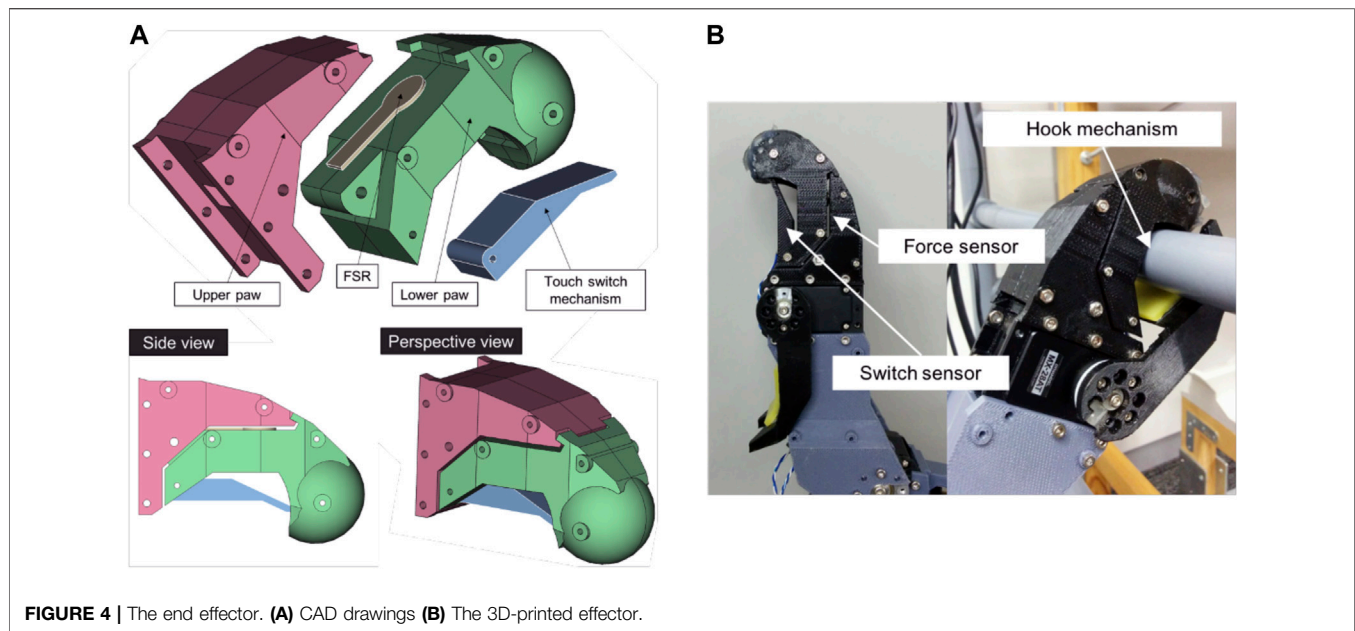
The hardware structure can be seen in **Figure 8**. We use an ATmega 8 microcontroller as the sub-controller for pre-processing the internal sensory inputs from the force sensor, touch sensor, and IMU. A NUC PC core i3 serves as the main controller for processing several advanced systems such as perception, motion control, communication, and interfacing.

The sub-controller processes analog signals from the force sensor, touch sensor, and IMU sensor through its analog to digital converter input. The data stream is then transferred to the main controller via a USB connection. All external sensory information is also conveyed via USB connections. The main controller generates digital motor control signals for all of the servomotors. There are 12 servo motors Dynamixel MX-106, four servo motors Dynamixel MX-64, and seven servo motor Dynamixel MX-28.

The electrical system is powered by two 4-cell lithium-polymer batteries holding 2700 mAh (14.8 V) and one 4-cell lithium-polymer battery holding 2200 mAh (14.8 V). The batteries are expected to power the robot for around 15 min.

MOVEMENT-RELATED CAPABILITIES

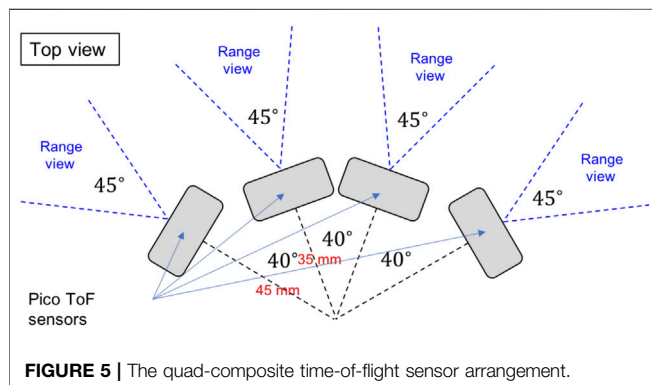
We implemented the robot's movement-related capabilities by integrating external and internal sensory information. This integration allows external sensory information to inform movement behaviors in short adaptation times, as happens in animals: when an obstacle suddenly appears

**TABLE 2 |** NG-IMU sensor specifications.

Model	NG-IMU
Sensors	Gyroscope, Accelerometer, Magnetometer, Pressure, Humidity
Update Rate	400 Hz
Static Accuracy (pitch/Roll)	<1 [deg] RMS
Static Accuracy (Heading)	<2 [deg] RMS
Communication	USB, Serial, WiFi
Size and weight	50 × 33 × 8 [mm], 10 [gram]

TABLE 3 | Time-of-flight sensor specifications.

Model	CamBoard pico flexx
Dimension, weight	68 × 17 × 7.35 mm, 8 g
Measurement range	0.1–4 m
Framerate	Up to 45 fps (3D frames)
Resolution	224 × 171 (38k) pixels
Viewing angle (H × V)	62° × 45°

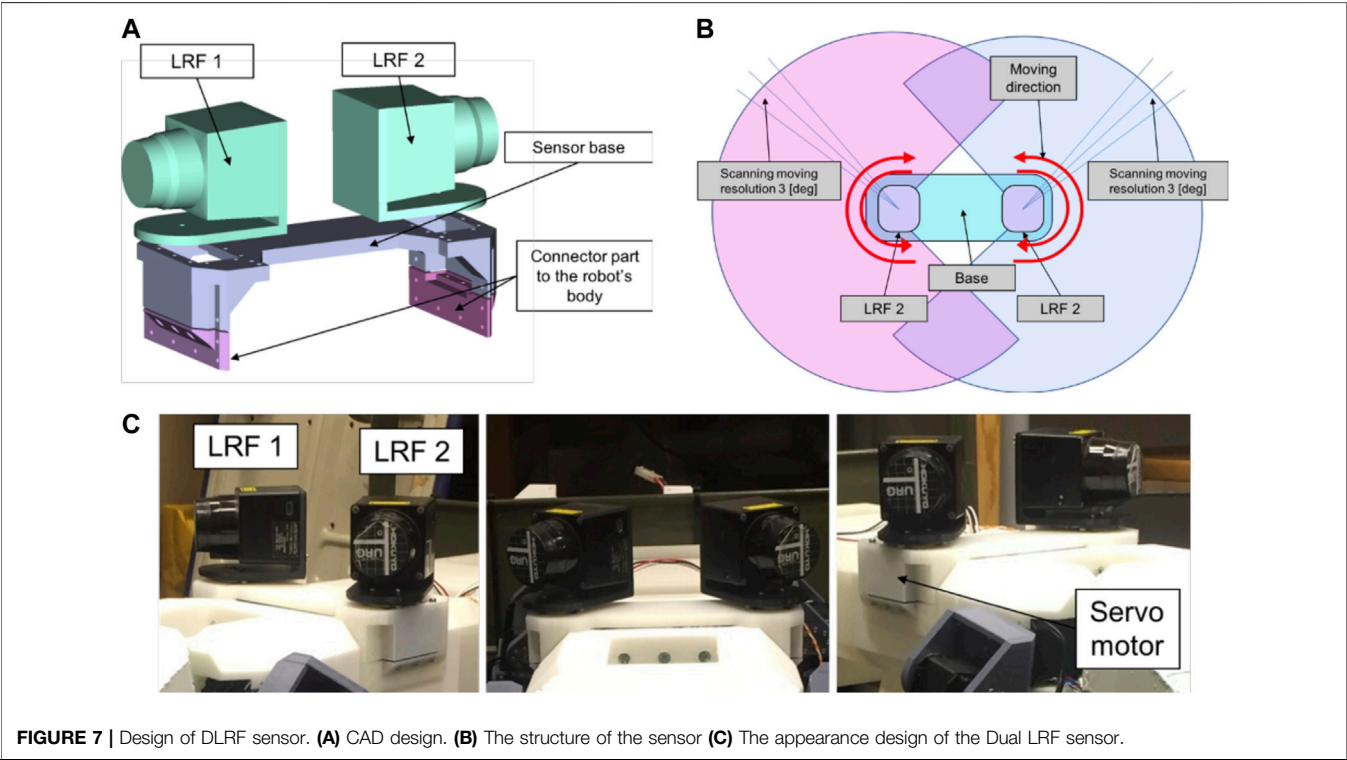
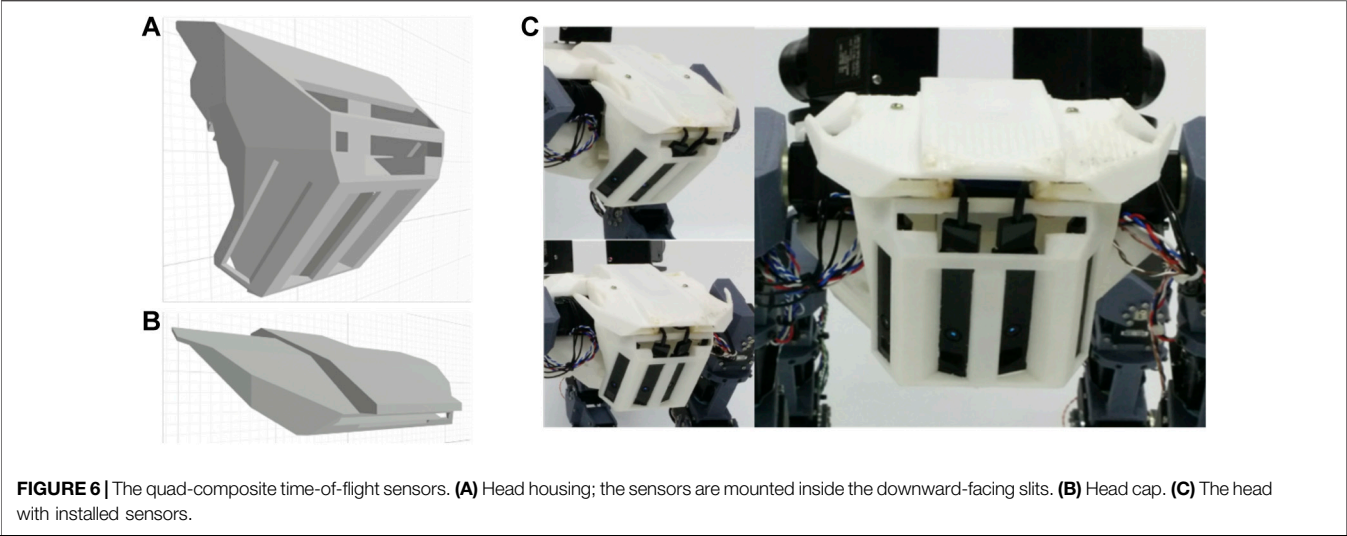


during the walking swing phase, the swing is changed in response, bringing the foot into a safe area. This mechanism illustrates the importance of external sensory information (in this case, vision) for movement behavior.

To use depth information or a 3D point-cloud data as the external sensory information, our robot's processing system includes 1) a dynamic-density topological map-builder with an attention model, 2) an affordance perceptor using the topological map, and 3) a neural network-based locomotion model.

Dynamic-Density Topological Map-Building With Attention Model

We present a novel algorithm to realize an attention mechanism for robot movement, based on the dynamic density of a growing neural gas. The aim of this model is to reduce the data representation overhead associated with the 3D point-cloud data. The basic real-time Growing Neural Gas (GNG) technique has been implemented in our previous path planning model (Saputra et al., 2017). We extended the GNG by adding a dynamic-density model. The algorithm's details are given in (Saputra et al., 2019b)(Saputra et al., 2019a). A comparison between the common GNG and the



proposed GNG augmented with dynamic attention can be seen in the link of **Video 1**.

TABLE 4 | LRF sensor specifications.

Model	URG-04LX-UG01
Weight	160 g
Measurement range	20–5600 mm
Scanning time	100 ms
Scanning accuracy	60–1000 mm: ±30 mm; 1000–4095 mm: ±3 mm
Measurement range	240°

Affordance Perception Model

The concept of affordance originated from Gibson, in ecological psychology (Gibson, 1977). Turvey describes affordance as the environment’s dispositional properties. The actor’s effectivity or dispositional properties will supplement what the environment provides. Affordance provides important details governing the actor’s potential behavior and capability. A difference in the robot’s embodiment can therefore lead to different affordance perceptions (Turvey, 1992). The aim of our proposed

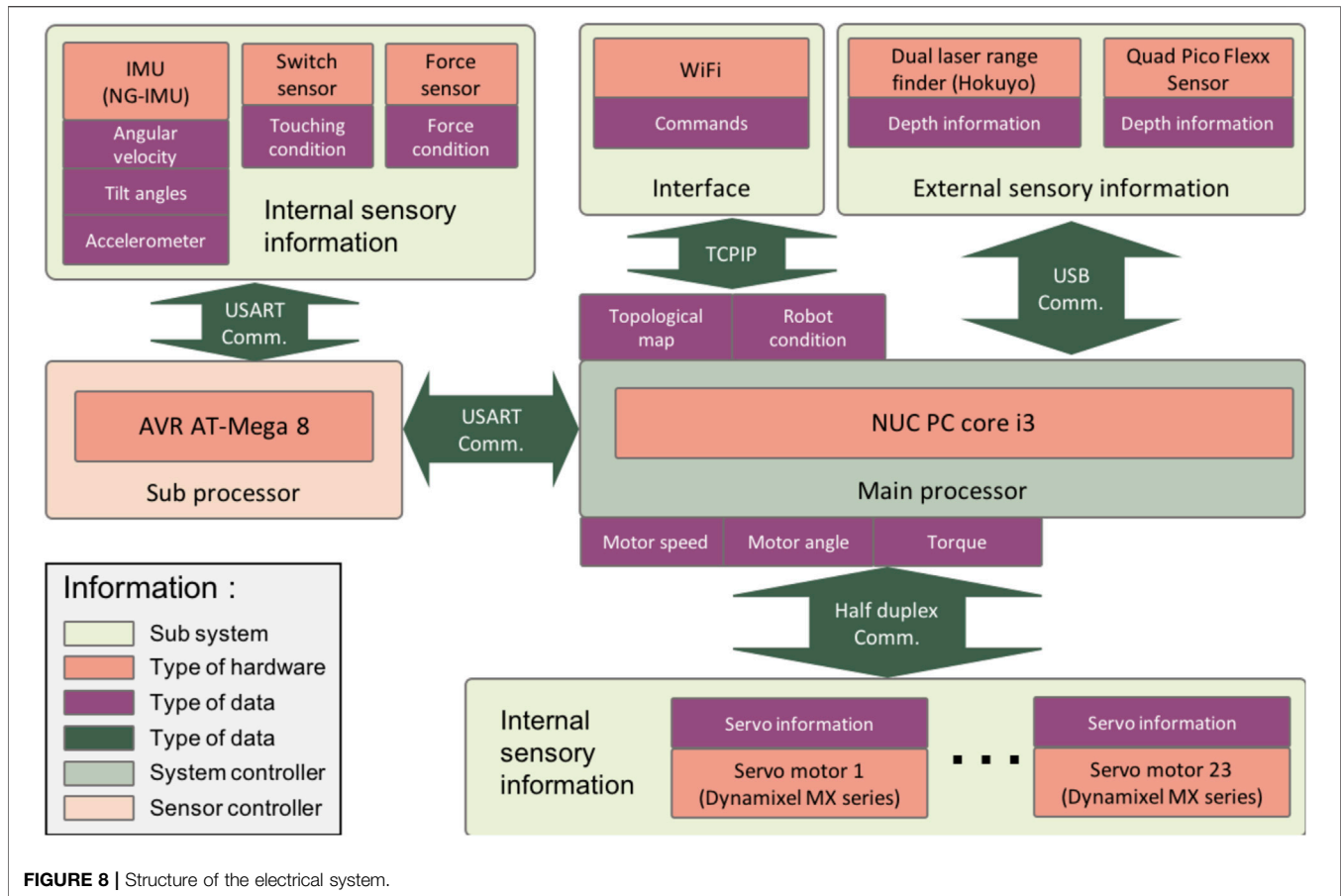


FIGURE 8 | Structure of the electrical system.

affordance perception model is to find a suitable integration between environmental conditions and possible actions for the robot. We built affordance perception systems for the robot's locomotion, ladder detection, and grasping.

Affordance Detection for Locomotion

In the locomotion system, the active behavior is regulated by perceiving the affordances. Prospective actions are therefore produced according to the affordance information obtained. In our model, affordances are detected by examining planes in the topological map generated by the dynamic-density growing neural gas (DD-GNG). The affordances of interest are horizontal (or nearly horizontal) surfaces that the robot can step on. These are found by calculating the plane's slope. We calculated the normal vector of triangular facets in the topological structure using Eq. 1, as illustrated in Figure 9.

$$N = \frac{(\mathbf{n}_0 - \mathbf{n}_1) \times (\mathbf{n}_0 - \mathbf{n}_2)}{\|(\mathbf{n}_0 - \mathbf{n}_1) \times (\mathbf{n}_0 - \mathbf{n}_2)\|} \quad (1)$$

After that, the slope of plane facet (γ_i) in every surrounding surface needs to be calculated using Eq. 2. A safe-to-step-on factor can then be calculated by considering how vertical the plane is.

$$\gamma_i = \cos^{-1} \left(\frac{\overrightarrow{Ob_i^{(v)}} \Delta \overrightarrow{N_{(ver)}}}{\|\overrightarrow{Ob_i^{(v)}}\| \Delta \|\overrightarrow{N_{(ver)}}\|} \right) \quad (2)$$

Where, $\overrightarrow{Ob_i^{(v)}}$ is the normal vector of the i th obstacle plane and $\overrightarrow{N_{(ver)}}$ is the vertical unit reference vector, [010].

Affordance Detection for Vertical Ladders

The model aims to present low-cost real-time vertical ladder-detection from 3D point-cloud data. The output from the

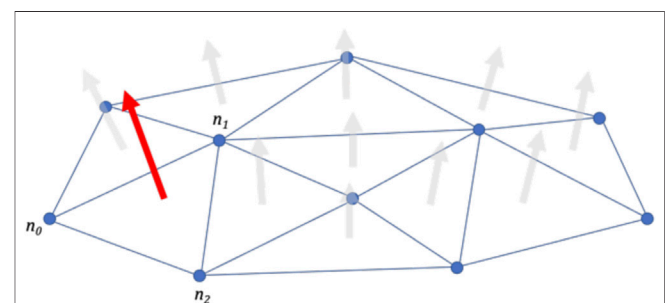


FIGURE 9 | Calculating the normal vector of a plane triangle.

TABLE 5 | Table of parameters.

v_i	Inhibition effect of its self-adaptation
y_j	Signal from other j -RG neurons, y_j calculated as $y_j = \max(x_j, 0)$
$w_{(RG,i)}$	Synaptic weight of j -RG neuron and i -RG neuron
τ and T	The inner-state and self-adaptation effects
α_i	sensory feedback of i -RG neuron
$\alpha_{i,0}$	Basic stimulation of the i th neuron
$w_{(FR,i)}$ and $w_{(SR,i)}$	The synaptic weights of the force afferent (F_i) and the swing-phase afferent (S_i) of the i th leg to the i th RG neuron
$w_{(NS,i)}$	The synaptic weights of the nociceptor afferent (N_i), a pain receptor that detects the condition of leg damage and sends damage stimuli to RG neurons
G_{STIM}	The gain parameter controlling the relationship between speed stimulation S_{STIM} and the sensory network
τ_f	Frequency control parameter

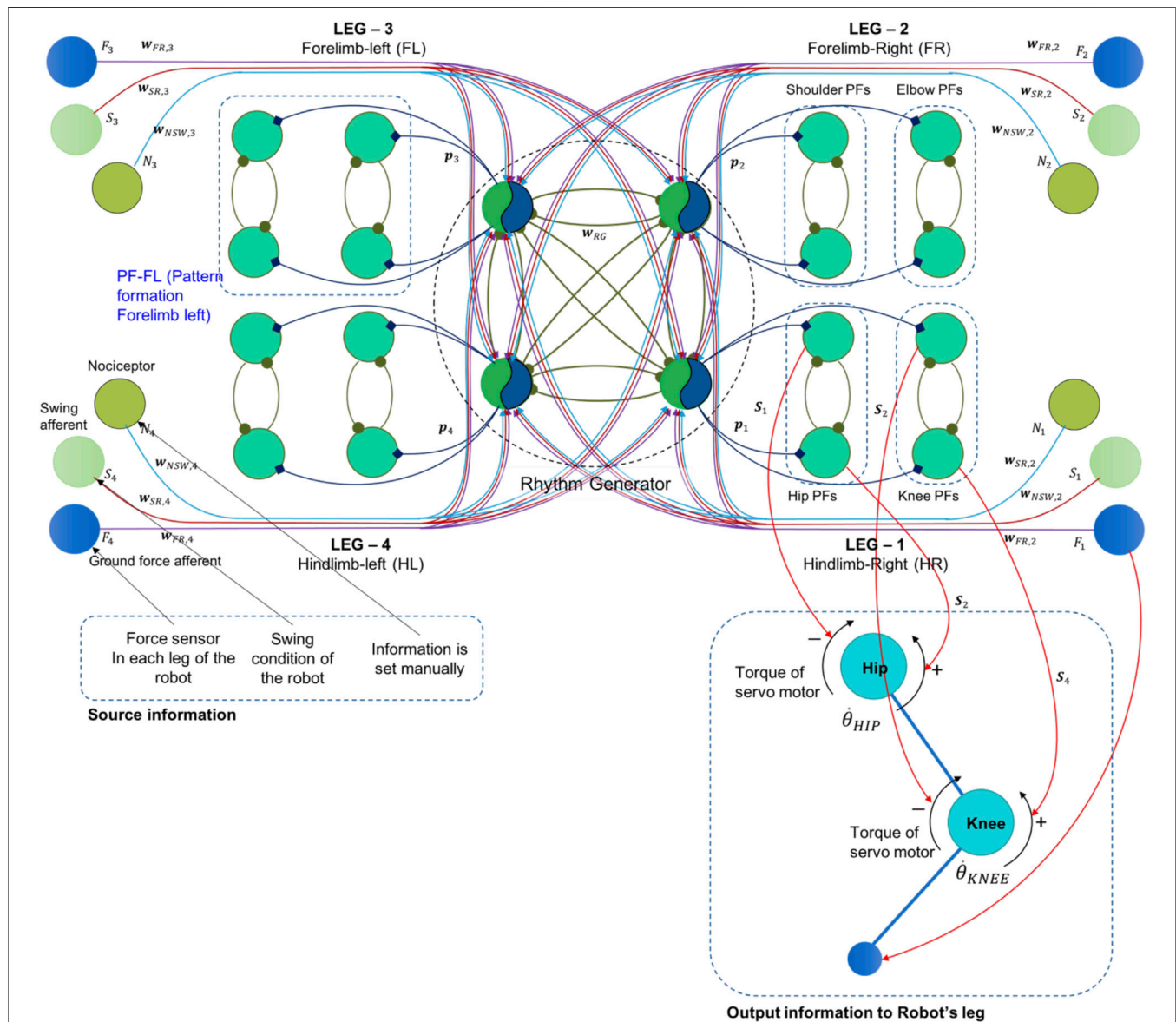
**FIGURE 10 |** The single-rhythm CPG model with a two-layered CPG. The rhythm generator neurons received feedback signals from a force sensor, a pain receptor, and a swing sensor in each leg.

TABLE 6 | Optimized parameter of CPG.

τ	T	b	τ_f	Time step (s)	$\alpha_{i,0}$	y^{ref}	Q	R	
1.0	12.0	1.5	3	0.01	1.0	0.98	0.5	30	
$W_{(RG,j)}$	$W_{(RG,1)}$	$W_{(RG,2)}$	$W_{(RG,3)}$	$W_{(RG,4)}$	$W_{(FR,j)}$	$W_{(FR,1)}$	$W_{(FR,2)}$	$W_{(FR,3)}$	$W_{(FR,4)}$
$W_{(RG,1)}$	0.00	2.431	1.32	2.431	$W_{(FR,1)}$	0.00	1.002	0.960	1.023
$W_{(RG,2)}$	1.32	0.00	2.431	2.431	$W_{(FR,2)}$	0.960	0.00	1.023	1.002
$W_{(RG,3)}$	2.431	2.431	0.00	1.32	$W_{(FR,3)}$	1.002	1.023	0.00	0.960
$W_{(RG,4)}$	2.431	1.23	2.431	0.00	$W_{(FR,4)}$	1.023	0.960	1.002	0.00
$W_{(SR,j)}$	$W_{(SR,1)}$	$W_{(SR,2)}$	$W_{(SR,3)}$	$W_{(SR,4)}$	$W_{(NS,j)}$	$W_{(NS,1)}$	$W_{(NS,2)}$	$W_{(NS,3)}$	$W_{(NS,4)}$
$W_{(SR,1)}$	0.00	0.00	2.059	0.00	$W_{(NS,1)}$	0.00	0.001	0.00	0.01
$W_{(SR,2)}$	0.02	0.00	0.00	0.00	$W_{(NS,2)}$	1.875	0.00	0.00	0.00
$W_{(SR,3)}$	0.00	0.00	0.00	0.02	$W_{(NS,3)}$	0.00	0.00	0.00	1.94
$W_{(SR,4)}$	0.00	1.987	0.00	0.00	$W_{(NS,4)}$	0.00	0.00	0.001	0.00

DD-GNG is used as input to the affordance model. Feature-extraction is needed to identify suspected artifacts for the next stage of processing. Thereafter, vertical ladder-rung detection is processed using an inlier-outlier system. The ladder detection system thereby represents the ladder as a set of nodes and edges. Next, we detect the graspable locations by considering the robot's embodiment. The details of the proposed detection system can be seen in (Saputra et al., 2019a).

Affordance Detection for Grasping

This affordance detection process aims to detect possible gripping positions on the object. The process generates a seven-dimensional representation of grippable locations: (3D location, 3D rotation, and object diameter). We put an RGB camera above the robot's quad-composite ToF sensor to detect the target object. Detection of target objects is performed by a computer vision algorithm. After that, the topological structure will be generated by using the proposed DD-GNG. The density of the topological structure is centralized on the desired object. Based on the inlier-outlier process, the possible gripping information is determined from topological map information and the robot gripper embodiment. Gripping possibilities can then be ranked from 'best' to 'worst' in any identified gripping solution. Details of this process can be seen in previous research (Saputra et al., 2019b).

Locomotion Model

Our locomotion model responds to current CPG development challenges in quadruped locomotion research. We present an efficient and solid CPG model that dynamically integrates with sensory feedback for generating various gaits, and allows for leg malfunction compensation without greatly increasing the number of parameters involved. The model has two feedback mechanisms based on sensorimotor coordination (Rossignol and Frigon, 2011)(Lam and Pearson, 2002). In the first feedback mechanism, sensory feedback is used to adjust CPG modulation. This is done by feeding

proprioceptive signals representing the leg's force exertion and swing phase back to the rhythm generator neurons (RG). This feedback is reduced by the second feedback mechanism, when legs are injured. A nociceptor neuron in the injured leg sends a signal to modify the effects of that same leg's other sensory signals to the RG. Furthermore, we integrate the locomotion functions with supraspinal-level functions generated from cognitive information. Our overall model mimics the descent of influence from attention mechanisms driven by visual information down to muscle activation. Our model addresses the problem of providing short-term adaptation in response to perceiving a sudden obstacle **Table 5**.

We designed a single-model CPG in which each RG neuron represents the movement pattern of one leg, and each pattern formation (PF) neuron represents the activation of one muscle. Since we use four muscles in one leg (flexor and extensor muscles of hip and knee joint), each limb structure in the CPG network comprises one RG neuron and four PF neurons. Our model uses two CPGs, one for the forelimbs, and one for the hindlimbs. The overall CPG design can be seen in **Figure 10**. We extend the CPG model from our previous model published in (Saputra et al., 2020b). We used the Matsuoka neural-oscillator model to generate a dynamic signal. The inner state of the RG neuron can be seen in this following equation:

$$\tau \frac{d}{dt} x_i = \left(v_i - x_i - \sum_{j=1}^n w_{(RG,ij)} y_j + \alpha_i - b v_i \right) (\tau_f S_{STIM}) \quad (1)$$

$$T \frac{d}{dt} v_i = (y_i - v_i) (\tau_f S_{STIM}) \quad (2)$$

$$\alpha_i = \alpha_{i,0} + \sum_{j=1}^n w_{(FR,ij)} F_i N_j - \sum_{j=1}^n \left(G_{STIM,A} (S_i) \left(w_{(SR,ij)} N_j \right) - \sum_{j=1}^n \left(G_{STIM,B} (S_i) w_{(NS,ij)} N_j \right) \right) \quad (3)$$

$$G_{STIM,A} = 3 / (1 + \exp(-8 S_{STIM} + 15)) \quad (4)$$

$$G_{STIM,B} = 2 \exp(\log(0.5) (2 S_{STIM} - 4)^2) \quad (5)$$



FIGURE 11 | The robot's dynamic gait pattern (A) on natural terrain (B) on flat terrain. (C) Dynamic gait pattern on flat terrain with injured forelimb. (D) On flat terrain with injured hindlimb. (E) On natural terrain with injured forelimb. (F) On natural terrain with injured hindlimb. The video of robot's performance can be seen in the link of [Video 2](#).

The signal from RG neurons will be transmitted to the PF neurons. PF neuron will generate spike activation for swinging action in certain leg. The spike signal of PF neurons (P_i) is calculated in the [Eq. 6](#), where the references signal (h_i^{ref}) is calculated in [Eq. 7](#), R is subtraction constant parameter, γ^{ref} is discount rate of h_i^{ref} , and q is the spike threshold. We also provide a source code of the CPG model in the attached link of [Supplementary Material S3](#).

$$p_i(t) = \begin{cases} 1 & \text{if } (y_i + h_i^{ref}(t)) > q \\ 0 & \text{Otherwise} \end{cases} \quad (6)$$

$$h_i^{ref}(t) = \begin{cases} \gamma^{ref} \Delta h_i^{ref}(t-1) - R & \text{if } (P_i(t-1) = 1) \\ \gamma^{ref} \Delta h_i^{ref}(t-1) & \text{Otherwise} \end{cases} \quad (7)$$

$$PF_{i,k}(t) = e^{\left(c_1 \left(\frac{|P_{i,k}(t) - \mu|}{\mu \Delta w} \right)\right)}, P_{i,k}(t) = P_{i,k}(t) + p_i(t) \quad (8)$$

In the process, RG neurons have a rhythmic pattern signal and generate the spike signal to the PF neurons. The parameter $PF_{i,k}(t)$ in [Eq. 8](#) is the signal generated by k th of PF neuron in i th leg. It will activate the muscle stimulation explained in the previous research (Saputra et al., 2020b)(Saputra et al., 2020a). The output of the muscle

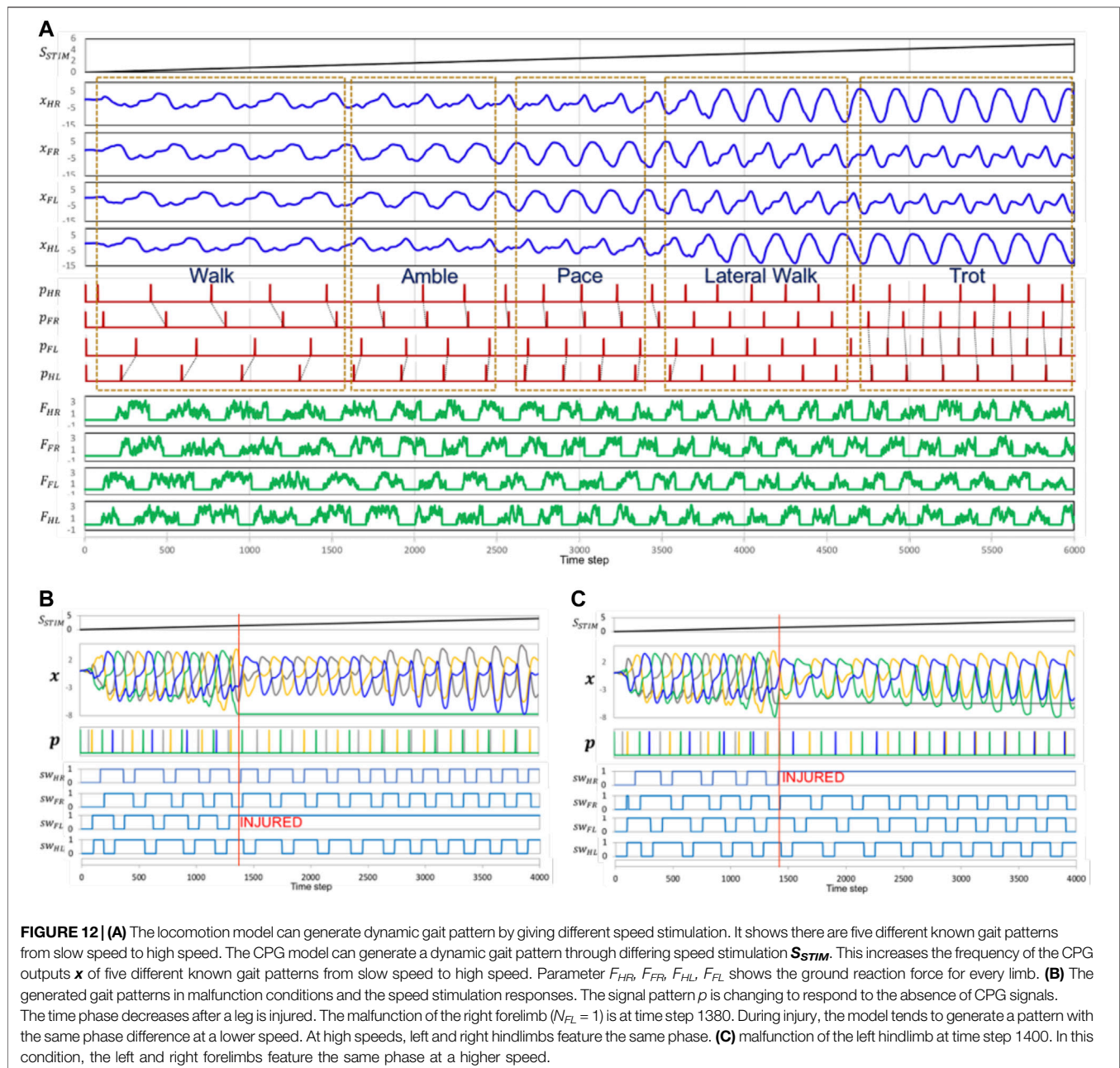
stimulation (S_i) will be converted to the direction the torque of servo actuator in the robot's leg. The connection information can be seen in the [Figure 10](#). Torque of one servo motor is driven by two muscle stimulation for different direction, flexor muscle stimulation is for CW direction and extensor stimulation is for CCW direction. Regarding to the [Figure 10](#), the total torque and the servo angular velocity are approached by [Eqs. 9 Eqs. 10](#), where (r) is the attachment length of muscle assumption, defined as 0.03 m.

$$\tau_{HIP}(t) = rS_1(t) + rS_2(t) \quad (9)$$

$$\dot{\theta}_{HIP}(t) = \dot{\theta}_{HIP}(t-1) + (S_1(t) - rS_2(t))/r \quad (10)$$

ROBOT IMPLEMENTATION

In order to test and demonstrate the robot's capabilities, we had the robot move across natural terrain, walk with a leg malfunction, avoid a sudden obstacle while walking, and climb on a vertical ladder. The optimization process of CPG model and muscle activation function can be seen in



our previous papers (Saputra et al., 2020b)(Saputra et al., 2020a).

Moving on Natural Terrain

We trialed the robot on natural terrain (grassed soil with varying slope) and flat terrain (a carpeted floor). The robot's gait pattern was controlled using the proposed neural-network locomotion generator. The optimized parameter of CPG model as pattern generation can be seen in **Table 6**.

Sample snapshots of the robot's performance can be seen in **Figures 11A,B**. We set S_{STIM} from zero and gradually increase along the value of time step ($S_{STIM} = \text{time step}/1200$). The

result can be seen in **Figure 12A**. The CPG model can generate dynamic gait pattern. The robot can produce dynamic gait patterns to walk, amble, pace and trot successfully across both terrains.

Moving With a Leg Malfunction

We tested the robot in two conditions: 1) with an injured forelimb, and 2) with an injured hindlimb. Both tests began with the robot in normal gait. After a few seconds, we set one of the legs to its 'injured' state. In this case the locomotion model cannot generate signal to the injured leg. However, the torque force of the leg is still active. In both tests, the robot responded by appropriately transitioning its without falling down. These tests were conducted on both artificial and

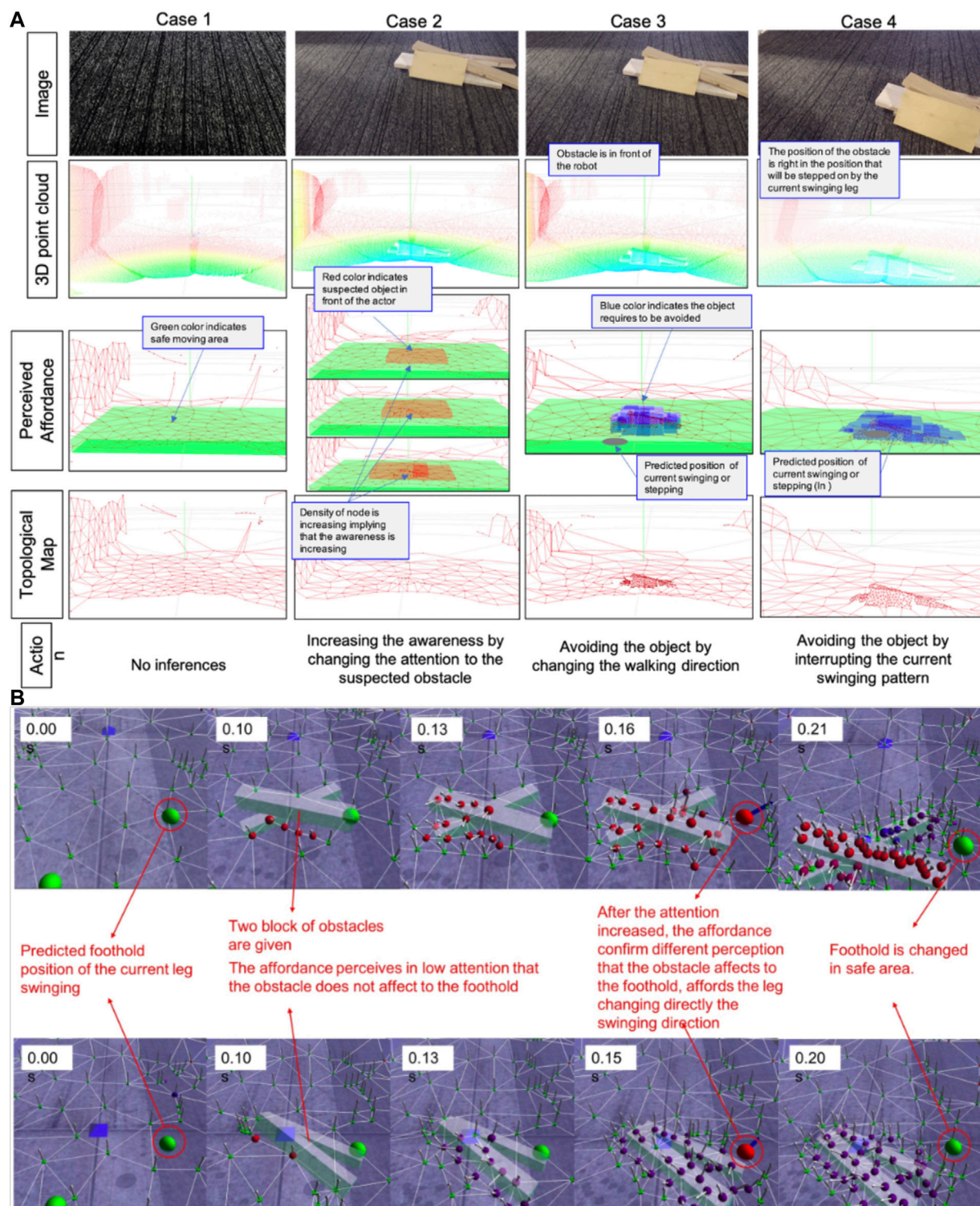


FIGURE 13 | (A) The result of different condition perception in different levels of data (3D point-cloud being the raw data from the depth sensors, topological map structure represent the attention model, perceived affordance, and generated action) **(B)** The snapshots show the integration between affordance and attention in computer simulation.

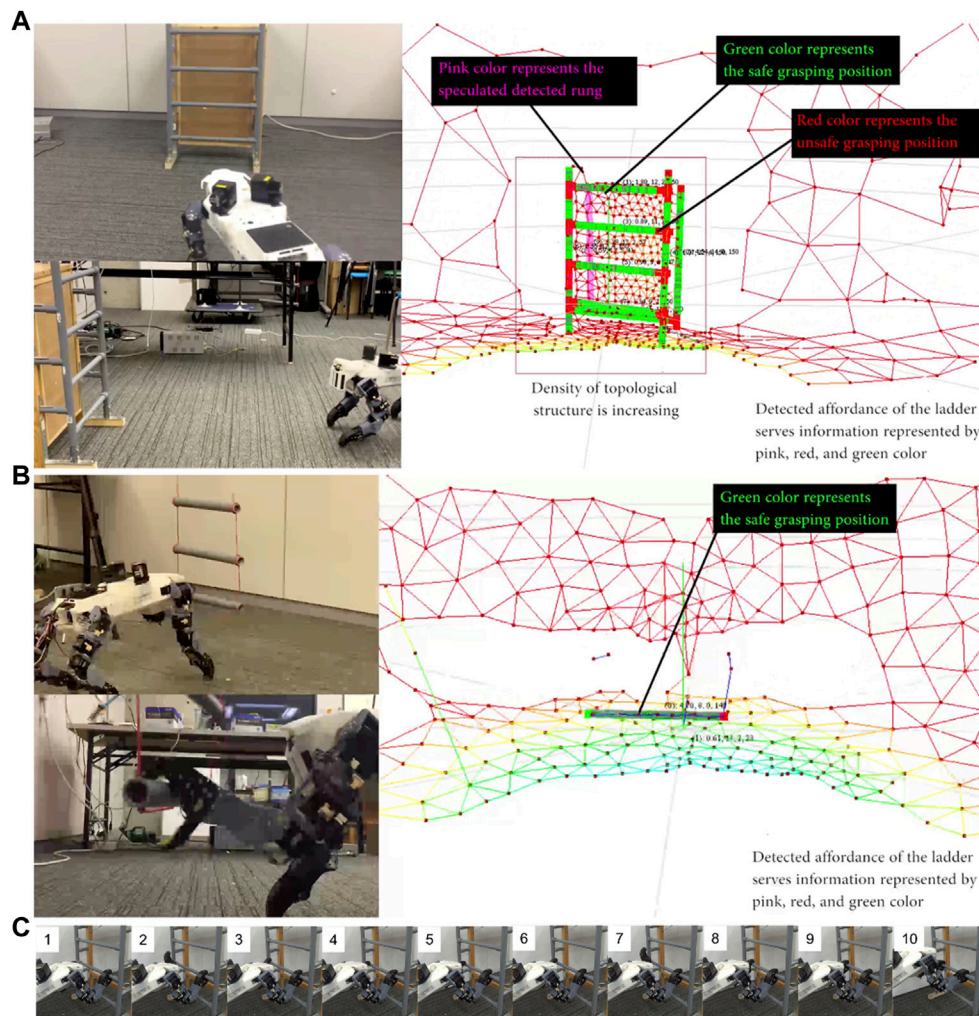


FIGURE 14 | (A) The robot detects the ladder's affordances while approaching it. **(B)** Robot detects graspability of a swinging ladder and grasps a rung of the moving ladder. **(C)** The snapshot video of the robot performance detailed in the link of **Video 5**. The robot approaches and climbs a ladder, then transitions back to a horizontal posture to stand on the tabletop (frames 9 – 10).

natural terrain. Snapshots of the robot's performance can be seen in **Figures 11C–F**. The corresponding video can be seen in the link of **Video 2**. Furthermore, the movement transition when leg got injured can be analyzed in **Figures 12B,C**.

Avoiding a Sudden Obstacle While Moving

In this trial, we set the robot to travel straight ahead. Once it was moving, we suddenly put a few small pieces of woods in front of the robot's front leg. This experiment tested how effectively the locomotion generator could produce short-term adaptations in response to external sensory information. The affordance process perceived the object before the robot took any action. The four columns in **Figure 13A** show affordance perception and adaptation in progress. An increase in map density (case 3) corresponds to the obstacle's location. The robot performance avoiding

sudden obstacle dropped into its path can be seen in the link of **Video 3**.

In order to show the integration of affordance and attention in robot locomotion, we first analyze the attention and affordance result in simulation, as shown in this link **Video 6** and **Figure 13B**. Simulation proved that the degree of attention may affect the accuracy of affordance detection. The topological structure (nodes and edges) represent the attentional model. The green ball represents the predicted foothold position for the current swinging movement. We suddenly put an obstacle around that intended foothold position 0.1 s after the leg starts swinging. A few nodes appear with non-homogeneous normal vectors (red color's nodes), meaning that the affordance detector has perceived some sudden obstacle with low accuracy. In this condition, the affordance system asks the attention process to focus on the obstacle. Then, the

red-colored nodes promptly generate new nodes. After 0.11 S, the number of nodes has greatly increased around the obstacle, showing that the affordance detector has perceived the obstacle with high accuracy. The robot is then directed to change its swing to a safe area (green nodes).

Climbing on Vertical Ladder

Before setting a climbing task, we tested the robot's ability to detect and interpret a vertical ladder detection using an inlier-outlier method. Affordance detection, in this case, is directed toward finding feasibly graspable locations. The detail affordance detection is explained in the (Saputra et al., 2019b). **Figure 14A** shows the robot detecting and tracking the ladder structure in real time, identifying which parts it can safely grasp. The detail video can be seen in the link of **Video 4**.

The robot's next task is to walk to the ladder and climb up it onto a higher floor, all without handrail support. This task entails transitions from horizontal motion to vertical motion, and then from vertical motion to horizontal motion. To tackle this problem, we propose an additional behavior generation model using independent stepping and pose control in the robot. Posture, safe movement areas, possible touch points, graspability, and target movement all need to be determined from the robot's sensors. As noted in our earlier research, four kinds of behavior are required: approaching, body-placing, stepping, and grasping (Saputra et al., 2019c). The proposed model was first optimized through simulation. The robot, in turn, successfully moved from the lower level to the upper level, negotiating the ladder between them (**Figure 14C**). The video of the robot performance climbing the vertical ladder can be seen in the link of **Video 5**.

CONCLUSION AND FUTURE PLANS

We developed a robot inspired by domestic feline morphology. The main contribution of the proposed robot is finding some benefit of biological morphology for robotics to tackle unsolved terrain. We imitate the morphology of the Cat animal in the robot structure and the paw mechanism. In the sensory system, we design the novel structure of 3D point cloud sensors for improving the efficiency. Then, the robot is built to show some novel bio-inspired model. The robot responds to both internal and external sensory information, processing the sensory input through several bio-inspired novel capabilities that enable the robot's motion through complicated terrains. The robot, though built on a low-cost budget (estimated as 12,000 USD), has been successfully trialed in several environmental conditions. The locomotion model of the robot can generate a dynamic gait pattern by stimulated only one single speed parameter. There are five patterns generated in the robot performance, walk, amble, pace, symmetrical walk, and trot gait. There are, however, still some practical problems still to be solved. Our continuing research will focus on these three areas:

- Improving stability: We will improve the robot's use of its inertial sensor data in manipulating the current stability model.
- Soften footfall: the robot's step is currently heavy. We will add a damper mechanism to soften footfall, inspired by feline leg structure.
- Improving durability: the robot needs to run for longer. This may be achieved by increasing battery capacity and body efficiency, for example by decreasing the robot's weight.
- Advanced terrain handling: further experimentation is required to develop the robot's performance in more complex environments. We will design and build an artificial ruin in which to develop and test the robot.

LINK TO ONLINE VIDEO

- (1) Video 1: <https://youtu.be/9MEojC5SjdA> Shows 3D point clouds data generated by Quad ToF sensor, Comparison of the proposed dynamic density topological generator with other model, The proposed model can specified the density in the obstacle area automatically.
- (2) Video 2: <https://youtu.be/4NeW1u3OfFo> Shows the robot performance in natural and rough terrain, dynamic gait transition in different speed, and robot's performance during malfunction condition.
- (3) Video 3: <https://youtu.be/TYACHd9G88E> Shows the Robot Performance Avoiding Sudden Obstacle While Moving
- (4) Video 4: <https://youtu.be/4sZH1vKzNp0> Shows the performance of real time vertical ladder affordance detection while approaching the ladder and performance of moving ladder affordance detection.
- (5) Video 5: https://youtu.be/Y_lmzQf-3Lk Shows the novel capabilities of the robot moving through the vertical ladder without handrail support.
- (6) Video 6: <https://youtu.be/hfL9vE847Es> Shows the integration between affordance and attention in computer simulation.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

AS, NT, KW contributed to design and development of mechanical and electrical hardware. AS and NK contributed to cognitive model development. AS and AJ contributed to neural-based robot controller. All authors contributed to writing and refining the manuscript.

FUNDING

This work was partially supported by a Grant-in-Aid for Scientific Research (18J21284) from Japan Society for the Promotion of Science.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frobt.2021.562524/full#supplementary-material>.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Effect of Thoracic Connective Lesion on Inter-Leg Coordination in Freely Walking Stick Insects

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Edited by:

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University of Palermo, Italy

Reviewed by:

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University of Porto, Portugal
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Specialty section:

This article was submitted to
Biomechanics,
a section of the journal
Frontiers in Bioengineering and
Biotechnology

Received: 19 November 2020

Accepted: 17 March 2021

Published: 20 April 2021

Citation:

Niemeier M, Jeschke M and
Dürr V (2021) Effect of Thoracic
Connective Lesion on Inter-Leg
Coordination in Freely Walking Stick
Insects.
Front. Bioeng. Biotechnol. 9:628998.
doi: 10.3389/fbioe.2021.628998

Multi-legged locomotion requires appropriate coordination of all legs with coincident ground contact. Whereas behaviourally derived coordination rules can adequately describe many aspects of inter-leg coordination, the neural mechanisms underlying these rules are still not entirely clear. The fact that inter-leg coordination is strongly affected by cut thoracic connectives in tethered walking insects, shows that neural information exchange among legs is important. As yet, recent studies have shown that load transfer among legs can contribute to inter-leg coordination through mechanical coupling alone, i.e., without neural information exchange among legs. Since naturalistic load transfer among legs works only in freely walking animals but not in tethered animals, we tested the hypothesis that connective lesions have less strong effects if mechanical coupling through load transfer among legs is possible. To do so, we recorded protraction/retraction angles of all legs in unrestrained walking stick insects that either had one thoracic connective cut or had undergone a corresponding sham operation. In lesioned animals, either a pro-to-mesothorax or a meso-to-metathorax connective was cut. Overall, our results on temporal coordination were similar to published reports on tethered walking animals, in that the phase relationship of the legs immediately adjacent to the lesion was much less precise, although the effect on mean phase was relatively weak or absent. Lesioned animals could walk at the same speed as the control group, though with a significant sideward bias toward the intact side. Detailed comparison of lesion effects in free-walking and supported animals reveal that the strongest differences concern the spatial coordination among legs. In free walking, lesioned animals, touch-down and lift-off positions shifted significantly in almost all legs, including legs of the intact body side. We conclude that insects with disrupted neural information transfer through one connective adjust to this disruption differently if they experience naturalistic load distribution. While mechanical load transfer cannot compensate for lesion-induced effects on temporal inter-leg coordination, several compensatory changes in spatial coordination occur only if animals carry their own weight.

Keywords: walking, leg coordination, locomotion, neural coupling, load transfer

INTRODUCTION

Adaptive, coordinated walking requires appropriate and simultaneous control of multiple legs (e.g., Graham, 1985; Dürr et al., 2018; Ritzmann and Zill, 2019). While it is clear that the interplay of rhythmic movements of all legs is monitored and controlled by neuronal circuits and proprioceptive systems (Tuthill and Wilson, 2016), neurophysiological and behavioural evidence on leg coordination support slightly different weighting of the relative importance of proprioceptive feedback in the generation of a gait.

Neurophysiological evidence from insects suggests that temporal patterning of activity in leg motor nerves arises from local neuronal networks of each leg, convened into central pattern generators (Bidaye et al., 2018), whose action can be adjusted by both intra- and inter-limb sensory feedback (Büschges, 2005). Accordingly, the gait originates from central neural network dynamics that is adjusted by proprioceptive input. In comparison, behavioural evidence, particularly from stick insects and crayfish, has been summarised in a set of coordination rules that describe the pairwise interaction between neighbouring legs (Cruse, 1990). In various software and hardware models of insect locomotion (e.g., Cruse et al., 1998; Dürr et al., 2019; Schilling and Cruse, 2020) these coordination rules have been implemented as sensory-motor feedback mechanisms. As the pairwise coupling through these feedback mechanisms dominates the execution of each step cycle, the gait does not originate from central neural network dynamics but emerges from distributed interaction of the body and its environment (Schilling et al., 2013). While this allows for several aspects of behavioural flexibility through de-centralised inter-leg coordination (Dürr et al., 2018), the neuronal mechanisms that underlie pairwise inter-leg coupling are not entirely clear.

The present study aims to quantify the contribution of local, load-dependent sensory feedback in insect walking without ipsilateral neural coordination. Experiments on tethered walking stick insects showed that inter-leg coordination is strongly affected by cutting thoracic connectives. Following connective lesions, animals showed shifted touch-down and lift-off positions of the tarsi and temporally uncoordinated step cycles of neighbouring legs (Dean, 1989). This strongly suggested that neural information exchange among legs is important. However, as rhythmic movement persisted in the leg posterior to the lesion, the generation of a local step cycle was still possible without neural input from the anterior hemi-ganglion.

More recently, experiments on freely walking stick insects showed that step cycles of ipsilateral neighbouring legs can be coordinated due to mechanical coupling alone (Dallmann et al., 2017). This study suggests that load transfer among legs generates sensory information about unloading that can be registered by campaniform sensilla (Zill et al., 2004) which, in turn, drive local reflex circuits involved in inter-leg coordination. Similar sensorimotor mechanisms were also discussed in cockroaches (Pearson and Iles, 1973; Greene and Spirito, 1979; Zill et al., 2009). Since load transfer and the corresponding proprioceptive impact on leg movement must differ considerably between tethered and freely walking animals (at least if the tether

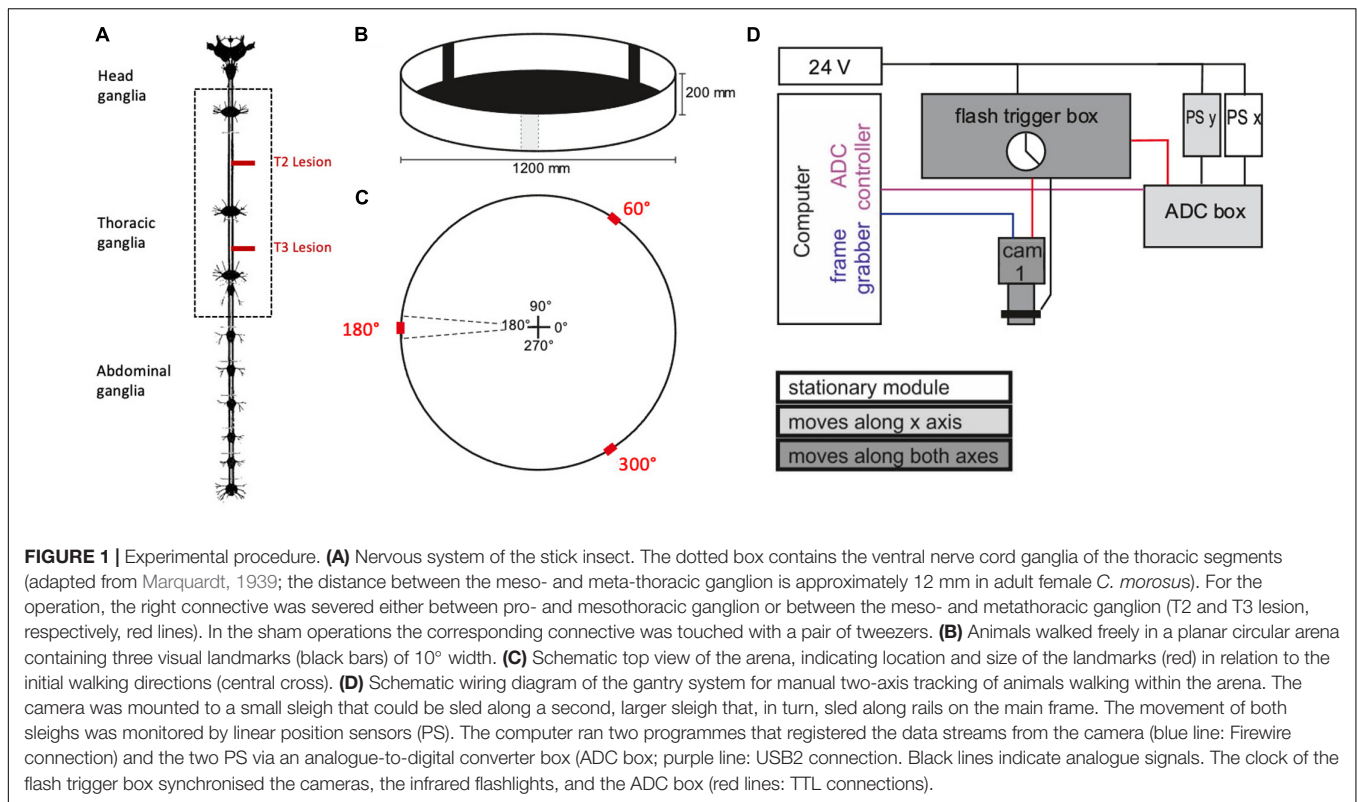
carries or supports the body weight), it is unknown to what extent the results of the connective lesion experiments by Dean (1989) hold for non-tethered walking animals. In contrast to animals in most tethered walking experiments, freely walking animals have to carry their own weight and, therefore, experience load transfer among legs. Moreover, interaction forces between body and substrate differ, not least during yaw rotation of the whole body. Here we investigate how these differences affect temporal and spatial inter-leg coordination in the absence of ipsilateral neural coupling by repeating Dean's connective lesion experiments in freely walking stick insects. To do so, we recorded protraction/retraction angles of all six thorax-coxa joints in the Indian stick insect *Carausius morosus* (de Sinéty, 1901) after cutting the right connective in the mesothorax or metathorax and compared them with those of animals that had undergone a corresponding sham operation. To ensure natural load transfer among legs, animals were recorded while walking freely across a plane horizontal arena, using marker-based motion capture. We show that stick insects can still walk at similar speed as sham-operated controls, although temporal coordination of legs adjacent to the lesion remains disturbed. Moreover, a detailed comparison of the effects of connective lesions between supported and free walking animals reveals that compensatory adjustments to disrupted neural information transfer concern mainly parameters of spatial coordination among legs, not temporal coordination.

MATERIALS AND METHODS

Animal Preparation

For this study, we used 20 adult, female stick insects of the species *Carausius morosus* (de Sinéty, 1901) from a laboratory colony bred at Bielefeld University. The animals were divided in two cohorts of 10 animals. From each cohort, five animals were assigned to a "treatment group," whereas the other five were assigned to a "sham group." Animals of the treatment group underwent an operation in which the right connective was severed between either the pro- and mesothoracic ganglion (Cohort 1) or between the meso- and metathoracic ganglion (Cohort 2). To do so, the animal was fixed on plasticine, ventral side up, and a small incision was made in the cuticula of the meso- or metasternum, using the splinter of razor blade. Then, both connectives were localised by gently moving the tracheae, and the right connective was slightly lifted and cut with fine scissors. Afterward, the incision was closed and sealed with beeswax. The animals of the sham group underwent a corresponding sham operation, in which the same incisions were made to the cuticula, and the connectives were touched gently with tweezers but not cut. Thus, each cohort had its own control group, making sure that any observed changes in locomotion were caused by the treatment, i.e., cutting the connective, and not by the operation itself.

For motion capture, the animals were marked with nine retroreflective markers ($\varnothing$ 1.5 mm, Prophysics, Zurich, Switzerland). Three of these marked the leg bases and were



placed on the dorsal thorax segments between the coxal bases. The other six marked the leg posture, and were placed on the distal, dorsal cuticle of each femur. Markers were fixed to the cuticle with clear nail polish. Marker positions on the body were photographed with a calibrated camera on a stereo lens (Olympus SZ61T with SC30 camera) at an accuracy of 0.1 mm.

Experimental Procedure

Experiments were carried out in a planar, circular arena (Ø 1,200 mm, height of margin: 200 mm) that was placed below a camera gantry (**Figure 1**). Before starting the experiment, the animals got a 10 min break for recovery after the operation. Afterwards, they were placed into the arena following a pseudo-random distribution of four cardinal starting directions within the arena (0°, 90°, 180°, 270°). The wall of the arena was illuminated from the outside with a set of eight projectors and a corresponding set of mirrors. As an incentive for walking, three black bars on a white background (width: 10°) were projected onto the arena rim at positions 60°, 180°, and 300°. These bars also served as visual landmarks (**Figure 1C**).

Prior to each recording the camera view was centred on a point that marked the middle of the arena. Once an animal had been placed onto this point, the video recording was started and the walking animal was followed by shifting the camera on the gantry. The recording was stopped as soon as the animals reached the rim of the arena or stopped walking.

In total, we acquired 69–89 trials per cohort, with each cohort contributing at least 6,200 step cycles to the data

set. The total number of trials and step cycles are listed in **Supplementary Table 1**.

Data Acquisition

For analysing the pro- and retraction movements, a zoomed-in top view of the walking stick insect was recorded by an infrared-sensitive digital video camera (Basler A602f-2, Basler AG, Ahrensburg, Germany) with a custom-built infrared LED flashlight for illumination and a manual zoom lens (Pentax H6Z810). The camera was mounted to the sled of a custom-made gantry (Item International, Solingen, Germany) with two horizontal movement axes. The camera position above the arena was recorded by two contact-free, linear position sensors (PMS-1-A-1000-K-2410, Megatron, Munich-Putzbrunn, Germany) placed on both axes of the gantry. The camera shutter, flashlight and camera position record were synchronised to via TTL pulses generated by a custom-built flash trigger box (Michael Dübber, Electronics workshop of Zoological Institute, University of Cologne; **Figure 1D**). The experimenter could manually move the camera along the two gantry axes, while observing the live image on a computer screen.

Videos were recorded with 50 frames per second at resolution of 480 × 640 pixels, and captured via Firewire (IEEE 1394) using a custom-written frame grabber software (Sven Hellbach and Peter Iseringhausen, Bielefeld University) that generated videos in AVI format, along with a separate text file with time stamps for individual frames. Camera position was recorded via USB using an analogue-to-digital converter (Data Translation DT9802, Data Translation GmbH, Bietigheim-Bissingen, Germany) that also

registered a binary camera exposure signal for later alignment of video and camera position data.

Data Analysis

Data analysis was done in MATLAB (The Mathworks, Natick, United States) using custom-written scripts and graphical user interfaces (GUIs). In a first step, the position records from the gantry system and the time stamps of the video recording software were aligned, yielding the 2D position time course of the camera. In a second step, the recorded videos were processed, yielding image positions of the nine markers for each video frame. To do so, markers were assigned and labelled manually in the first frame and then tracked semi-automatically using threshold-based clustering of marker pixels and a nearest-neighbour tracking algorithm. In a third step, the gantry position data, time stamps, and extracted marker coordinates were combined with calibration data for the camera projection and arena properties in separate files per trial.

These combined data files allowed calculation of both external, arena-centred information such as body orientation and velocity, and local, body-centred information about leg coordination. For the latter, positions were expressed relative to a “root marker” (in our case, the marker on the posterior metathorax) and aligned with the body axis. The resulting body-centred marker trajectories were used to calculate the time courses of protraction/retraction angles of all thorax-coxa joints. Protraction/retraction of a leg was defined as the angle between the line connecting the femoral and thoracic marker and the line perpendicular to the body axis. As a result, an angle of zero indicates that the femur was orthogonal to the body axis, and a positive angle indicates that the femur pointed forward. Extraction of local maxima and minima from protraction/retraction time courses yielded the times of movement reversals at the thorax-coxa joints. These served as estimates of the lift-off and touch-down events and thus, the onset/offset of stance and swing phases. Note that this definition of swing and stance phases is common in the literature (e.g., Wendler, 1964; Dean, 1989) but neglects small phase shifts between the protraction/retraction cycle of the thorax-coxa joint and the actual onset/offset of ground contact (e.g., Theunissen et al., 2015, see their Figure 9). Also, all positional step cycle parameters like step length, anterior and posterior extreme positions correspond to angles and will be given in degrees.

Body position and orientation within the arena were calculated by combining the camera position relative to the gantry and marker positions within each video frame. Forward and sideward translational velocities [mm/s] and yaw rotational velocity [deg./s] were calculated from the shift and rotation of the animal between subsequent frames and smoothed by use of a sliding median filter with a window of 60 ms (3 frames). For further information about data analysis and sample data, see **Supplementary Material**.

Because each one of the five animals per cohort contributed a lot of steps, the statistical analysis had to take into account the large but unbalanced samples per animal, for $n = 5$ independent samples per cohort. This was done in a two-step

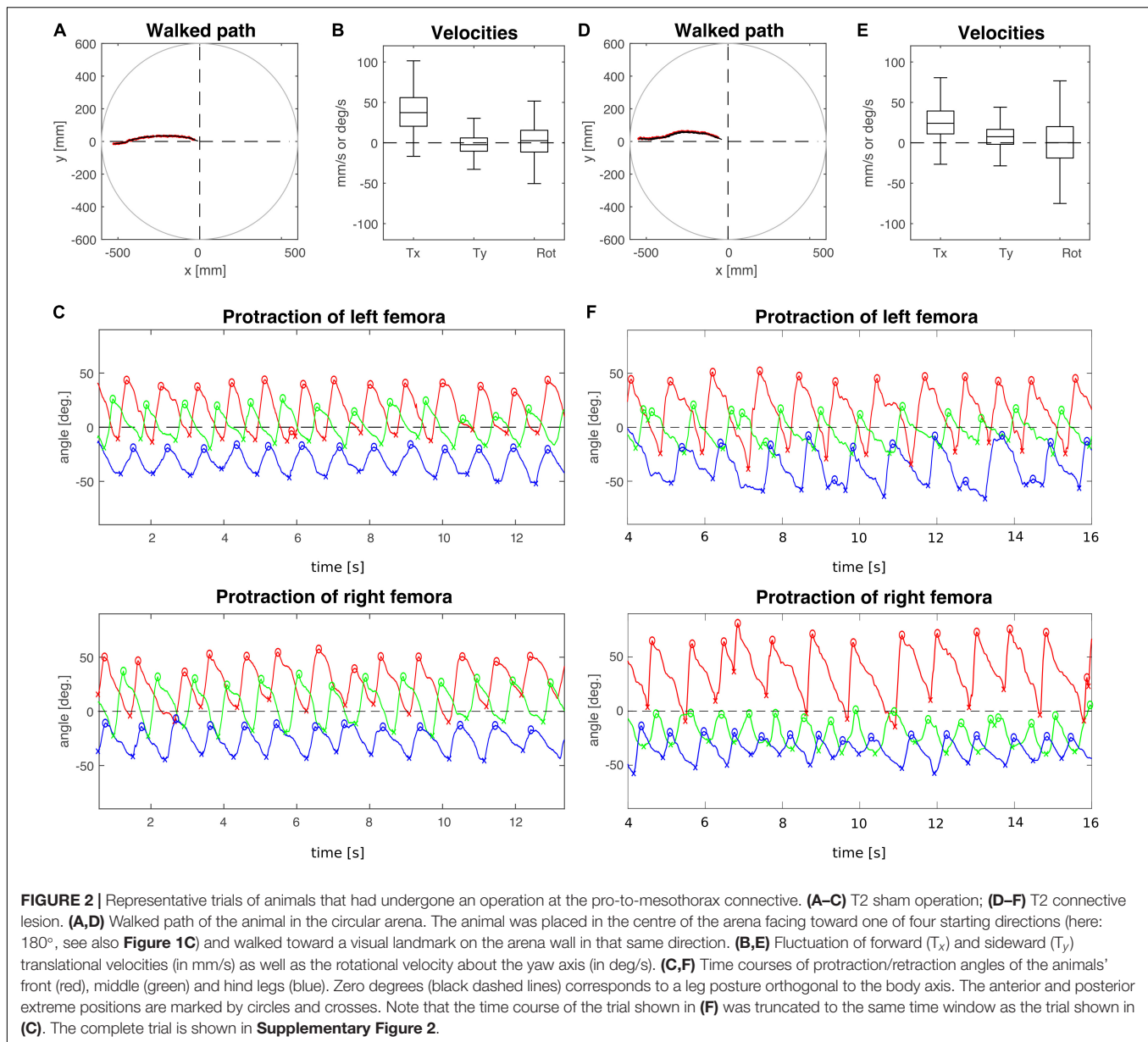
procedure by first re-sampling balanced pooled distributions with the original total sample size, and then bootstrapping the median and its 95 and 99% confidence intervals from 10,000 balanced samples. Statistical significance of pairwise comparisons was concluded whenever the 95% confidence intervals (95% CI) did not overlap ($p < 0.05$). The corresponding pairwise effect sizes were calculated as differences between cohort medians, divided by their mean 95% CI. Circular statistics on phase differences between step cycles were calculated on per-animal means, using the MATLAB toolbox CircStat (Berens, 2009).

RESULTS

General Observations

To analyse the effect of connective lesions on walking behaviour, we will first provide a general overview of the walking parameters of representative, single trials and later quantify the effects on both temporal and spatial parameters of inter-leg coordination across the different cohorts. **Figure 2** compares trials from animals with a lesion (T2 lesion) or sham operation (T2 sham) at the pro-to-mesothorax connective. Despite the fact that both animals walked a similar path, several aspects differed between the sham-operated and lesioned animal. First, the lesioned animal was slower and showed a leftward bias in sideward velocity (**Figures 2B,E**). Furthermore, the local minima and maxima of the protraction angles revealed pronounced shifts of several extreme positions and/or working ranges of the different legs (**Figures 2C,F**). Compared to the sham-operated animal, the left front and hind legs (intact side) of the lesioned animal took bigger steps by shifting their posterior extreme positions (PEP) to the rear. Also, the left hind leg extended the stance phase such that it tended to lift off later than the front leg (compare blue and red crosses at local minima in **Figure 2F**). On the right side (treatment side), the anterior extreme position (AEP) of the front leg is strongly shifted forward, resulting in much larger steps. Moreover, the working range of the right middle leg decreased and shifted rearwards.

In contrast, the animal with a lesioned right meso-to-metathorax connective shown in **Figure 3** (T3 lesion) was still capable of walking at a similar forward velocity as the sham-operated animal (T3 sham), but also revealed a bias in sideward translational velocity to the left (**Figures 3B,E**). The protraction angles of the legs show that the hind leg of the (right) treatment side executed only very small and seemingly uncoordinated protraction movements. Also, its working range was strongly shifted rearwards. At the same time, the opposite (intact side) hind leg showed a strongly increased step length, caused by a forward shift of the AEP and a rearward shift of the PEP. Also, this leg stayed retracted at nearly the same angle for some time before lift-off. This may indicate a further rearward shift of the foot by extension of the femur-tibia and/or depression of the coxa-trochanter joints which was not monitored. Compared to the sham-operated animal, the working ranges of the right front and middle legs of the lesioned animal were enlarged and shifted forward. The opposite



front and middle legs showed little to no change in their protraction/retraction time courses.

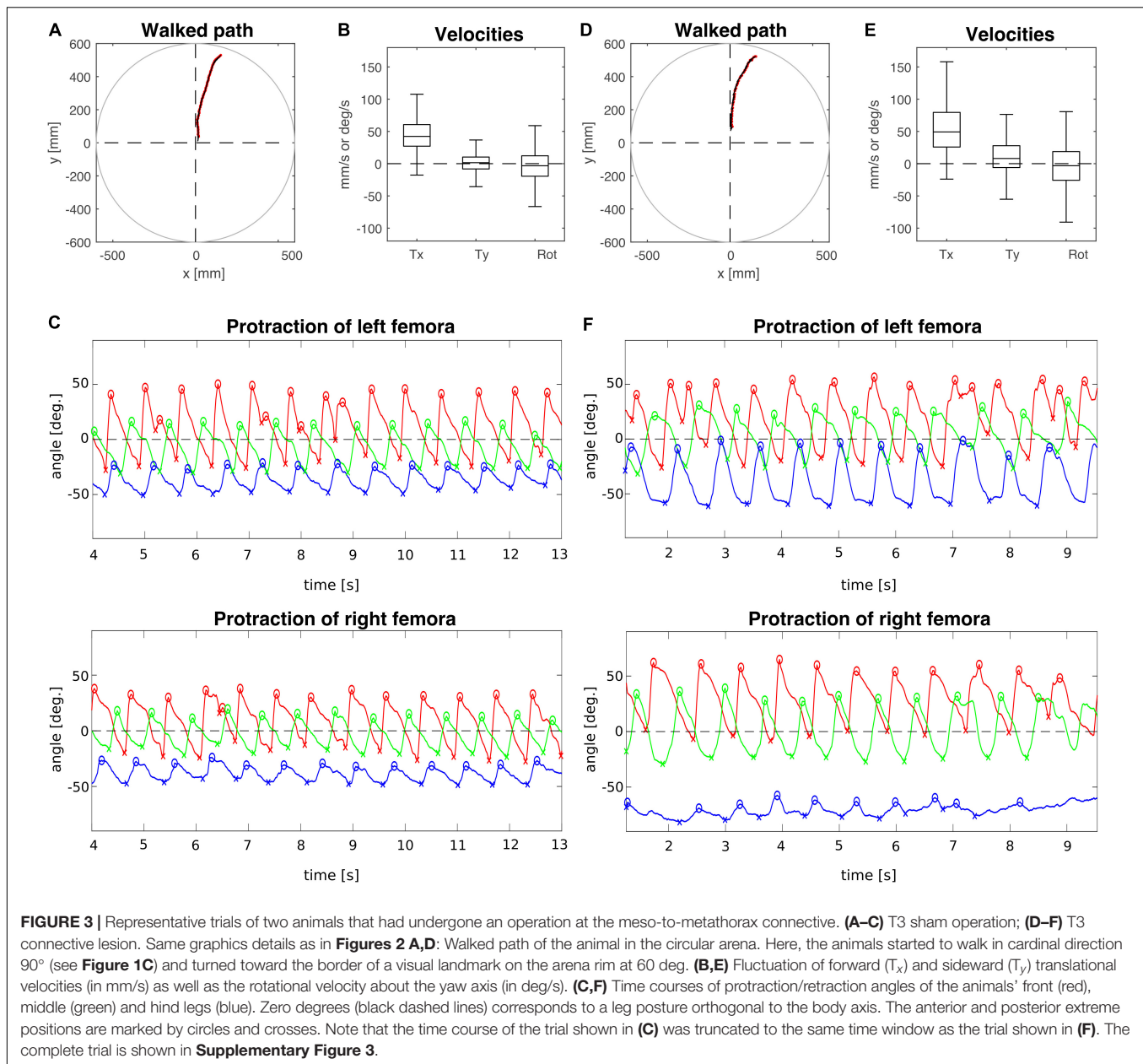
Taken together, these representative trials show that a number of effects were induced on the treatment side, but several adjustments concerned the opposite, intact body side, too. In the next sections, we examine the consistency of these lesion-induced differences across entire cohorts.

Effects on Velocity and Step Cycle Parameters

As animals were walking freely on a horizontal plane, we could determine all three degrees of freedom of motion in the plane and assess lesion-induced effects on both translational velocities (T_x : forward; T_y : sideward) and rotational velocity about the yaw axis.

Figure 4A shows that animals with a lesioned pro-to-mesothorax connective walked with significantly increased sideward velocity ($T_{y_{sham}} = -0.8$ mm/s, $T_{y_{lesion}} = 4.2$ mm/s, $p < 0.05$) and tended to walk slightly slower than sham-operated animals, but the latter difference was not statistically significant ($T_{x_{sham}} = 30.4$ mm/s, $T_{x_{lesion}} = 18.2$ mm/s, n.s.). Similarly, animals with a meso-to-metathorax connective lesion (**Figure 4B**) walked at a similar forward velocity as sham-operated animals ($T_{x_{sham}} = 36.2$ mm/s, $T_{x_{lesion}} = 31.1$ mm/s, n. s.). As for the other lesion, these animals walked at a significantly increased sideward velocity ($T_{y_{sham}} = 0.2$ mm/s, $T_{y_{lesion}} = 3.3$ mm/s, $p < 0.05$). Neither lesion resulted in a change of median yaw rotation.

Since these differences in velocity can be due to changes in the step length and step cycle period, we took a closer look at these parameters. **Figure 5A** shows that R1 and R2 legs of



animals with a lesion of the right pro-to-mesothorax connective, i.e., the legs immediately anterior and posterior to the lesion, had significantly longer step cycle periods than sham-operated animals ($R1_{sham} = 0.6$ s, $R1_{lesion} = 0.9$ s, $p < 0.01$; $R2_{sham} = 0.7$ s, $R2_{lesion} = 1.0$ s, $p < 0.01$). The step cycle period of all other legs showed no statistically significant differences. Following a lesion of the meso-to-metathorax connective lesion (**Figure 5B**), both hind legs (L3, R3) as well as the right front leg (R1) showed a significantly increased step cycle period after the lesion ($L3_{sham} = 0.7$ s, $L3_{lesion} = 0.8$ s, $p < 0.01$; $R3_{sham} = 0.7$ s, $R3_{lesion} = 0.8$ s, $p < 0.05$; $R1_{sham} = 0.5$ s, $R1_{lesion} = 0.7$ s, $p < 0.05$). Generally, lesioned animals showed a large variance in step cycle period (**Figure 5B**). For effect sizes see **Table 1** (T2 lesion) and **Table 2** (T3 lesion).

Other than step cycle period, step length was generally affected more, both in terms of effect size and in number of legs (**Figure 6**), corroborating the effects seen in the single trials shown in **Figures 2, 3**. After cutting the right pro-to-mesothorax connective, the leg posterior to the lesion took smaller steps ($R2_{sham} = 35.9$ deg., $R2_{lesion} = 25.7$ deg., $p < 0.01$) while the leg anterior to the lesion took larger steps ($R1_{sham} = 52.3$ deg., $R1_{lesion} = 61.2$ deg., $p < 0.05$). Furthermore, the contralateral hind and middle legs showed significantly increased step lengths ($L2_{sham} = 35.7$ deg., $L2_{lesion} = 40.3$ deg., $p < 0.01$; $L3_{sham} = 26.9$ deg., $L3_{lesion} = 40.1$ deg., $p < 0.01$). Similarly, animals with a lesioned meso-to-metathorax connective showed altered step lengths of the legs anterior and posterior to the lesion (**Figure 6B**). The right hind leg took significantly smaller steps

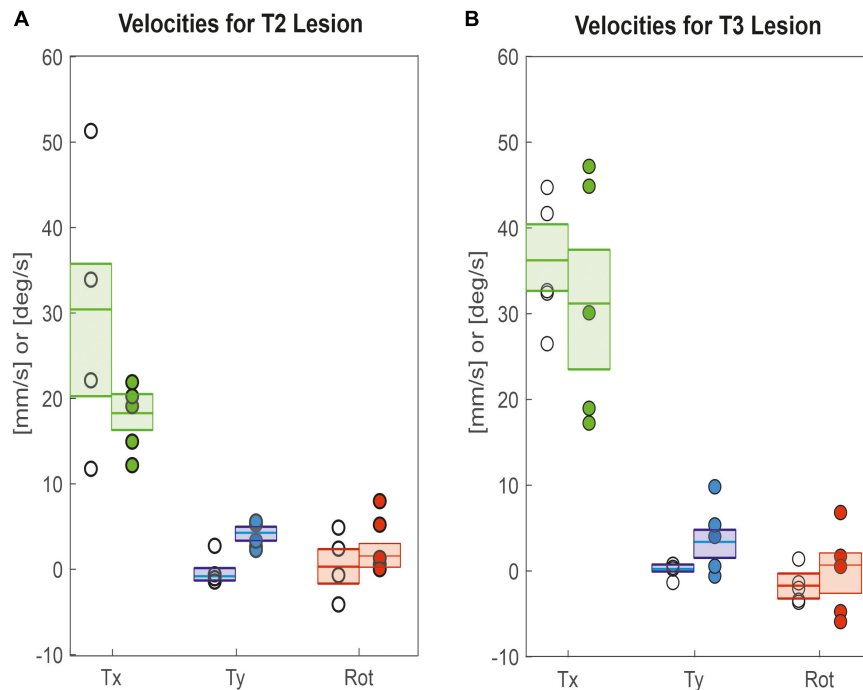


FIGURE 4 | Lesion effects on translational and rotational velocities. Tx: Forward translational velocity (green); Ty: Sideward translational velocity, with positive values indicating shifts to the left (blue); Rot: Rotational velocity, with positive values indicating ccw rotation (red). **(A)** Pro-to-mesothorax connective; **(B)** meso-to-metathorax connective. Symbols show median velocity per animal (lesion: filled circles; sham operation: open circles). Boxes comprise all trials of the cohort and show the median velocities and the bootstrapped 95% CI.

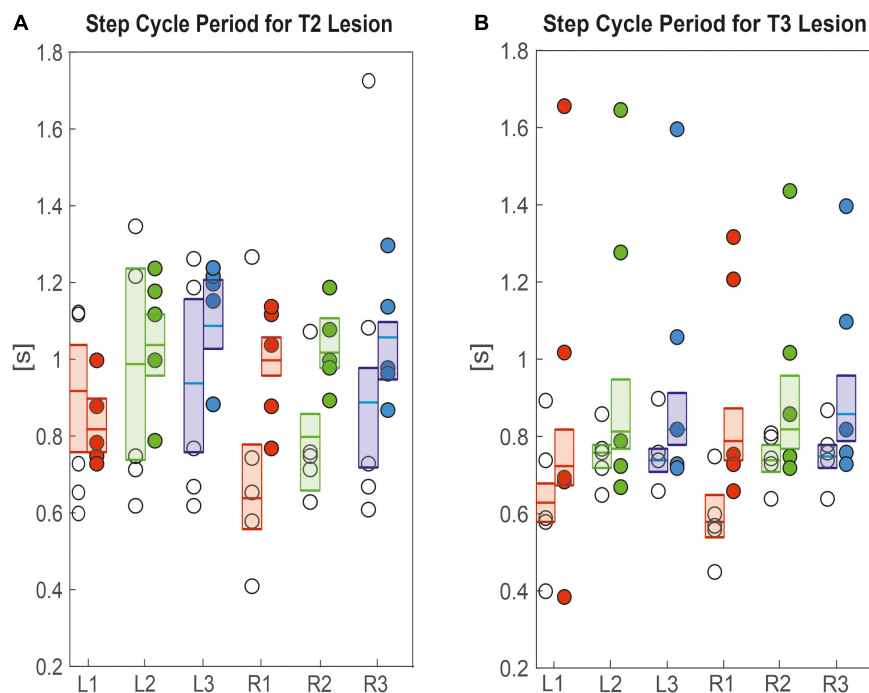


FIGURE 5 | Effects on step cycle period. **(A)** Pro-to-mesothorax connective; **(B)** meso-to-metathorax connective. Symbols show the median step cycle period per animal after lesion (filled circles) or a sham operation (open circles). Boxes comprise all trials of the cohort and show the median and the bootstrapped 95% CI.

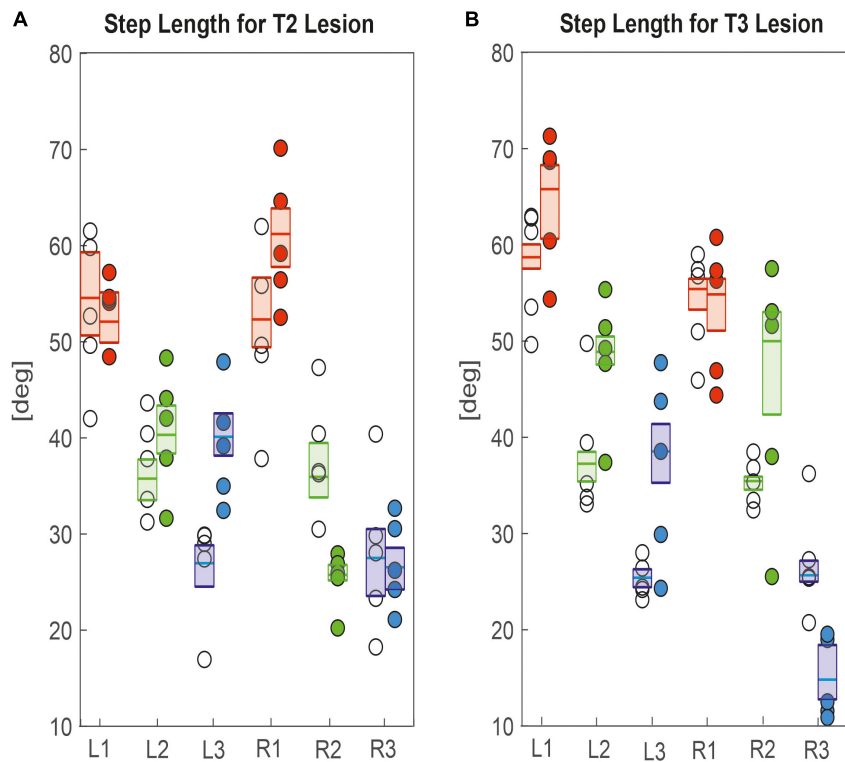


FIGURE 6 | Effects on step length. **(A)** Pro-to-mesothorax connective; **(B)** meso-to-metathorax connective. Symbols show median step length per animal with connective lesion (filled circles) or sham operation (open circles). Boxes comprise all trials of the cohort and show the median step length and the bootstrapped 95% CI.

($R3_{sham} = 25.6$ deg., $R3_{lesion} = 14.8$ deg., $p < 0.01$) while the middle leg took larger steps ($R2_{sham} = 35.4$ deg.; $R2_{lesion} = 49.9$ deg., $p < 0.01$). Moreover, all three contralateral legs took longer steps compared to sham-operated animals (for p -values and effect sizes see **Table 2**).

Taken together, the similar forward velocity with and without lesion of the pro-to-mesothorax connective was mirrored by fairly consistent step cycle periods in four of six legs, whereas the changes in step length overall larger and left only two leg unaffected (**Table 1**). Similarly, our finding that animals with a cut meso-to-metathorax connective could walk equally fast as sham-operated animals was mirrored by an overall weaker change in step cycle period (concerning three legs) and overall stronger and more wide-spread change in step length (concerning five legs).

Spatial Coordination

Given the leg-specific changes in step length, we further examined how these changes in step length related to forward or rearward shifts of the actual touch-down and lift-off positions. To this end **Figures 7, 8** show the protraction/retraction angles at the onset of swing or stance, which we interpret as equivalents of the anterior (AEP) and posterior extreme positions (PEP) of all legs. **Figure 7** shows the effect a cut pro-to-mesothorax connective. All six legs significantly shifted both AEP and PEP, though with strongly different effect sizes (**Table 1**). The strongest effect was

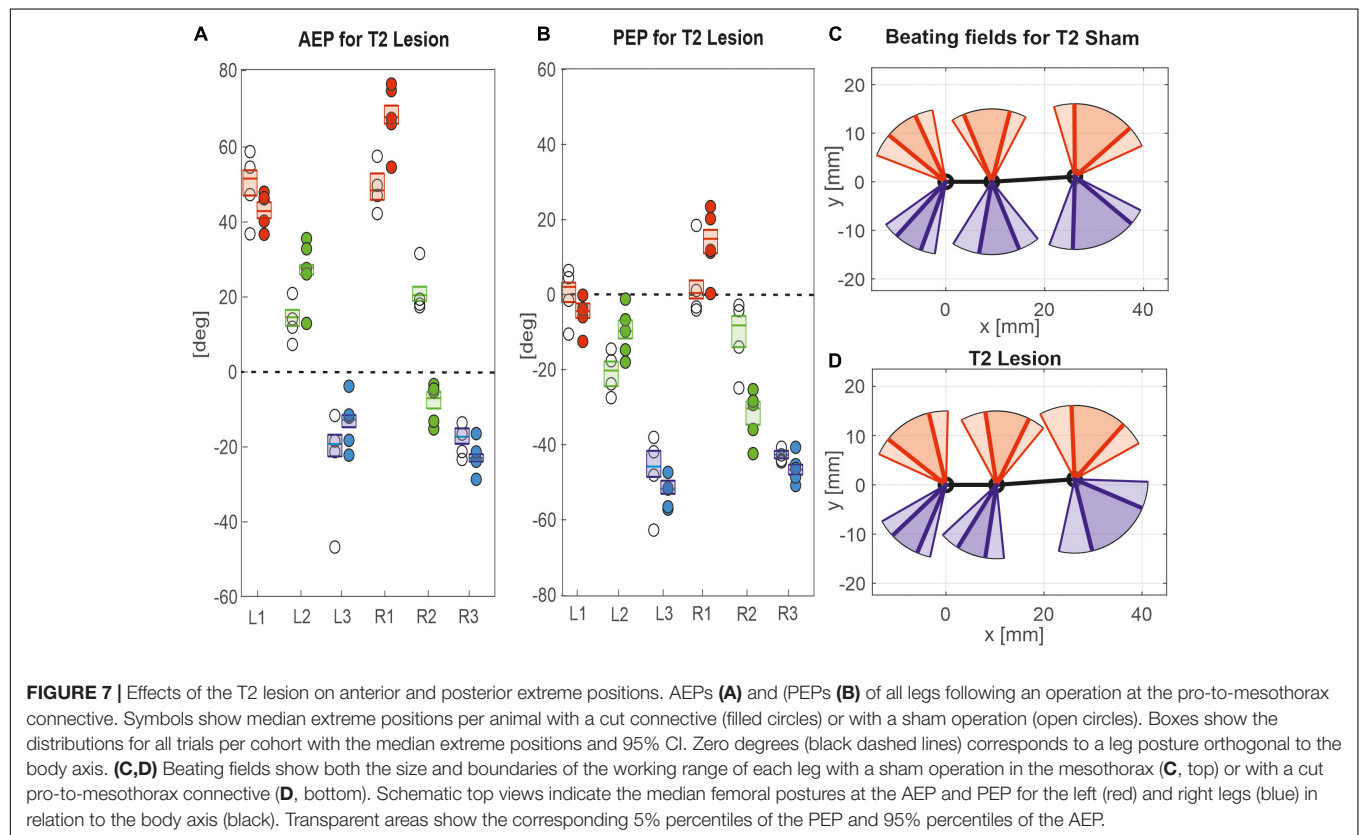
observed for the median AEP (**Figure 7A**) and PEP (**Figure 7B**) of the right middle leg, both of which strongly shifted to the rear compared to sham-operated animals ($R2$: $AEP_{lesion} = -6.9$ deg., $p < 0.01$; $PEP_{lesion} = -30.3$ deg., $p < 0.01$). Also, the working range of the right front leg shifted anteriorly by forward shifts of both the AEP and PEP ($R1$: $AEP_{lesion} = 67.9$ deg., $p < 0.01$; $PEP_{lesion} = 14.8$ deg., $p < 0.01$). Furthermore, the AEP of the contralateral hind leg also shifted forward ($L3$: $p < 0.05$), thus leading to the increase of step length observed in **Figure 6A**. Finally, both AEP and PEP of the contralateral middle leg shifted anteriorly ($L2$: $AEP_{lesion} = 27.7$ deg., $p < 0.01$; $PEP_{lesion} = -9.7$ deg., $p < 0.01$), resulting in a forward shift of the working range with a small change in step length only (compare beating fields in **Figures 7C,D**).

Similar to the results described above, a lesion of the meso-to-metathorax connective affected the touch-down and lift-off locations of most legs, again with very different effect sizes (**Table 2**). Again, effects were strongest anterior and posterior to the lesion (**Figure 8**). The median AEP and PEP of the right hind leg both shifted to the rear ($R3$: $AEP_{lesion} = -44.7$ deg., $p < 0.01$; $PEP_{lesion} = -62.9$ deg., $p < 0.01$), whereas the median AEP of the right middle leg strongly shifted forward ($R2$: $AEP_{lesion} = 27.1$ deg., $p < 0.01$) with no change of the PEP. As a consequence, the narrowed working range of the right hind leg revealed a strong rearward shift, whereas the broadened working range of the right middle leg shifted only little (compare **Figures 8C,D**). Of the legs

TABLE 1 | Summary of the changes in step parameters induced by a lesion of the pro-to-mesothorax connective.

T2 lesion	Lesion									Sham		
	Local changes						Bilateral asymmetry			Bilateral asymmetry		
	L1	L2	L3	R1	R2	R3	FL	ML	HL	FL	ML	HL
AEP	↓ 1.57	↑↑ 3.84	↑↑ 1.43	↑↑ 3.29	↓↓ 6.67	↓↓ 1.85	↑↑ 5.48	↓↓ 9.94	↓↓ 3.89		↑ 1.45	
PEP	↓ 1.42	↑↑ 1.83	↓ 1.14	↑↑ 2.6	↓↓ 3.05	↓↓ 1.73	↑↑ 3.81	↓↓ 3.75	↑ 1.67		↑↑ 1.61	
LENGTH		↑ 0.98	↑↑ 3.02	↑ 1.33	↓↓ 2.79		↑↑ 1.61	↓↓ 4.4	↓↓ 3.1			
DURATION				↑↑ 2.25	↑↑ 1.33		↑ 1.5			↓ 1.12		

The statistical significance and direction of the effect (arrows) as well as the effect size (numbers) are shown for local changes in single leg step cycles and bilateral leg pairs of lesioned and sham-operated animals. Arrows indicate the direction and significance level (one arrow: $p < 0.05$; two arrows: $p < 0.01$). Effect sizes more than twice the 95% CI are coloured in dark red, effect sizes larger than four times the 95% CI are coloured in bright red. Grey shading of local changes columns indicates the location of the lesion.



contralateral to the lesion, all legs showed a significant anterior shift of the AEP, while the effect on the PEP differed among legs: Whereas the PEP of the left middle leg shifted forward (i.e., in the same direction as the AEP), it shifted rearward in case of the left hind leg (i.e., in the opposite direction of the AEP) resulting in a strong increase in step length (compare beating fields of L3 in **Figures 8C,D**).

Taken together, these results show leg-specific, local shifts of both AEP and PEP, with particularly strong effects on the legs anterior and posterior to the lesion. The fact that all legs of the

intact (left) body side also underwent significant changes after lesion highlights the complex interplay of local adjustments in spatial coordination, potentially caused by direct effects of the lesion as well as by local compensatory effects on both body sides.

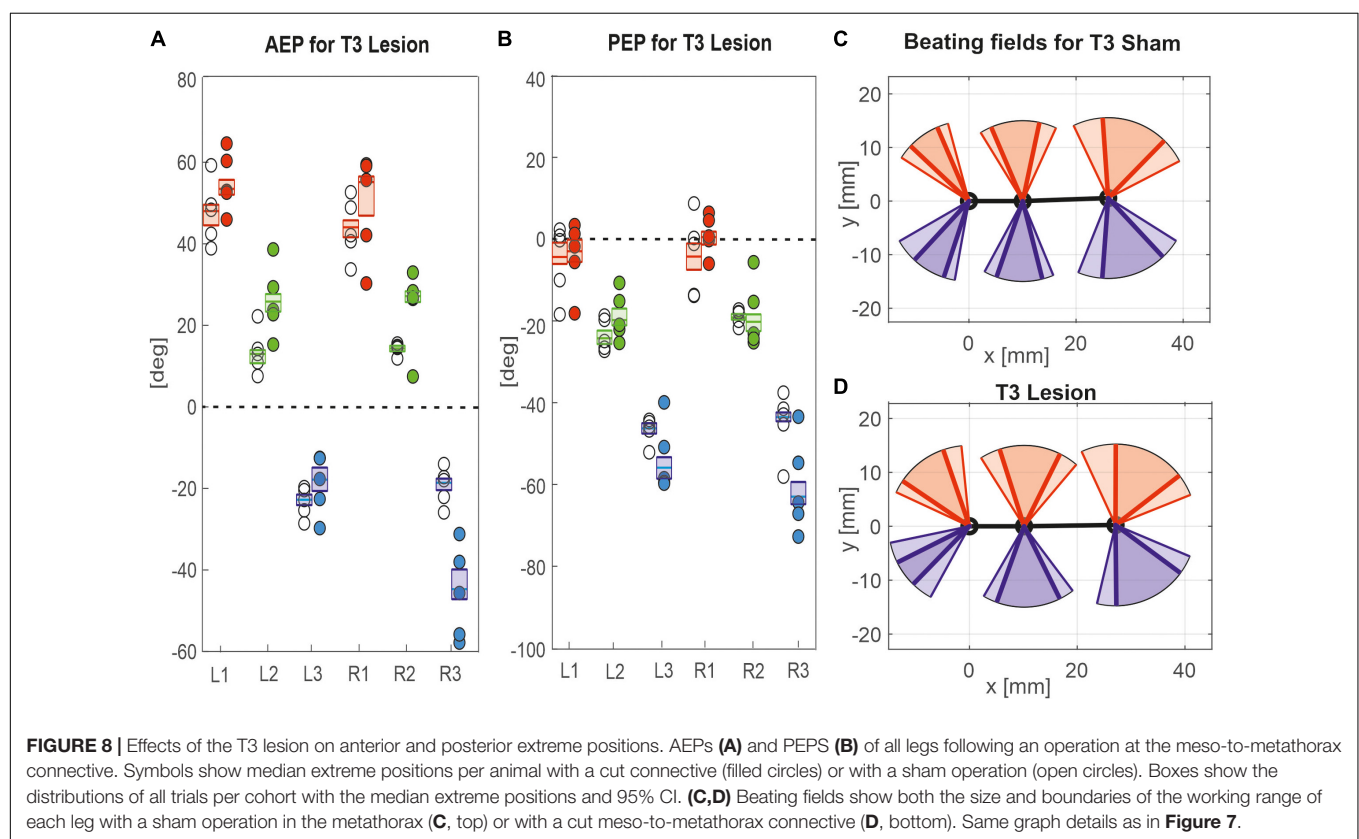
Temporal Coordination

Given the fact that the observed spatial adjustments were not equal across all legs, despite the fact that animals with connective lesions could walk along the same paths as sham-operated animals (**Figures 1, 2**), and even at a similar speed (**Figure 2**),

TABLE 2 | Summary of the changes in step parameters induced by a lesion of the meso-to-metathorax connective.

T3 lesion	Lesion									Sham		
	Local changes						Bilateral asymmetry			Bilateral asymmetry		
	L1	L2	L3	R1	R2	R3	FL	ML	HL	FL	ML	HL
AEP	↑↑ 1.25	↑↑ 3.41	↑ 1.18	↑ 1.61	↑↑ 6.37	↓↓ 5.15			↓↓ 4.11			↑↑ 1.53
PEP		↑ 1.19	↓↓ 2.46			↓↓ 5.12			↓ 1.32		↑ 2.17	↑ 1.16
LENGTH	↑ 1.38	↑↑ 3.86	↑↑ 3.29		↑↑ 2.41	↓↓ 2.76	↑↑ 1.67		↓↓ 4.03	↓↓ 1.14		
DURATION			↑ 0.8	↑↑ 1.68		↑ 0.95						

The statistical significance and direction of the effect (arrows) as well as the effect size (numbers) are shown for local changes in single leg step cycles and bilateral leg pairs of lesioned and sham-operated animals. Same details as in **Table 1**.



a major question was to find out which changes in temporal coordination kept walking sufficiently coherent. In particular, we were interested in potential changes in pairwise coupling of ipsilateral leg pairs according to Cruse's rule 2, i.e., the rule that a receiver leg commences a swing movement shortly after touch-down of its (posterior) neighbouring sender leg. Therefore, for each ipsilateral leg pair we registered the onset of a swing phase of the anterior (receiver) leg and related it to the step cycle of its posterior neighbour (sender leg). The same was done for contralateral leg pairs, expressing the phase of the onset of swing on the operated (right) body side relative to the step cycles of their

neighbours on the intact (left) body side. In all cases, the reference step cycle of the sender leg was defined as the interval between the two subsequent anterior extreme positions, i.e., touch-down events. This choice allowed us to interpret the phase shift in the context of Cruse's coordination rule 2, but also in relation to the unloading event due to load transfer from sender to receiver legs. The corresponding rose plots of **Figures 9, 10** show the mean phase shift per animal and the dispersion of the pooled distribution, the latter being a measure of coupling strength between leg pairs. All circular statistics reported below were calculated on per-animal means.

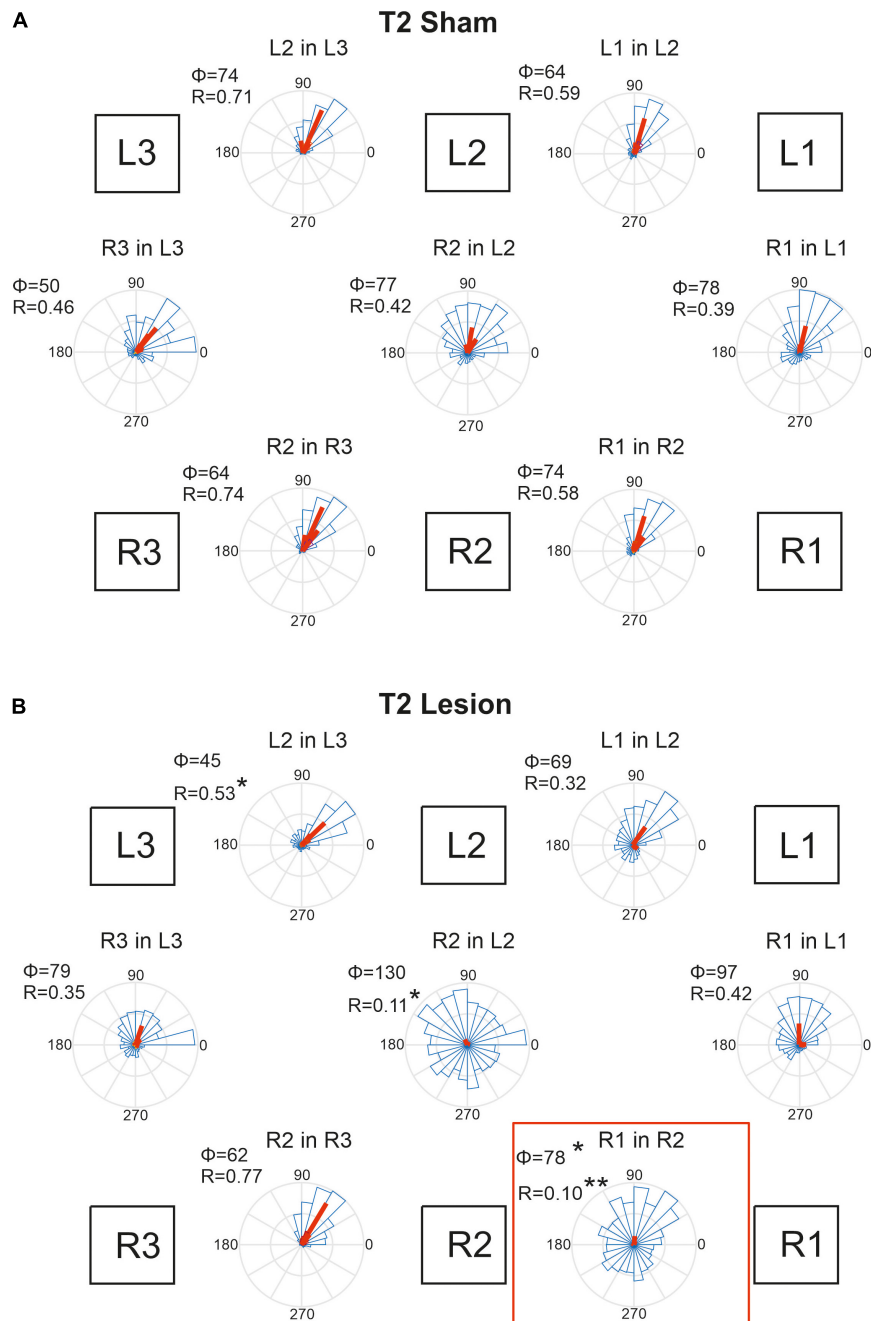


FIGURE 9 | Temporal coordination of step cycles after an operation in the mesothorax. **(A)** Sham-operated animals. **(B)** Animals with a lesion of the right pro-to-mesothorax connective (T2 lesion). Square boxes labelled L1–L3 and R1–R3 show the arrangement of the six legs. For each leg pair labelled “Leg1 in Leg 2”, rose plots show pooled distribution (blue) and per-animal mean phase shifts Φ (red) of the onset of swing by Leg 1 (receiver leg) in relation to the step cycle of (sender) Leg 2. Accordingly, $\Phi = 0$ indicates that L1 lifted off at the same time as L2 touched down. Circular histograms comprise all steps per cohort in 15 deg. bins. Statistics were calculated on per-animal mean phase vectors, with Φ and R giving the corresponding angle and length of that vector, respectively. Significance levels, * $p < 0.05$; ** $p < 0.01$.

Figure 9A shows that the phase shifts were very similar for all leg pairs in case of the T2 sham operation. Typically, the receiver leg lifted off in the late first quarter of the step cycle of the sender leg, with mean phase angles ranging between 50 and 78 deg. This coherent pattern of coordination was disrupted after

the lesion of the right pro-to-mesothorax connective (**Figure 9B**, T2 Lesion). After lesion, the right front leg started its swing phase without obvious coupling to the step cycle of the right middle leg. Although the mean phase shift changed only little compared to that of the sham-operated cohort (R1 in R2: $\phi_{sham} = 74$;

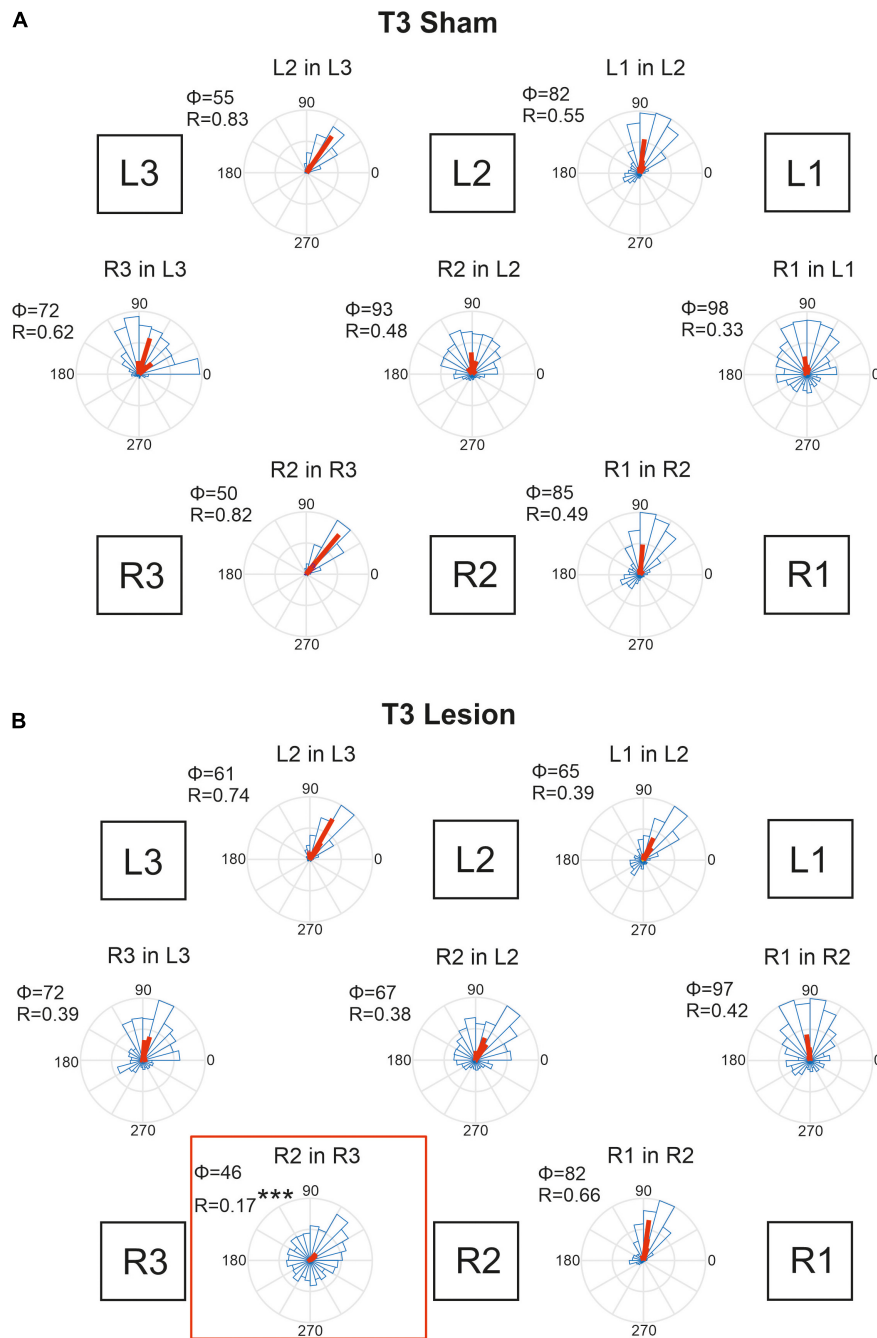


FIGURE 10 | Temporal coordination of step cycles after an operation in the metathorax. **(A)** Sham-operated animals. **(B)** Animals with a lesion of the right meso-to-metathorax connective (T3 lesion). Same graph details as for **Figure 9**. Significance level *** $p < 0.001$.

$\phi_{lesion} = 78$, $p < 0.05$, Watson-Williams test), we observed a strong increase in dispersion of phase and, as a result, decreased coupling strength (R1 in R2: $r_{sham} = 0.58$, $r_{lesion} = 0.10$, $p < 0.01$, Kuiper test). Both effects were statistically significant. Not only the temporal coordination of the ipsilateral leg pair adjacent to the lesion was affected, but also the contralateral coupling between the left and right middle legs: The right middle leg tended to start its swing movement later in the step cycle of the

left middle leg (R2 in L2: $\phi_{sham} = 77$, $\phi_{lesion} = 130$; n.s.), but the dispersion was similarly increased as for the ipsilateral leg pair (R2 in L2: $r_{sham} = 0.417$; $r_{lesion} = 0.11$, $p < 0.05$). Owing to the variation of per-animal mean phase, only the effect on dispersion was statistically significant. A further effect concerned the ipsilateral coupling of the hind and middle legs of the (left) intact body side, that showed a reduced mean phase angle (L2 in L3: $\phi_{sham} = 74$, $\phi_{lesion} = 45$, $p < 0.05$). Related to these changes

we observed a tendency for increased phase angles between contralateral front and hind leg pairs. Whereas the mean phase shift of these contralateral pairs was very similar to that of the left ipsilateral leg pairs in sham-operated animals (compare L2-in-L3 to R3-in-L3, and L1-in-L2 to R1-in-L1 in **Figure 9A**), there is a consistent increase of phase angle for all legs of the operated side with reference to their contralateral neighbours on the intact body side. Given the fact that the coordination of R2-in-R3 remained unaffected by the lesion, despite the weaker coupling of R2 and either L2 and R1, we suggest that the changes in contralateral coordination and ipsilateral coordination on the intact side are secondary effects. They could be a consequence of maintaining coherence among the six legs, with the primary lesion effects concerning R1-in-R2 and R2-in-L2.

Animals that had undergone a sham operation in the metathorax (**Figure 10A**) showed similar temporal coordination pattern as did the cohort with a sham operation in the mesothorax (**Figure 9A**). In all contralateral and ipsilateral leg pairs the receiver leg commenced swing with a phase lag between 50 and 98 deg, relative to touch-down of the sender leg. A small but notable difference between the T2 sham (**Figure 9A**) and T3 sham cohorts (**Figure 10A**) concerned the slightly larger mean phase shifts of the front legs (R1-in-R2 and L1-in-L2) compared to that of the middle legs (R2-in-R3 and L2-in-L3).

Figure 10B shows that the T3 lesion of the right meso-to-metathorax connective had a similar effect on the adjacent ipsilateral leg pair as described above for the T2 lesion cohort. After the lesion, the lift-off of the right middle leg was almost randomly distributed in the step cycle of the posterior right hind leg. Whereas the mean phase shift remained similar as in sham-operated animals, angular dispersion was very large, i.e., coupling strength was weak (R2 in R3: $\varphi_{sham} = 50$, $\varphi_{lesion} = 47$, n.s.; $r_{sham} = 0.82$; $r_{lesion} = 0.17$, $p < 0.001$). The phase relation between the contralateral hind legs, however, did not change after the lesion ($\varphi_{sham} = 72$, $\varphi_{lesion} = 72$, n.s.) and coupling strength decreased only slightly and non-significantly ($r_{sham} = 0.62$, $r_{lesion} = 0.39$, n.s.). A secondary effect involving the intact (left) legs and contralateral coupling was weaker than described for the T2 lesion above. As yet, we observed a slightly decreased phase angle for the contralateral pair of middle legs in **Figure 10B** (R2 in L2), but this change was statistically non-significant.

Taken together, these results show that connective lesions affected the temporal coordination of leg pairs only locally, i.e., not consistently among legs. After both types of lesion, the main effect concerned the leg posterior to the lesion, indicating that ipsilateral coupling is strongly affected by disruption of neuronal information transfer from anterior to posterior legs.

DISCUSSION

Coordination Rules, Load Transfer, and Motor Flexibility

Recent findings in cockroaches and stick insects revealed that mechanical transfer among ipsilateral legs can be sensed by campaniform sensilla at the base of the insect leg, and may contribute to maintain temporal coordination (cockroach: Zill

et al., 2009; stick insect: Dallmann et al., 2017) without involving intersegmental neurons. On the other hand, several studies have investigated the effect of thoracic connective lesions on inter-leg coordination (e.g., *Blatta*: Hughes, 1957; *Periplaneta*: Pearson and Iles, 1973; Greene and Spirito, 1979; *Carausius*: Dean, 1989), and all of them concluded that neural information transfer through thoracic connectives is important for temporal coordination of the adjacent, ipsilateral pair of legs. However, all analyses in the mentioned studies dealt with inter-leg coordination in tethered animals [some, with anecdotal remarks on free walking], and except for Greene and Spirito (1979); for method see Spirito and Mushrush, 1979] the animals were supported, thus altering the nature and reducing the magnitude of sensory feedback about load. Moreover, only the study of Dean (1989) has analysed the effect of connective lesions on spatial coordination among legs. Owing to the significance of spatial coordination for the resulting load distribution among legs and, therefore, for mechanical load transfer between legs (for examples in biology and biomimetics see Dallmann et al., 2017; Dürr et al., 2019, respectively), the aim of the present study was to assess the potential of mechanical load transfer in insect walking without neural coupling of ipsilateral leg pairs. To this end, we analysed both spatial and temporal inter-leg coordination of unrestrained walking stick insects with and without severed thoracic connectives.

A conceptual framework for behavioural analysis of inter-leg coordination has been established by Cruse and coworkers, who derived a set of inter-leg coordination rules (Cruse, 1990) that has set the stage for detailed experimental analysis (temporal coordination: e.g., Kindermann, 2002; Dürr, 2005; spatial coordination: e.g., Schumm and Cruse, 2006; Theunissen et al., 2014) and modelling (e.g., Espenschied et al., 1996; Cruse et al., 1998; Schilling and Cruse, 2020) of hexapedal locomotion. Cruse's rules describe interactions among adjacent leg controllers that depend on their current state (being either the thrust-generating stance phase or the re-positioning swing phase) and local mechanosensory information about posture, ground contact and/or load. Last not least, because of the different coupling strengths between different leg pairs (Dürr, 2005; Grabowska et al., 2012) and context-dependent modulation of coupling strengths (Dürr, 2005), Cruse's concept of how gaits and gait transitions emerge through distributed interaction of pairwise, mutually coupled leg controllers offers a valuable framework for understanding motor flexibility in general (for review, see Dürr et al., 2018).

With regard to load transfer among legs, Cruse's rules 1 and 2 are of particular interest, both of which operate from a posterior "sender leg" to its anterior "receiver leg." Rule 1 states that during swing phase the sender leg inhibits the start of a swing movement in the adjacent receiver leg. Rule 2 regulates the onset of a swing movement of the receiver leg depending on the onset of stance in the sender leg. In both cases, the crucial timing event is the touch-down of the sender leg that, by taking on load, induces mechanical load transfer from the receiver leg to the sender leg. To test whether Cruse's rules 1 and 2 require neural information transfer, Dean (1989) tested ipsilateral coupling of leg pairs after cutting thoracic connectives. His results showed that the coordination of the legs immediately adjacent to the lesion was

hampered significantly, leading to the conclusion that Cruse's rules 1 and 2 should be implemented by some sort of anteriorly directed neural information travelling through the ipsilateral connective. Although Dean's conclusions are perfectly valid for an experimental situation without mechanical load transfer, recent insights into the mechanisms underlying mechanical load transfer in insects (Zill et al., 2009; Dallmann et al., 2017) call for a re-investigation under naturalistic load distribution. To this end, we measured temporal and spatial coordination parameters of visually guided but mechanically unrestrained walking stick insects (*Carausius morosus*) in a planar arena after severing one thoracic connective.

To account for Hughes' warning that "in any experiment involving operations such as these it is often difficult to distinguish the effects produced by the specific operation from those resulting from the general injury" (Hughes, 1957, p. 323) we designed the study to compare lesioned animals with animals that underwent a corresponding sham operation (other than Dean, 1989, who conducted a "before-after" study). A potential limitation of our experimental design concerns our decision to opt for a relatively small number of individuals ($N = 5$ per cohort) with the benefit of having many step cycles per animal and reliable estimates of per-animal means. To improve comparability with Dean's results, we did not differentiate between distinct classes of step types (Theunissen and Dürr, 2013). Although short steps are known to be relatively infrequent in planar walking, it is worth to bear in mind that neglecting them would have mainly concerned observations on front legs, where short steps are most frequent. Finally, to account for the fact that insects are known to adjust to connective lesions (Greene and Spirito, 1979) or genetic manipulation of mechanoreceptive input (Isakov et al., 2016) over time, we focussed on immediate effects of the lesion only (as opposed to long-term effects that, in cockroaches, establish over a period of about 3 weeks; Greene and Spirito, 1979).

As a further methodological note, it is useful to bear in mind the differences in data acquisition by Dean (1989) and us: Dean's optical recording system measured the tangent of the protraction/retraction angle, rather the leg angle itself, as reported here. This makes it difficult to compare effect sizes, as both angle and dispersion estimates by Dean (1989) were subject to a non-linear transformation.

Under Load, Connective Lesions Affect Spatial Coordination More Widely and Strongly Than Temporal Coordination

In a qualitative description of the effects of a T2 lesion in free walking stick insects, Dean (1989) noted that "the ipsilateral middle leg usually remained in a posterior position, where it was dragged over the ground. Because the ipsilateral front and rear legs together provide sufficient support for the animal during their common stance, the middle leg was sometimes able to make long, slow swing movements" (Dean, 1989, p. 116). This turned out quite differently in our experiments, as the middle leg posterior to the lesion regularly engaged in rhythmic movements, albeit with an altered working range (see **Figure 2**).

Qualitatively, Dean's observation that in tethered animals a connective lesion strongly affected the legs immediately adjacent to the lesion, with multiple other, often minor effects, was the same in our free walking animals. However, the results differed quite strongly when comparing some details, even for the adjacent leg pair. For example, Dean (1989) found after a T2 lesion that "the mean AEP and PEP of the ipsilateral [...] middle leg, showed little change but their standard deviations increased" (p. 116). Comparing his Table 4 with our **Table 1** reveals that in free walking, the effects on that middle leg were among the strongest found in free walking animals (the rearward shift of the AEP was more than six times the 95% CI). In case of the PEP, shifts even were of opposite sign: We found a strong rearward shift, Dean found a slight forward shift. At the same time, we did not find a consistent increase of the 95% CI, which is in contradiction with Dean's observation of increased spread after lesion. Related to these differences, Dean (1989) reported that after a T2 lesion the middle leg frequently showed unusually long swing movements and "often stepped onto the tibia or femur of the front leg" (p. 116), an observation that we cannot confirm for unrestrained walking stick insects. This difference may have to do with the pattern of more distributed and overall stronger changes in spatial coordination after T2 lesion as reported here. For example, the strong, opposite effects on the working ranges of the ipsilateral front and middle legs (our **Figure 7**) would have greatly reduced the likelihood of an overstepping middle leg. This is in line with the fact that increased overstepping in Dean's animals was accompanied by much less divergence of the front and middle leg working ranges.

Moreover, we found strong anterior shifts of the entire working range of the contralateral middle leg (**Figure 7D**) and an increased step length in both the contralateral middle and hind legs (**Table 1**). Both of these effects occurred on the intact body side, where Dean (1989) reported effects with opposite shift directions for the contralateral middle leg AEP and PEP, as well as the hind leg AEP (rearward shifts for Dean, his Table 4; forward shifts for us, our **Table 1**). Assuming that the single major difference between Dean's and our experimental design concerned the load distribution and load transfer among legs, we propose that the load distribution experienced by the animal substantially affects adjustments in spatial inter-leg coordination. To some extent, this also concerned the temporal coordination, as Dean (1989) did not report a significant change in temporal coordination of the legs on the intact body side. In contrast, we did find significant adjustment in the coupling of the contralateral hind and middle legs (L2 in L3, **Figure 9**).

Dean (1989) himself noted quite different effects of a T3 lesion in supported and free walking stick insects. His qualitative observations on free walking animals were that "the most obvious effect [...] was an apparent weakness in the rear leg, an inability to make a strong swing movement. [...] The ipsilateral rear leg spent much of its time extended near its posterior extreme position (PEP) where it dragged along the surface. This leg contributed support to the animal [...]. Only when it was unloaded by the other legs could it occasionally make a short swing" (Dean, 1989, p. 107). He described a different behaviour

for tethered walking (with reduced load), when the ipsilateral hind leg stepped more regularly.

Our own observations on free walking insects confirm that, after a T3 lesion, the ipsilateral hind leg moved only little. Overall, the difference between Dean's study and ours appeared less pronounced for the T3 lesion than for the T2 lesion. Much like Dean (1989), we found that the ipsilateral hind leg does not make normal swing movements, although protraction/retraction of the hind leg femur oscillated rhythmically (**Figure 3**). Nevertheless, these rhythmic movements concern the femur and do not necessarily imply that the hind leg conducted a genuine, active swing movement with each femoral protraction. In principle, part of this movement could be passive, as induced by a lateral pull by the contralateral legs. As the difference between active and passive movement is impossible to tell from our top view videos (see **Supplementary Videos**), further studies would have to record protractor activity and track the movement of the hind leg tarsus.

Our findings on temporal coordination after T3 lesion largely corroborate Dean's findings, in that the coordination of the ipsilateral hind and middle legs was hampered, with greatly increased dispersion, albeit little or no effect on mean phase (R2 in R3; **Figure 10**). Effects of T3 lesion on spatial coordination look fairly similar in both studies (compare Dean's Table 2 with our **Table 2**), except for two differences: First we report a lot more effects than Dean (1989); second, Dean reported a slight rearward shift of the contralateral hind leg AEP (intact body side), whereas we found a substantial forward shift, i.e., in the opposite direction, with an associated strong increase of the step length. Thus, as for the T2 lesion effects discussed above, we find that spatial adjustments on the contralateral (intact) side differ between tethered and unrestrained walking.

Load Transfer in Temporal and Spatial Coordination

Perhaps the most important difference between the results on tethered walking stick insects (Dean, 1989) and ours concerns the somewhat dysfunctional swing movements and the increased frequency of overstepping that were found in tethered but not in unrestrained walking. What is more, our **Figures 2, 3** demonstrate clearly that the overall walking behaviour remained functional after connective lesion, as animals were still capable of walking along the same paths and without significant reduction of forward velocity. In fact, the significant increase in sideward velocity after connective lesion (**Figure 4**) implies that the difference in net translational velocity, i.e., the resultant of forward and sideward translation, would be even smaller than the difference in forward translation alone. Increased sideward translation indicates that connective lesions induced an asymmetry of the lateral forces exerted by the feet during stance. We suggest that this asymmetry is reflected by significant increase of step length on the intact (left) body side, which we found in the two rear legs after T2 lesion (**Figure 6A**, L2 and L3) and in all three legs after T3 lesion (**Figure 6B**, L1–L3). On the lesioned (right) body side, step length increased only in the leg immediately anterior to the lesion (R1 in **Figure 6A** and R2 in **Figure 6B**), whereas the leg posterior to the lesion

took much shorter steps, and the remaining third leg did not change step length at all. The fact that step duration, i.e., cycle period (**Figure 5**), did not mirror these changes in step length (see **Tables 1, 2**) suggests that movement velocities must have differed strongly among legs, potentially on a stride-to stride basis. Given the strong variance of step duration (see 95% CI's and per-animal means in **Figure 5**), we propose that legs locally adjusted movement velocity to maintain the much more consistent changes in step length and the associated touch-down (**Figures 7A, 8A**) and lift-off positions (**Figures 7B, 8B**). This is consistent with the observation that temporal coordination became highly variable for the leg pair immediately adjacent to the lesion (**Figure 9**: R1 in R2; **Figure 10**: R2 in R3) while changing only little or not at all in almost all other leg pairs (except contralateral coupling R2 in L2 and ipsilateral coupling of intact L2 in L2 after T2 lesion, **Figure 9**). Thus, we conclude that animals compensated for hampered inter-leg coordination in a single leg pair by concerted action of all legs, leading to substantial adjustment of spatial coordination with comparatively little change in temporal coordination.

Concerning the contribution of load transfer among legs to temporal coordination according to Cruse's coordination rule 2, Dallmann et al. (2017) provided strong evidence for two important aspects of mechanical inter-leg coupling: First, local unloading of a middle leg may be related to a single, most likely cause, that is the touch-down of the posterior hind leg (i.e., the sender leg); second, local unloading precedes the switch of depressor to levator activity, i.e., the transition from stance to swing. Assuming that this evidence would hold for the experimental situation of the present study, we expected that normal ipsilateral coordination should have persisted even after connective lesion. This was clearly not the case. Nevertheless, while the fact that both lesions resulted in highly variable phase relationships clearly points at the role of neural information transfer through the ipsilateral connective, the small (**Figure 9**) or even non-significant (**Figure 10**) change in mean phase lag among animals indicates the persistence of some weak coordinating effect. Whether or not this weak effect could be driven by ipsilateral load transfer or rather by an influence coming from the intact contralateral leg cannot be decided based on our results. As yet, the results of Dallmann et al. (2017) indicate that mechanical load transfer among two legs may only be effective if the distance between feet is small. Accordingly, our finding of increased distance between the sender leg AEP and receiver leg PEP (**Figures 7C,D, 8C,D**) adjacent to the lesion should have reduced efficacy of mechanical load transfer and weakened its potential effect on inter-leg coordination.

Mechanical load transfer alone cannot maintain inter-leg coordination after connective lesion in cockroaches either. "In a male *Blatta* with the right pro-mesothoracic commissure cut, the legs of the uninjured side showed a perfect rhythm L3, L2, L1 and this was true of the right side to some extent, but sometimes R1 fell out of the rhythm" (Hughes, 1957, S. 323). Similarly, Greene and Spirito (1979) found in that slow walking, tethered but load-bearing *Periplaneta americana*, connective lesions caused strong immediate effects on ipsi- and contralateral phase differences in the leg pair posterior to the lesion. Similar to our own results,

they found that the main effect concerned the precision of coordination (i.e., strongly increased variance), whereas the mean phase changed relatively little. Moreover, the remaining leg pairs maintained rigid coordination, but with slightly altered mean phase. Quite fitting to our own study, the authors concluded that “it should be stressed at this point that these co-ordination measures are not independent; a change in the relationship between any one pair of legs will necessarily be accompanied by changes in other pairs. Thus, the entire system must be considered as an entity” (Greene und Spirito 1979, S. 251). Overall, due to the extensive adjustments of all legs to a local defect in neuronal information transfer, it would be far-fetched to stress the significance of a single local mechanism of inter-leg coordination. Our results show that stick insects adjust to connective lesion quite differently if they experience a naturalistic load distribution. However, since altered load distribution during walking on inclines causes relatively weak effects on footfall patterns of the legs or body posture, but rather strong effects on muscle activity (Dallmann et al., 2019) future studies may need to relate load-induced changes in distributed muscle activity to ensuing kinematic changes in conjunction with local lesions.

As the experimental situations of Dean’s study (1989) and ours mainly differed in load distribution among legs, we conclude that these differences must be related to load. Future modelling studies using suitable dynamic simulation environments (e.g., see Schilling and Cruse, 2020), biomimetic robots with distributed load sensing (e.g., see Dürr et al., 2019) or conceptual robot models with load-dependent step-cycle generation (e.g., Owaki et al., 2013) could test the main prediction of our study: A change in load distribution (e.g., tethered vs. free walking) can account for compensatory spatial coordination after disruption of information exchange between neighbouring legs, so as to maintain the walking speed before the disruption. A corollary of this prediction is that such spatial compensatory actions

occur at the cost of increased step-by-step variation of temporal coordination among legs with disrupted information exchange. Furthermore, we expect to see significant spatial adjustment on the contralateral (intact) side of the disrupted information exchange.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MN, MJ, and VD designed research and edited the manuscript. VD established the setup and analysis software, and advised MN and MJ. MN and MJ performed the experiments, analysed the data, prepared all the figures, and drafted the manuscript. VD acquired the funding. All authors contributed to the article and approved the submitted version.

FUNDING

This work was supported by the Cluster of Excellence 277 CITEC, funded through Excellence Initiative of the German Research Council.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fbioe.2021.628998/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Dynamic Turning of a Soft Quadruped Robot by Changing Phase Difference

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Dynamic locomotion of a quadruped robot emerges from interaction between the robot body and the terrain. When the robot has a soft body, dynamic locomotion can be realized using a simple controller. This study investigates dynamic turning of a soft quadruped robot by changing the phase difference among the legs of the robot. We develop a soft quadruped robot driven by McKibben pneumatic artificial muscles. The phase difference between the hind and fore legs is fixed whereas that between the left and right legs is changed to enable the robot to turn dynamically. Since the robot legs are soft, the contact pattern between the legs and the terrain can be varied adaptively by simply changing the phase difference. Experimental results demonstrate that changes in the phase difference lead to changes in the contact time of the hind legs, and as a result, the soft robot can turn dynamically.

OPEN ACCESS

Edited by:

Dai Owaki,
Tohoku University, Japan

Reviewed by:

Yuichi Ambe,
Tohoku University, Japan
Eduardo J. Izquierdo,
Indiana University Bloomington,
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Specialty section:

This article was submitted to
Computational Intelligence in
Robotics,
a section of the journal
Frontiers in Robotics and AI

Received: 15 November 2020

Accepted: 22 March 2021

Published: 22 April 2021

Citation:

Tanaka H, Chen T-Y and Hosoda K
(2021) Dynamic Turning of a Soft
Quadruped Robot by Changing Phase
Difference. *Front. Robot. AI* 8:629523.
doi: 10.3389/frobt.2021.629523

Keywords: quadruped robot, soft robotics, pneumatic artificial muscle, body-environment interaction, dynamic turn

1. INTRODUCTION

Quadruped locomotion is more stable than bipedal locomotion and more adaptive than wheeled locomotion to the terrain (He and Gao, 2020). However, if each leg is controlled to follow a given trajectory based on force or touch information, the movement of the robot cannot be very fast and adaptive. Thus, Compliance of each leg should be a key to resolve the problem. Spröwitz et al. (2013) developed a robot Cheetah-cub, a quadruped robot with compliant legs. Recently, to realize fast and adaptive locomotion, some studies (e.g. Hyun et al., 2014) have proposed using low-reduction gears and impedance control. Pneumatic artificial muscles are also good candidates for realizing fast and adaptive quadruped locomotion, because they have natural compliance and can react against the external forces without a time delay (Narioka et al., 2012). However, these muscles have a large control latency, and it is very difficult to be control them precisely. To change the robot behavior, for example, changing the direction of the movement, we have to develop a different method for controlling the actuators.

This study describes a quadruped robot driven by pneumatic artificial muscles, and investigates the turning behavior by changing the phase difference among the legs. Pneumatic muscles are light; however, they can generate relatively large power. The compliance of the actuator absorbs the impact that is associated with landing without feedback control. In addition, the artificial muscles can be arranged similar to the muscles of animals, which may provide bio-inspired design guidelines for the hardware and control. The tunable compliance of the actuator enables multi-modal locomotion (Hosoda et al., 2008). It is even possible for a musculoskeletal robot to generate a gait pattern, without needing any computational resources (Masuda et al., 2020). However, it is difficult to control them precisely to change the behavior of the robot, because they are quite nonlinear and have a large control latency.

The target behavior of this paper is turning, which has been a complex locomotion task. In static locomotion, the robot can turn by changing the trajectory of its legs (Chan and Liu, 2016). To realize dynamic turning, however, it is necessary to analyze the dynamic effects such as centripetal force (Tsujita et al., 2005). Some researchers have proposed the application of computational techniques, such as optimization or learning methods (Bledt et al., 2018; Fahmi et al., 2019; Hwangbo et al., 2019), without explicitly dealing with the dynamic effects. The RHex robot utilizes hardware compliance for dynamic turning. The robot turns dynamically by changing the phase difference between the left and right sets of legs (Haldane and Fearing, 2014). Haldane et al. analyzed the turning moment that generates roll oscillation, leading to the turning motion of the robot in the simulation. This paper also utilizes phase difference for a pneumatically driven quadruped robot. We propose a simple controller for a quadruped robot that changes the phase difference among the legs, and analyze the contact pattern of the soft legs for dynamic turning.

The remainder of this paper is organized as follows. First, we describe the design of a quadruped robot driven by McKibben pneumatic artificial muscles. Each leg has two degrees of freedom (DOF) and is driven by a fixed-valve pattern. The diagonal legs are in phase, and the phase difference between the left and right legs can be changed. Then, we experimentally investigate whether the turning can be controlled by changing the phase difference. We recorded the contact patterns of the leg during the experiments, and found a relation between the patterns and turning motion. The main contributions of this paper are (1) developing a pneumatically driven soft quadruped robot that can turn, (2) determining the relationship between the contact patterns of the legs and turning behavior, and (3) finally, experimentally realizing the turning of the robot experimentally.

2. HARDWARE DESIGN

During locomotion without slipping, a robot is strongly restrained on the ground and receives a strong ground reaction force (GRF). A change in the contact timing of the leg can cause the robot to fall over, depending on the hardware design. For example, unlike a conventional motor-driven robot, a soft robot can contact the ground adaptively without falling over, even if the contact timing is changed (Rosendo et al., 2014). Therefore, we focus on softness and develop a soft quadruped robot named “PneuHound.” In this section, we introduce the hardware design of the developed robot.

2.1. Mechanical Design of Quadruped Robot

Figure 1 provides an overview of the design of “PneuHound.” The length, width, height, and weight of the whole body are 500, 300, 300 mm, and 3.5 kg, respectively. The main structure is composed of aluminum components. Air and electrical power are supplied externally. More detailed information about the design is provided in **Table 1**.

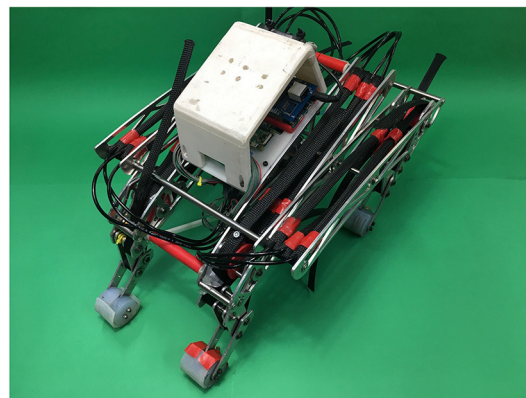


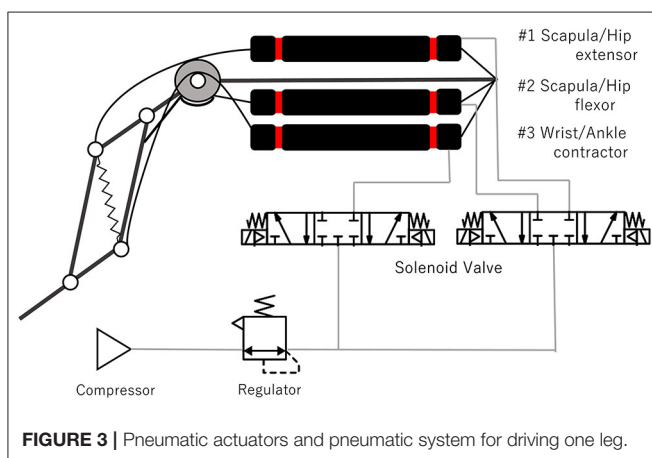
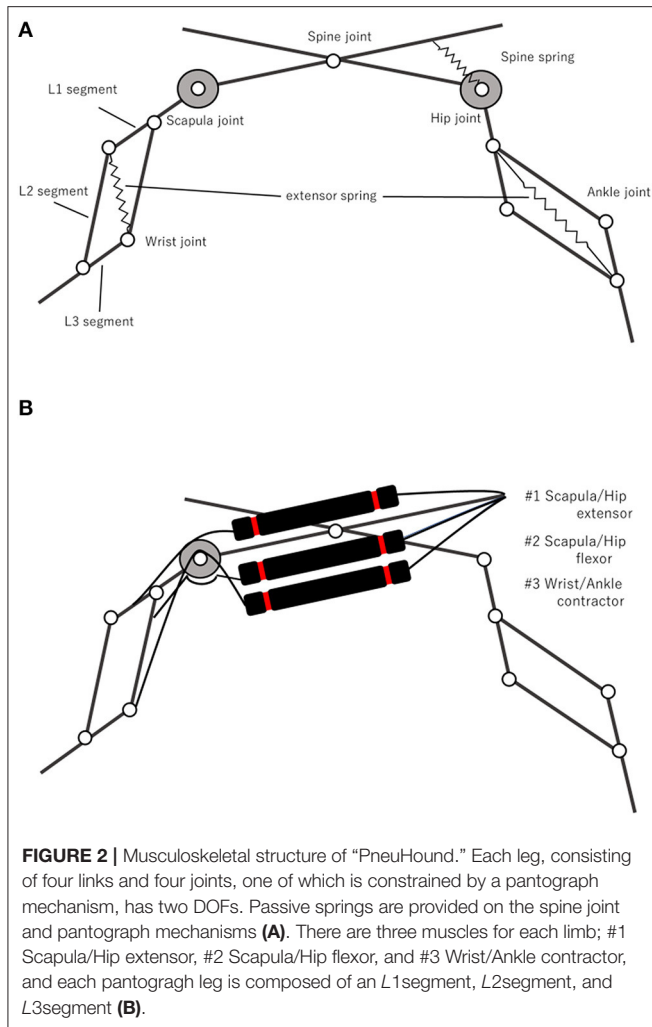
FIGURE 1 | Pneumatic quadruped robot “PneuHound.” The main objective of this robot is to perform dynamic turning by changing the phase difference among its legs.

TABLE 1 | Key properties of PneuHound.

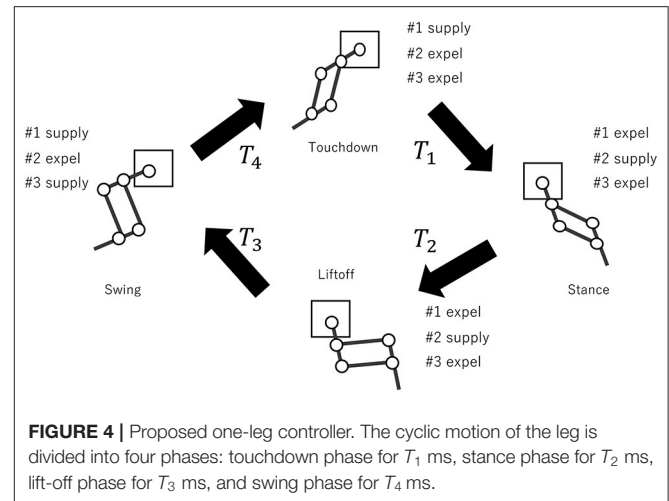
Property	Value
Length × width × height	500 × 300 × 300 mm
Total weight	3.5 kg
Fore leg weight	0.24 kg
Hind leg weight	0.26 kg
Number of valves	8
Number of muscles	12
L1 segment length in fore legs	55 mm
L2 segment length in fore legs	52 mm
L2 segment length in fore legs	70 mm
L1 segment length in hind legs	65 mm
L2 segment length in hind legs	64 mm
L3 segment length in hind legs	70 mm

The musculoskeletal structure of “PneuHound” is shown in **Figures 2A,B**. The robot has nine DOFs in total: each leg has two DOFs, and the spine has one DOF. The leg design is based on those reported in previous studies (Spröewitz et al., 2011; Narioka et al., 2012). Each leg has a pantograph structure with four links and four joints, and a tension spring is provided on the diagonal of the pantograph structure. The fore and hind legs can be extended with springs to a maximum of 65 and 70 mm, respectively. Due to the difference between the lengths of the fore and hind legs, the spring constants are different: 2.4 and 2.9 N/mm for the fore and hind legs, respectively.

To manipulate the leg, the robot drives nine joints: scapula and wrist joints in the fore legs, hip and ankle joints in the hind legs, and the spine joint (**Figure 2A**). The scapula and hip joints are antagonistically driven by two muscles, the wrist and ankle joints are retracted by a muscle and extended by a spring, and the spine joint is driven only by a spring (**Figures 2A,B**). The moment arm of the muscles driving the scapula and hip joints can be adjusted through the diameter of the pulley, which is set as 40 mm. In contrast, the moment arm of the wrist and ankle flexors



is very small (5 mm); this ensures that the flexors can shorten the leg while minimizing the influence of the muscle driving the scapula and hip joints.



For running dynamically without slippage, the robot requires high ground friction. Hence, we install rubber pillars on the toes. The radius and height of the rubber pillars are 17.5 and 37 mm, respectively.

2.2. Pneumatic Actuator and Control Architecture

Animals possess biological muscles, which provide a high output force with compliance to enable locomotion. To impart softness to the robot, we use McKibben pneumatic artificial muscles, which are similar to biological muscles, as the actuators. For such artificial-muscle-type actuators, the principle of actuation is that supplying air to the muscle generates a contraction in the muscle, while exhausting the same air relaxes the muscle. The compliance offered by the actuator is proportional to the contraction, and the force provided by the actuator depends on the internal pressure and the muscle deformation, as shown in the following equation (Klute et al., 2002):

$$F \propto \frac{P_{air}}{\Delta/L_0}, \quad (1)$$

where F is the force, P_{air} is the internal pressure, L_0 is the relaxed length, and Δ is the deformation of the muscle. The actuators are made from a rubber tube with an 8-mm diameter, 1-mm thickness, and 200-mm length, covered with a polyester exterior braid having an 11-mm diameter. The actuators are connected to a valve through a tube with a 4-mm diameter.

Figure 3 shows the pneumatic system for driving one leg with three actuators. Two solenoid valves (5 ports and 3 position types, SYJ3340-6L, SMC Co.) are used for each limb. One of the valves supplies compressed air to both the extensor and the flexor driving the scapula and hip joints, while the other valve supplies compressed air to the contractor driving the wrist and ankle joints. The two actuators driving the scapula and hip joints constitute the antagonistic muscles. However, only one valve is connected to these muscles, and hence, the joint compliance can't be modulated by varying the pressure of the antagonistic muscles as achieved in previous studies (Hosoda et al., 2008;

Takuma et al., 2008). The supply air pressure was 0.54 MPa when the turning experiment was conducted. A micro-controller (Arduino-Due) with the custom amplifier board is used for valve control.

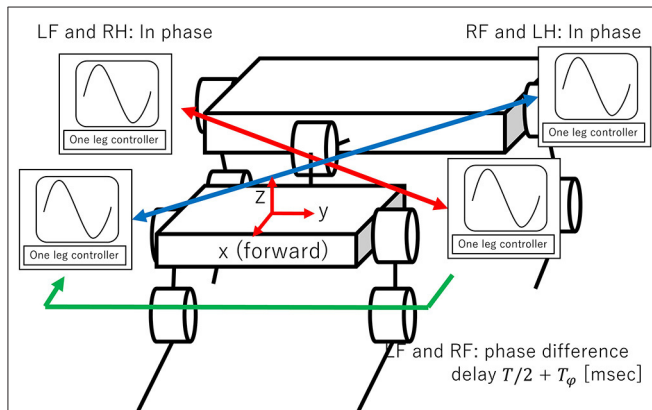


FIGURE 5 | Proposed interlimb controller. The phase difference is set as follows: LF and RH controllers and RF and LH controllers are in phase. Phase difference between two diagonal pairs (LF and RH controllers and RF and LH controllers) can be changed by varying T_ϕ .

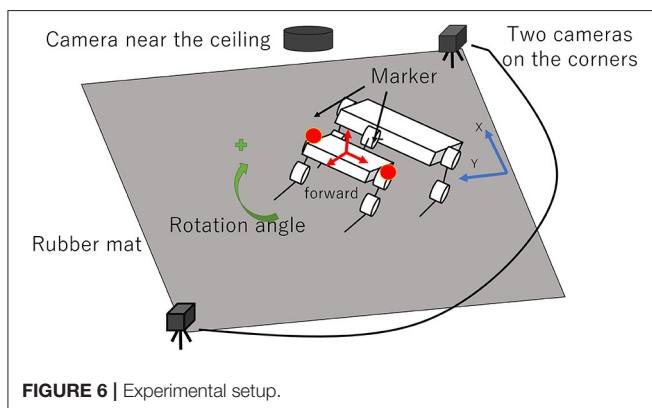


FIGURE 6 | Experimental setup.

3. CONTROLLERS FOR DYNAMIC LOCOMOTION

To achieve dynamic turning for a rigid quadruped robot, previous studies focused on controlling the phase difference among the legs to adjust the imbalance between left and right movements (Tsujita et al., 2005). This was only for compensating the imbalance, not for generating turning motion. In contrast, we control the phase difference among the legs to generate turning motion, based on a previous study (Haldane and Fearing, 2014). To design the locomotion controller, we divide it into one-leg and inter-limb controllers. In this section, we explain the design of each controller.

To generate the motions of the right hind leg (RH), right fore leg (RF), left hind leg (LH), and left fore leg (LF), we design the one-leg controller dividing the cyclic motion of a leg into four phases (Figure 4). The four phases are touchdown, stance, lift-off, and swing. To execute these phases, the valve-opening and -closing times, which determine the actuation pattern of muscles #1, #2, #3 (Figure 2B), are determined. For the touchdown phase, muscle #1 is supplied with air, while muscles #2 and #3 are expelled for T_1 ms. For the stance phase, muscle #2 is supplied, while muscles #1 and #3 are expelled for T_2 ms. For the liftoff phase, muscles #2 and #3 are supplied, while muscle #1 is expelled for T_3 ms. For the swing phase, muscles #1 and #3 are supplied, while muscle #2 is expelled for T_4 ms. Consequently, the period of the leg motion is calculated as $T = T_1 + T_2 + T_3 + T_4$ ms. We heuristically determined the parameters $T_1 \sim T_4$, such that the robot could run fast in the forward direction (i.e., $T_1 = 0.1T$, $T_2 = 0.4T$, $T_3 = 0.1T$, $T_4 = 0.4T$). Herein, the one-leg controller of each leg is denoted as the leg name followed by “controller” (for example, the one-leg controller of LF is denoted as “LF controller”).

Next, we design the inter-limb controller (Figure 5). The LF and RH controllers and the RF and LH controllers start at the same time. This means that the movements of the two diagonal pairs are in phase. To set the phase difference between these two diagonal pairs, the RF controller is started $T/2 + T_\phi$ ms after the LF controller. The phase difference can be changed from the trot gait ($T_\phi = 0$) by varying the parameter T_ϕ .

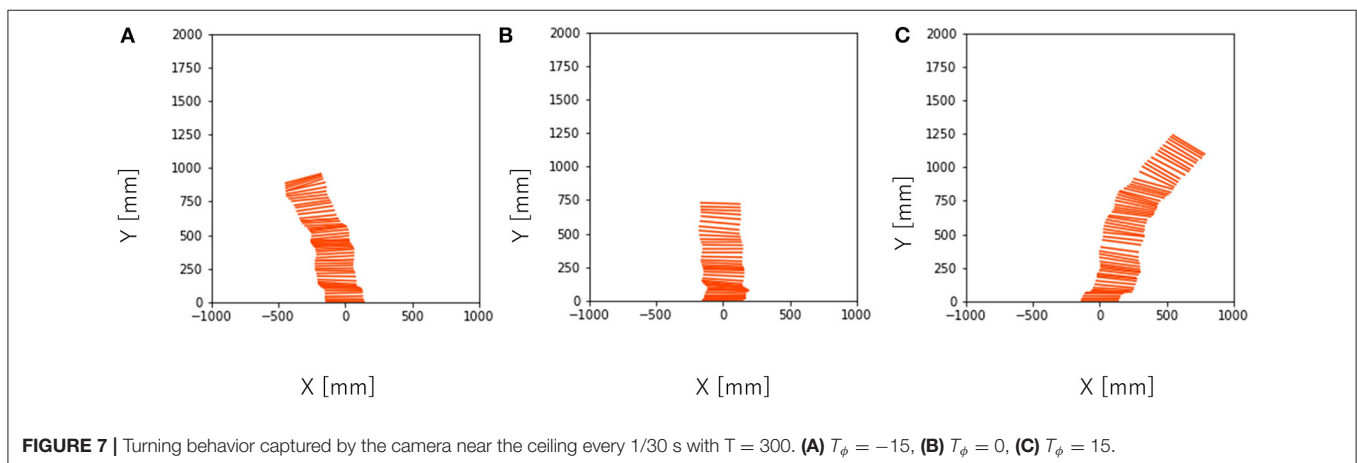


FIGURE 7 | Turning behavior captured by the camera near the ceiling every 1/30 s with $T = 300$. (A) $T_\phi = -15$, (B) $T_\phi = 0$, (C) $T_\phi = 15$.

4. EXPERIMENTAL SETUP

We used the experimental setup shown in **Figure 6**, which consists of the robot, a rubber mat, two cameras on diagonally opposite corners of the rubber mat, and a camera near the ceiling. The size of the rubber mat is 310 cm (L) $\times$ 180 cm (W). The two cameras on the corners of the rubber mat are synchronized, and their frame rate is 60 fps. The camera near the ceiling is 250 cm from the floor and captures the entire rubber mat; its frame rate is 30 fps. For a behavior analysis of the robot, we used

image-processing software (Dipp-MotionV, DITECT, Inc.), and two markers are attached to the left and right sides at the front of the robot.

In this research, we define dynamic turning as follows: First, we define “dynamic locomotion” as locomotion with a period in which two or fewer legs contact with the ground. Next, “dynamic turning” is defined as the dynamic locomotion with a turning motion.

In the following experiments, we observe four quantities: velocity, turning rate, duty ratio (the ratio of stance period

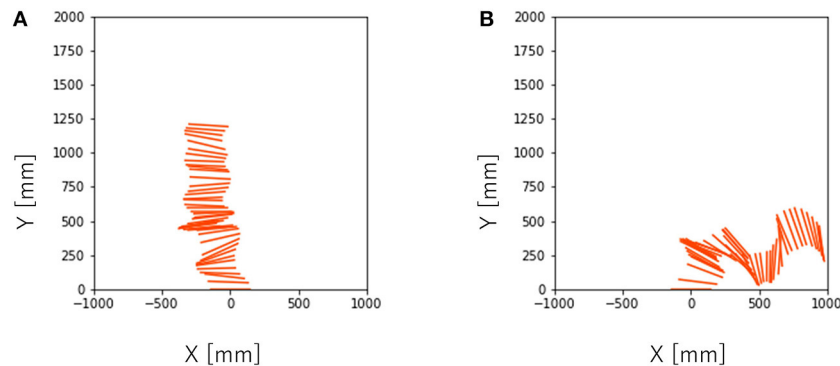


FIGURE 8 | Turning behavior captured by the camera near the ceiling every 1/30 s with $T = 450$. (A) $T_\phi = 0$, (B) $T_\phi = 15$.

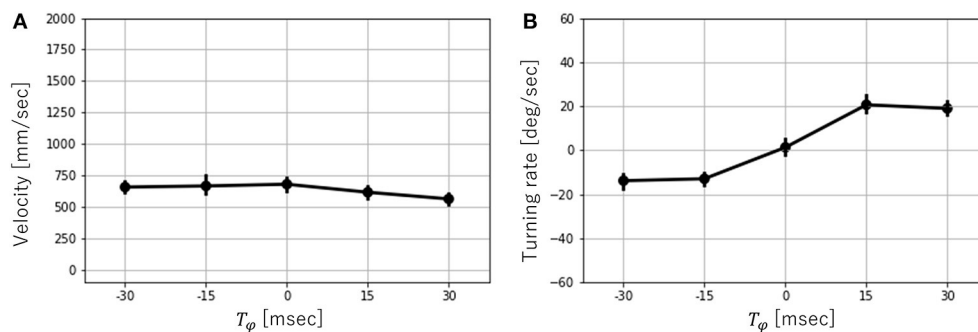


FIGURE 9 | (A) Velocity vs. T_ϕ and (B) Turning rate vs. T_ϕ with $T = 300$. Error bars show one standard deviation.

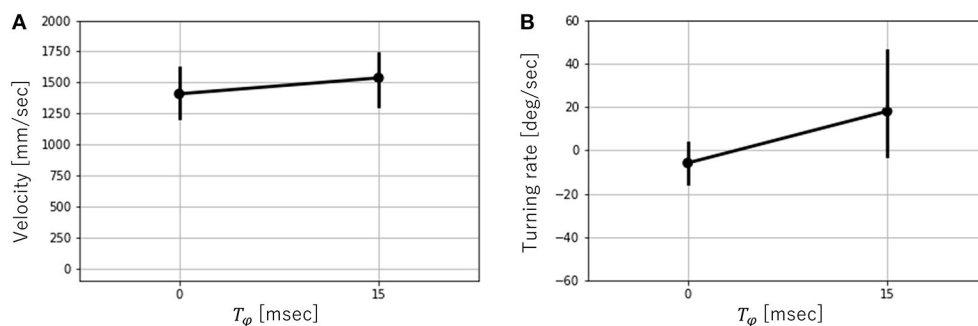


FIGURE 10 | (A) Velocity vs. T_ϕ and (B) Turning rate vs. T_ϕ with $T = 450$. Error bars show one standard deviation. It is noted that the mean and the standard deviation are calculated using the data the robot successfully ran.

divided by cycle period), and the ratio of the period that two or fewer legs contact with the ground divided by cycle time. The velocity is calculated with reference to the midpoint of the two markers on the robot. The turning rate is calculated using the two markers; the angle when turning right from the initial posture is considered as positive. The impulse received from the ground can be estimated from the ground contact time and gives the robot propulsion. Therefore, we use duty ratio as a simplified indicator of propulsion and investigate the changes in this parameter according to the phase difference among the legs. Contact between the legs and the ground is identified from the videos recorded by the two synchronized cameras, and the duty ratio is calculated accordingly. To verify whether the locomotion of the robot is dynamic turning, the ratio of the period when two or fewer legs contact with the ground divided by cycle time is calculated. We conducted experiments by varying T_ϕ from 0 ms in increments of ± 15 ms with $T = 150, 300, 450$.

5. RESULTS

5.1. Velocity and Turning Rate in Dynamic Turning

To investigate the effect of the phase difference among the legs on the dynamic turning, we conducted an experiment by varying T_ϕ where $T = 150, 300, 450$. With $T = 150$, the running was not successful because the supply time of the air was too short for the system to provide sufficient actuation force for running. With $T = 300$, the robot ran for $T_\phi = -30, -15, 0, 15, 30$. **Figure 7** shows the turning behavior of the robot with different parameters. With $T = 450$, the robot ran for $T_\phi = 0, 15$. **Figure 8** shows the turning behavior of the robot with different parameters.

Next, the effects of T_ϕ on the velocity and turning rate were examined when the robot ran successfully (that is, $T = 300, 450$). **Figure 9** shows the mean values and error bar of the velocity and turning rate with $T = 300$. A total of 10 trials were conducted for each parameter, and the average velocity and turning rate were obtained through the 2-s locomotion experiments. While the robot moved straight ahead with $T_\phi = 0$, it turned right for $T_\phi > 0$ and left for $T_\phi < 0$. The velocity varied slightly depending on the value of T_ϕ . In contrast, the turning rate varied significantly over the range of $-15 \leq T_\phi \leq 15$. However, it did not change considerably over the ranges of $-30 \leq T_\phi \leq -15$ and $15 \leq T_\phi \leq 30$. Next, the velocity and turning rate with $T = 450$

were investigated. Ten trials were conducted for each parameter, and the average velocity and turning rate were obtained through the 2-s locomotion experiments. However, only six trials were successful with $T_\phi = 0$, and only seven trials were successful with $T_\phi = 15$. **Figure 10** shows the mean values and error bar of the velocity and turning rate with $T = 450$. It is noted that the mean and the standard deviation are calculated using the data in which the robot ran successfully. The velocity with $T = 450$ was higher, and had a larger variation than that with $T = 300$. The turning rate with $T = 450$ had a larger variation than that with $T = 300$, and showed a similar change with $T = 300$ between $T_\phi = 0$ and 15.

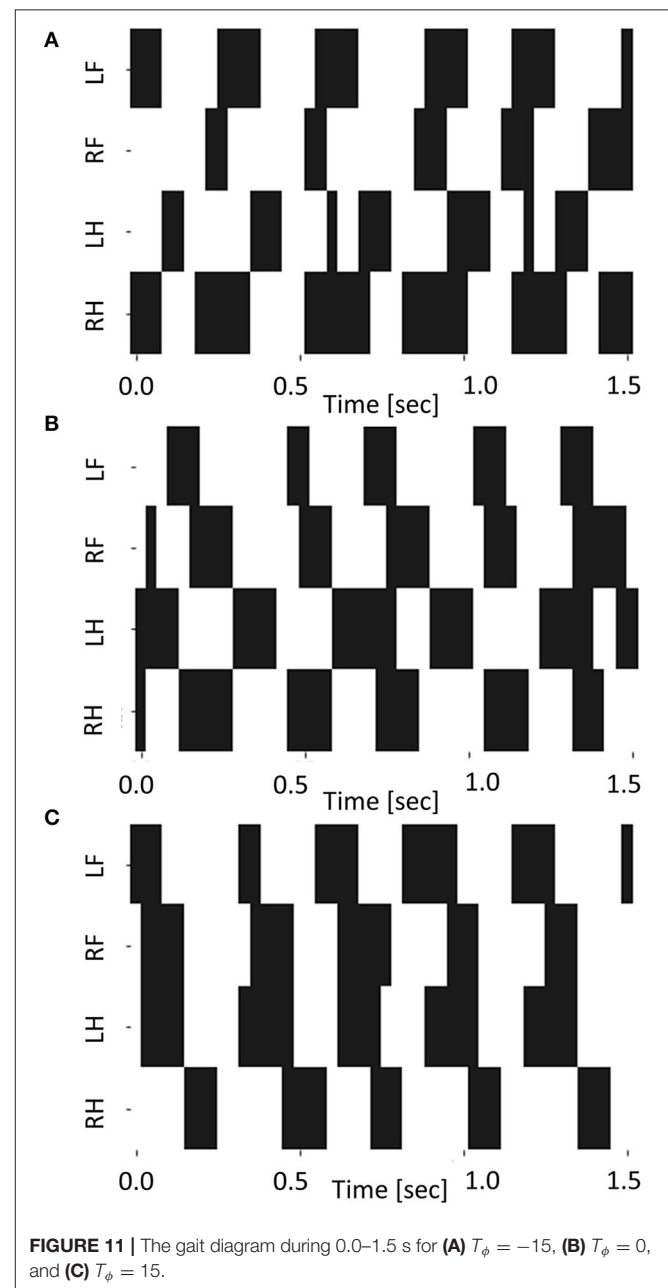


TABLE 2 | Ratio of the period that two or fewer legs contact with the ground divided by cycle time.

Phase difference	Ratio
$T_\phi = -30$	0.80
$T_\phi = -15$	0.86
$T_\phi = 0$	0.74
$T_\phi = 15$	0.86
$T_\phi = 30$	0.89

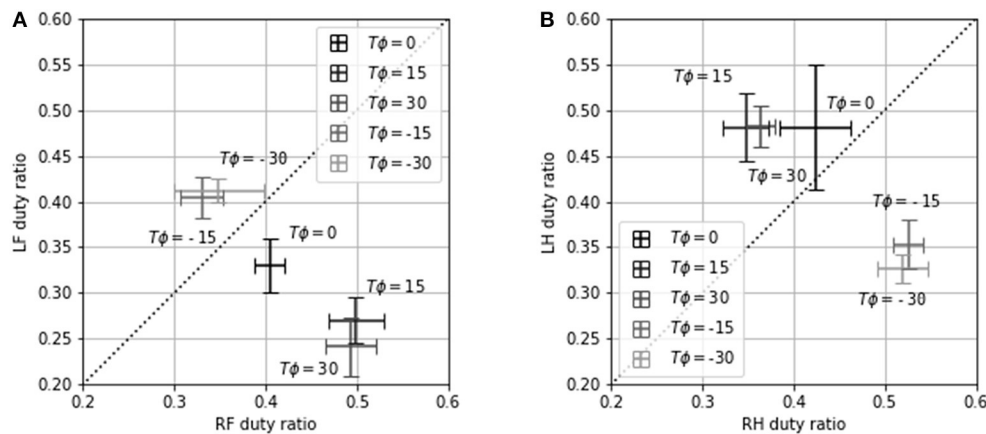


FIGURE 12 | (A) LF duty ratio vs. RF duty ratio and **(B)** LH duty ratio vs. RH duty ratio for $T_\phi = -30, -15, 0, 15, 30$. Error bars show one standard deviation.

5.2. Contact Pattern of Leg

In this experimental setup, we could capture the contact of the leg with $T = 300$. Hence, we conducted an experiment to investigate the dependence of the contact pattern of the leg on T_ϕ with $T = 300$. **Table 2** shows the ratio of the period that two or fewer legs contact with the ground divided by cycle time with $T = 300$. This table shows that the robot locomotion is dynamic turning considering **Figure 9** shows that the robot turned with $T = 300$. **Figure 11** shows the gait diagram during 0.0–1.5 s with different values of T_ϕ . In the gait diagram, the black regions represent the stance phase. The robot achieved different contact patterns by changing the value of T_ϕ . The results showed that the robot turned dynamically because there was a phase in which two or fewer legs were in contact with the ground. **Figures 12A,B** shows the mean value and error bar of the duty ratio of the fore and hind legs. The line along which the duty ratios of the “left and right legs” are equal is also shown in the figure. Five trails were conducted for each parameter, and the average duty ratio was obtained through experiments involving more than 10 steps of locomotion.

From the experimental results, we observed a strong correlation between the duty ratio of the hind legs and the turning rate. For $T_\phi \geq 15$, the duty ratio of LH was higher than that of RH (**Figure 12B**). Consequently, the left propulsion was stronger than the right propulsion, causing the robot to turn right (**Figure 9B**). For $T_\phi \leq -15$, the duty ratio of RH was higher than that of LH, causing the robot to turn left. However, the relationship between the duty ratios of LF and RF was the opposite of the relationship between the duty ratios of LH and RH. The propulsion of the hind legs was observed to have a stronger influence on the turning of the robot than the propulsion of the fore legs. Additionally, the variation in the duty ratio was a similar to that in the turning rate: The duty ratio and the turning rate varied significantly over the range of $-15 \leq T_\phi \leq 15$, but they did not vary considerably over the range of $-30 \leq T_\phi \leq -15$ and $15 \leq T_\phi \leq 30$. This indicates that the contact pattern was not changed significantly upon changing

the phase difference. As a result, the turning rate was not changed significantly either.

In addition, the experimental results show that the frequency of the periodic leg movement (that is, $1/T$) changed the turning motion. Stable turning motion was generated with $T = 300$. When the frequency of the leg movements increased, the running was not successful. On the contrary, when the frequency of the leg movement decreased, the turning became unstable.

6. DISCUSSION

We proposed a simple control method for dynamic turning of a quadruped soft robot driven by pneumatic artificial muscles as actuators. The experimental results show that the control parameter T_ϕ controls the direction of dynamic turning. Our results also indicate that when the gait deviates from trotting ($T_\phi = 0$) due to changes in T_ϕ , the contact pattern of the legs is changed, causing the robot to turn. However, the contact pattern does not change significantly depending on the size of the phase difference. Consequently, the turning rate does not change significantly either. In addition, the experimental results show that the frequency of the periodic leg movement changes the turning motion.

Haldane et al. reported that the phase difference between the left and right sets of compliant legs of a hexapod robot modulated the oscillations in height and roll angle. Additionally, they demonstrated that the roll oscillations enabled the robot to turn at high speeds through changes in the phase difference (Haldane and Fearing, 2014). In their study, to calculate the turning moment, the simulation setup parameters were simplified: the contact of the leg was defined only by the rotation angle of the motor. However, the interaction between the legs and the ground has to be carefully considered because various speeds and orientations are involved in the dynamic locomotion. Our study presents a significant finding: the contact pattern of a soft leg plays an important role in dynamic turning. In contrast, it seems

that the roll oscillations confirmed in their study did not exist in our system because the roll posture data of our robot were not steady. The turning controllers of our study and their study were similar. However, because the main structure of our robot's body is different from that of their robot, the turning mechanism may be different.

In previous studies, the turning direction of motor-driven robots have been precisely controlled using kinematic approaches. For example, generating a three-dimensional motion by increasing the DOF of the legs improves turning maneuverability (Estremera and de Santos, 2005; Kimura et al., 2007; Raibert et al., 2008). In this study, the trajectory of each leg in the air was kept unchanged since we aimed to investigate the effect of the phase difference among the legs. We believe that integration of the kinematic method with our control method for soft robot legs presents an important topic for further research on precise control of the turning direction with a simple controller.

Our research has three limitations. First, is that in this experimental setup, we could not capture the contact pattern of the leg with $T = 450$ because the robot turned in various directions. Therefore, we cannot confirm the effect of unstable turning on the contact of the legs. Second, we did not verify that the same simple controller would not produce turning in a non-soft robot. In this experimental setup, it was extremely difficult to control the stiffness of the leg for a quadruped robot. Third, the structure makes a different turning mechanism from the relevant study (Haldane and Fearing, 2014). We intend to investigate more about these three issues in the near future.

7. CONCLUSION

In this study, we demonstrated dynamic turning of a soft quadruped robot with a simple controller. Our findings show that a soft body simplifies a controller design even for complex tasks.

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We showed that a change in phase difference leads to a change in the duty ratio of the hind legs, enabling the robot to turn dynamically. Further investigation of the softness of quadruped robots can elucidate the complex interaction between the robot and the terrain, enabling the development of a specialized control method for such robots.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

HT: conception and design, development, analysis and interpretation, manuscript writing, and final approval of the manuscript. T-YC: construction of the robot and final approval of the manuscript. KH: development of fundamental concepts, project guidance, and final approval of the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

This work was partly supported by the JSPS KAKENHI Grant-in-Aid for Scientific Research on Innovative Areas Science of Soft Robotics (#18H05467).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frobt.2021.629523/full#supplementary-material>

- International Conference on Robotics and Biomimetics (ROBIO)*, (Guangzhou). 307–311. doi: 10.1109/ROBIO.2012.6490984
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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Brainless Walking: Animal Gaits Emerge From an Actuator Characteristic

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In this study, we discovered a phenomenon in which a quadruped robot without any sensors or microprocessor can autonomously generate the various gait patterns of animals using actuator characteristics and select the gaits according to the speed. The robot has one DC motor on each limb and a slider-crank mechanism connected to the motor shaft. Since each motor is directly connected to a power supply, the robot only moves its foot on an elliptical trajectory under a constant voltage. Although this robot does not have any computational equipment such as sensors or microprocessors, when we applied a voltage to the motor, each limb begins to adjust its gait autonomously and finally converged to a steady gait pattern. Furthermore, by raising the input voltage from the power supply, the gait changed from a pace to a half-bound, according to the speed, and also we observed various gait patterns, such as a bound or a rotary gallop. We investigated the convergence property of the gaits for several initial states and input voltages and have described detailed experimental results of each gait observed.

Keywords: legged robot, quadruped robot, motion control, gait analysis, motors, autonomous decentralized control, oscillator, vibration

OPEN ACCESS

Edited by:

Dai Owaki,
Tohoku University, Japan

Reviewed by:

Shinya Aoi,
Kyoto University, Japan
Alexander Thomas Badri-Spröwitz,
Max Planck Institute for Intelligent
Systems, Germany

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Specialty section:

This article was submitted to
Computational Intelligence in Robotics,
a section of the journal
Frontiers in Robotics and AI

Received: 15 November 2020

Accepted: 08 April 2021

Published: 29 April 2021

Citation:

Masuda Y, Naniwa K, Ishikawa M and
Osuka K (2021) Brainless Walking:
Animal Gaits Emerge From an
Actuator Characteristic.
Front. Robot. AI 8:629679.
doi: 10.3389/frobt.2021.629679

1 INTRODUCTION

Most of the legged animals have the ability to adaptively select their gait patterns according to their speed (Alexander, 1984). Although the mechanism of the gait selection in animals is still unclear, conventional animal experiments have provided us with some knowledge. A study investigating the oxygen consumption of running horses (Hoyt and Taylor, 1981) showed that horses choose an efficient gait depending on their running speed. The result suggests that animals choose an energetically appropriate gait to survive in nature with limited resources. A study comparing the characteristics of the transition points in various animals' gait (Heglund et al., 1974) showed that the ratio of stride frequency to body weight at the transition points from trot to gallop was linear in logarithmic coordinate. The result indicates that the control mechanism for selecting motion patterns depends on the basic dynamics of the body rather than on animal species. As described above, the control principle of selecting the gait patterns of animals is not only energy efficient but also common to animals with different morphologies.

If we can imitate the ability of gait generation and selection in animals, the locomotor ability of legged robots will be improved. However, since animal gait patterns emerge as a result of complex interactions between the brain, body, and environment, it is difficult to determine which factors dominate gait generation and selection. In order to understand the principles of animal locomotion, researchers have conducted a variety of animal experiments and proposed gait generation models

from various perspectives ranging from neural circuits to body dynamics. The neural network called the central pattern generator (CPG), which is located within the animal's spinal cord, is widely known as a mechanism for generating motor patterns (Grillner, 1985). Experiments using the hind limbs of cats (Brown, 1911) observed that they could generate alternating muscle activity between flexors and extensors without sensory information from the muscles. In other experiments focusing on the generation of motor patterns, decerebrated cats generated a walking gait on a treadmill (Rossignol, 2000), and observed the gait transitions from walking to fast walking and galloping (Stuart and Hultborn, 2008; Armstrong, 1988). After the discovery of the CPG, some researchers have been tried to replicate and understand the CPG (Marder and Bucher, 2001; Ijspeert, 2008; Aoi et al., 2017). In connectionist approaches based on mathematical neuron models, multi-layer CPG models (McCrea and Rybak, 2008) have been proposed, which are capable of generating several periodic motions. More abstract CPG models using oscillators, such as the Kuramoto oscillator (Kuramoto, 1975) and Matsuoka oscillator (Matsuoka, 1985), were adopted as control laws for robots (Ijspeert, 2008; Maufroy et al., 2010; Aoi et al., 2013; Fukuoka et al., 2015).

Although the CPG has the ability to generate motor patterns by itself, several simulations and robotic experiments have shown that the spinal reflex system, which is simpler than the CPG, can also generate motor patterns by itself. It is theoretically shown that the two stretch reflex system and the physical (nonneural) interaction between the muscles stabilize the alternating motion patterns between the antagonistic muscles in a one-joint neuromechanical model (Masuda et al., 2019). In a simulation study of bipedal walking (Geyer and Herr, 2010), a human model in the sagittal plane with some reflexes, including neural connections between the left and right limbs, generated a stable gait pattern. In a simulation study of quadrupedal gait (Ekeberg and Pearson, 2005), although a three-dimensional model of the cat's hind limbs has no neural connection between the left-right limbs, it generated a stable gait using a four-phase reflex rule. This reflex rule has also been implemented in a musculoskeletal robot (Rosendo et al., 2014). Another musculoskeletal robot with simpler reflexes (Masuda et al., 2020) has developed fast running motions by using a reciprocal excitatory reflex between the hip and knee extensors, even though there was no neural coupling between the left and right limbs, or explicit design of the walking phases and the leg trajectories. As a robot that generate multiple motion patterns, a quadruped walking robot (Owaki and Ishiguro, 2017), which uses a reflexive rule described by an oscillator model, generated various gait patterns, such as walk, trot, and gallop, depending on the speed, using only physical (nonneural) interactions between the limbs. These experiments suggest that the physical interactions between the limbs through the body and the ground play a greater role in the generation of adaptive gait.

In addition, some simpler gait generation phenomena have been reported, in which gait patterns emerge from body-environment dynamics alone, without even using reflexes. A prime example is the passive dynamic walker, which generates a bipedal gait through interaction with the

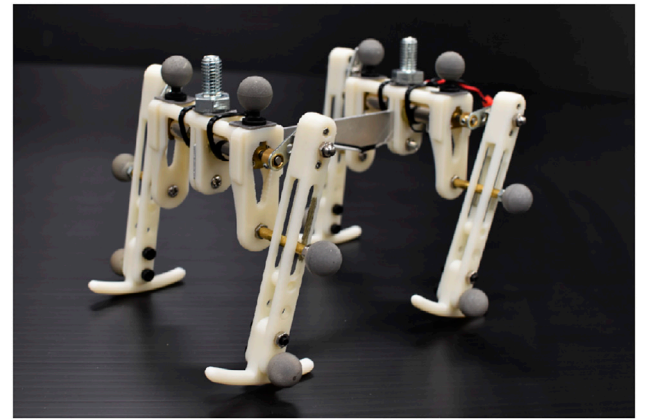
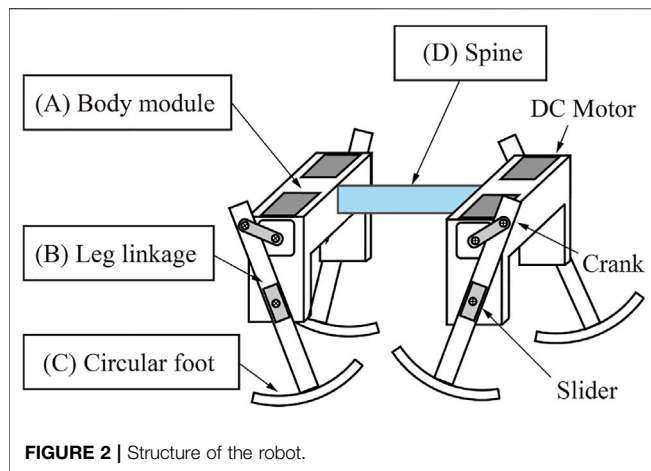


FIGURE 1 | Overview of the robot.

ground and gravity (McGeer, 1990; Collins et al., 2005). As passive walkers that generate gait patterns, experiments with passive quadrupedal walkers (Nakatani et al., 2009) and passive bipedal walkers (Owaki et al., 2008) have shown a variety of adaptive gait generations. Furthermore, as a motor control approach that utilizes the body, which is slightly different from passive walking, there are examples of gait generation that utilize the vibration modes of the robot body. In a simple robot with a body made of a flexible U-shaped curved beam and a single DC motor (Reis et al., 2013), the continuous rotation of the DC motor generates multiple gait patterns by entraining the coupled body-environment dynamics into a resonant mode. These results are a good example of the gait selection due to the interaction between the dynamics inherent in the robot body and the environment, without the need for control by the nervous system. Thus, it has been shown that animals and robots can generate gaits not only by CPGs but also by different levels of subsystems, such as simpler reflex systems and body dynamics alone. This suggests that the animal's ability to generate gait is not provided by a single functional module such as CPGs, but by parallel overlapping gait generation mechanisms that complement each other's functions. Therefore, there may be additional unknown mechanisms behind the phenomenon of gait generation and selection.

This article describes a novel gait generation mechanism that we discovered from a different perspective than previous studies. The major contribution of this study was discovering a phenomenon in which a quadruped robot without any sensors or microprocessor can autonomously generate the various gait patterns of animals using actuator characteristics and select the gaits according to the speed. The robot, shown in **Figure 1**, has one DC motor on each limb and a slider-crank mechanism connected to the motor shaft. Since each motor is directly connected to a power supply, the robot only moves its foot on an elliptical trajectory under a constant voltage. In other words, this robot does not have any computational equipment, such as sensors or microprocessors. Nevertheless, when we applied a voltage to the motor, each limb begins to adjust its gait autonomously and finally converged to a steady gait pattern.



Furthermore, by raising the input voltage from the power supply, the gait changed from a pace to a half-bound according to the speed, and also we observed various gait patterns, such as a bound or a rotary gallop. We investigated the convergence property of the gaits for several initial states and input voltages and describe detailed experimental results of each gait observed. A prototype of this robot was presented at an international conference on robotics (Masuda et al., 2017b). The analysis of the synchronization phenomenon of multiple DC motors in fundamental systems is described in Masuda et al., 2017a.

2 QUADRUPEL ROBOT

This section describes a quadruped robot that can generate gait patterns and perform adaptive gait selection even though it has no sensors, microprocessor, or other computing resources.

2.1 Mechanical Structure

Figure 2 shows the structure of the quadruped robot. The robot consists of fore and hind body modules, and the modules are connected with a spine. **Figure 3** shows the measurements of the robot. We designed the distance between the crank tip and foot tip to be 90 mm, and the foot width is 6 mm. The total mass of the robot, which includes the two body modules and four limbs, is 183 g.

Each module has right and left limbs, and each limb has a slider-crank mechanism connected to the shaft of a geared DC motor (Pololu 75:1 Micro Metal Gearmotor HP). **Figure 2A** shows the structure of the body modules. Each body module has two DC motors, so the robot has four motors in total, and all the motors are directly connected to a stabilized power source in parallel.

Each limb of the robot consists of a slider-crank mechanism. **Figure 2B** shows the robot limb. The limb has one degree of freedom, and the motor just rotates continuously under a constant voltage. Therefore the motor generates only an elliptical trajectory as it turns the crank, as shown in **Figure 3** right. The lengths of the major and minor axes of the elliptical trajectory are 54 and 20 mm, respectively.

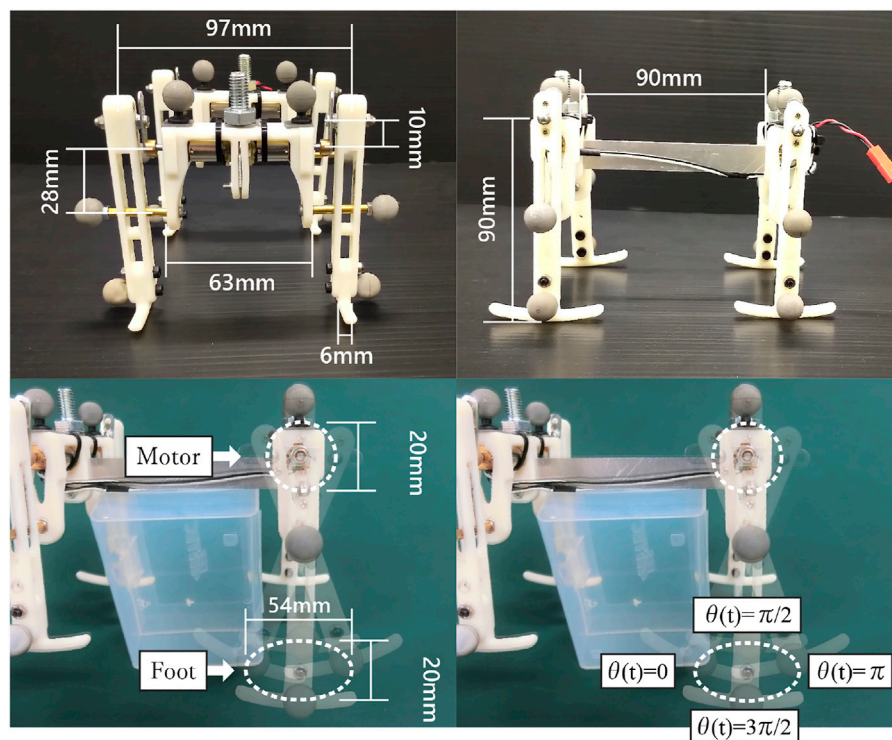


FIGURE 3 | Measurements of the robot. We designed the distance between the crank tip and foot tip to be 90 mm, and the foot width is 6 mm. The right figure shows the foot trajectory of the robot. The blue box in the center of the image is a stand for fixing the robot in the air.

We embedded a circular foot for smooth touch-down and take-off of the limb. **Figure 2C** shows the circular foot. The shape of the foot was designed as the arc of a circle. The radius of the arc of the circular foot is 85 mm, and the foot length is 49 mm.

3 CONTROLLER INHERENT IN MOTOR DYNAMICS

When the robot walks, each DC motor moves the foot on an elliptical trajectory under a constant voltage; thus, it generates a fixed foot trajectory. In spite of such a simple configuration, this robot generates a gait according to the locomotion speed, while adjusting the phases of the motors. The key to the phase adjustment is the torque–velocity characteristics of DC motors, as described below.

3.1 Modeling of DC Motor

Equation of motion and circuit for a DC motor with a constant voltage V applied is given by

$$J\ddot{\theta}(t) + D\dot{\theta}(t) = K_T i(t) + \frac{\tau(t)}{n}, \quad (1)$$

$$V = L_M \dot{i}(t) + Ri(t) + nK_E \dot{\theta}(t), \quad (2)$$

where $i(t)$ is the input amplitude, $\theta(t)$ is the motor angle, $\tau(t)$ is the load torque applied to the output shaft of the gearbox, n is the gear ratio, L_M is the inductance, and R is the armature resistance. J and D are the inertia and the viscous resistance coefficient, respectively, including the rotor, gears, and shafts. K_T and K_E are the proportionality coefficient between torque–current and the electromotive force constant.¹ Note that since $K_T = K_E$ from the reciprocity theorem, we write $K := K_T = K_E$ in the following.

Assuming that the inductance L_M of the motor are negligible, the dynamics of the motor **Eqs 1, 2** can be rewritten as follows:

$$n\epsilon J\ddot{\theta}(t) = (\omega - (n\epsilon D + 1)\dot{\theta}(t)) + \epsilon\tau(t), \quad (3)$$

where $\omega := V/nK$ is the rotation speed at no load and $\epsilon := R/n^2 K^2$ is the motor constant.

Finally, assuming that the inertia J and viscous resistance coefficient D are sufficiently small,² the relationship between the torque–velocity characteristics of the motor, that is, the angular velocity $\dot{\theta}(t)$ and the load torque $\tau(t)$ can be written as follows:

$$\dot{\theta}(t) = \omega + \epsilon\tau(t). \quad (4)$$

From the right-hand side of **Eq. 4**, in the absence of a disturbance torque $\tau(t)$ from the environment, the angular velocity converges to a constant $\dot{\theta}(t) = \omega$ that is proportional to the input voltage. In addition, when an external load $\tau(t) < 0$ from the environment is applied to a DC motor, the rotation

speed of the motor $\dot{\theta}(t)$ increases or decreases. The interesting point of this research is that the torque–velocity characteristics, which cause inconvenience in general motor control, are utilized as a control law to adjust the motor phases in response to external forces.

3.2 Phase Adjustment Function Emerged From Motor and Linkage

As introduced above, thanks to the torque–velocity characteristics of the motors, the interaction between the motors, body, and the environment changes the walking motion of the robot. Next, in order to understand the general behavior of the motors in a walking robot, we model the limb linkage with a DC motor.

The structure of the load torque $\tau(t)$ changes depending on the ground contact condition. For example, when a robot's foot is in the air, the dynamics are dominated by the inertia of the limb linkage, the rotor, and the shaft of the motor. On the other hand, when the foot is on the ground, the limb linkage is supported by the ground and the dynamics of the robot body dominates. However, the weight of the limb linkage was only 12 g compared to the body weight of 178 g. Therefore, in this study, we focus on the ground reaction force during the stance phase, which is the largest influence that the motor receives from the environment, and consider how the ground reaction force may affect the motor phase during walking.³

Moreover, during the stance phase, the robot receives forces from various directions depending on the condition of the environment (unevenness of the floor and friction coefficient) and the robot's motion (gait, body posture, and relative velocity to the environment). Since these external forces emerge from the complex interaction between the body, motor, and the environment, detailed modeling of floor reaction forces is not possible and does not make sense. However, we know that the reaction force the robot receives is typically an upward force under gravity. Therefore, we discuss the general effect of a typical ground reaction force: a vertical upward force to the ground.

In order to discuss the general effect of the vertical ground reaction force on the rotation of the motor, we assume that the body posture of the robot is constant with respect to the ground. Moreover, we also assume that the ground contact point is nearly under the motor shaft O and the slider shaft Q, thanks to the circular foot, as shown in **Figure 4**. From this assumption, the axial load from the slider shaft Q to the tip of the crank p can be written as $N(t)\cos\phi(t)$. Here, $N(t)$ is the vertical ground reaction force received by the foot of the robot, and $\phi(t)$ is the relative angle between the limbs and the body. Therefore, the torque from the tip of the crank p to the motor shaft is $\tau(t) = aN(t)\cos\phi(t)\cos(\phi(t) + \theta(t))$. Here, since $\cos(\phi(t) + \theta(t)) = (b/a)\sin\phi(t)$ by kinematics of the

¹Note that, although J , D , K_T , and K_E are also constants that depend on the gear ratio n , we omitted them for simplicity.

²In most motors, the inductance and viscous resistance coefficient are kept small. For the inertia term, the rotor and shaft with gears were only 2 g and 1 g.

³Although the dynamics of the limb linkage also exists during the stance phase, we ignore its influence because the weight of the limb linkage is small compared to the body weight, and the displacement of the center of gravity of the limb linkage is very small because the toes are fixed to the ground.

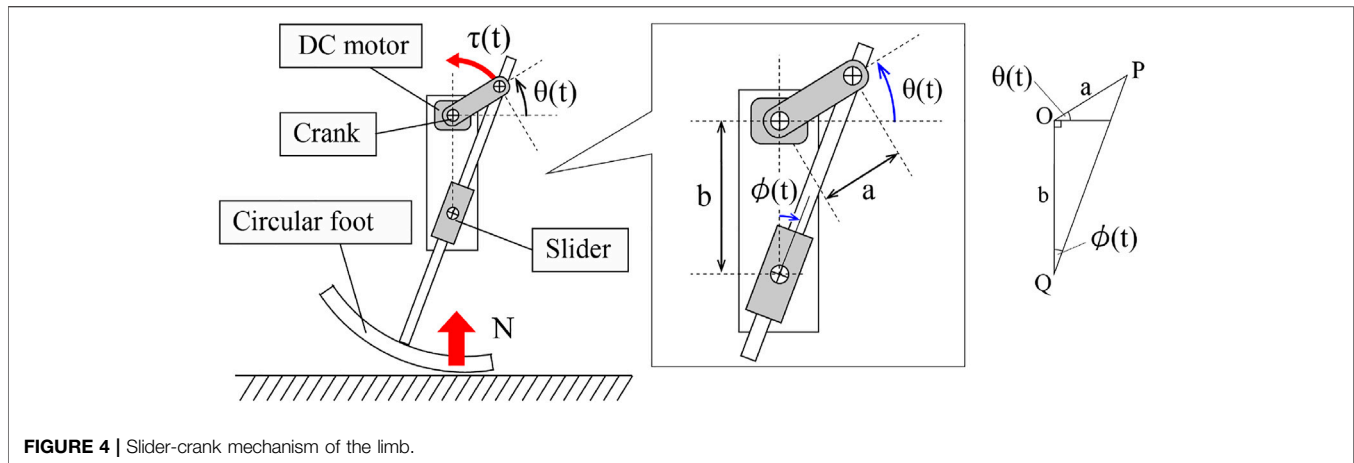


FIGURE 4 | Slider-crank mechanism of the limb.

linkage, the load torque of the motor, $\tau(t)$, can be written as follows:

$$\tau(t) = \frac{b}{2} N(t) \sin 2\phi(t), \quad (5)$$

where a and b is the length of the crank and the distance from the motor shaft to the slider, respectively.

Then, the motor model Eq. 4 can be rewritten using Eq. 5 as follows:

$$\dot{\theta}(t) = \omega + \varepsilon \frac{b}{2} N(t) \sin 2\phi(t). \quad (6)$$

Here, note that the leg angle $\phi(t)$ is a function of the motor phase: $\phi(\theta, t) = \arctan(\cos\theta(t)/\sin\theta(t) + b/a)$. Here, let us see the second term on the right side of Eq. 6. Interestingly, since the state variable $\theta(t)$ is in the second term, the load torque $(b/2)N(t)\sin 2\phi(t, \theta)$ from the environment can be interpreted as a state feedback rule of the motor angle $\theta(t)$. That is to say, DC motors Eq. 6 are the physical devices that have all the three functions of “actuate, sense, and control” necessary for adaptation to the environment.

Now, let us consider the behavior of a quadruped robot when the ground reaction forces are applied to the limbs. In Eq. 6, we consider the case where a ground reaction force $N(t) > 0$ is applied to the foot. When the motor phase is $-\pi/2 \leq \theta(t) < \pi/2$, the load torque becomes $(b/2)N(t)\sin 2\phi(t, \theta) > 0$ ⁴ and the motor speed increases, and when the motor phase is $\pi/2 \leq \theta(t) < 3\pi/2$, the motor speed decreases. Under a sufficiently large ground reaction force $N(t) \gg 0$, Eq. 6 has a stable equilibrium point $\theta = \pi/2$ and an unstable equilibrium point $\theta = 3\pi/2$.⁵ Thanks to the torque-velocity

characteristics of the motor and the limb, which supports the body weight and stays around the equilibrium point $\theta = \pi/2$, and when the external force decreases, the motor quickly drives the limb to kick the ground.

4 EXPERIMENTAL RESULT

In this section, we report on the speed-adaptive gait generation and selection due to the torque-velocity characteristics of the motor.

Figure 5 shows the experimental setting. All of the motors were connected to a power supply in parallel. In the following, we call the limbs [Left-Fore, Right-Fore, Left-Hind, and Right-Hind] as [LF, RF, LH, and RH]. The phases of the motors and the robot posture are calculated from data with a motion capture system (OptiTrack Prime13, NaturalPoint). Markers are set on the top of the motor, the tip of the crank, and the pivot of the slider. Since the robot has neither microprocessor nor sensor, we derived the limb configuration $\theta(t)$ kinematically by measuring the 3D positions of several optical markers equipped with the links by a motion capture system. The experimental videos are on <https://www.youtube.com/watch?v=VzXPOAgaCQU&feature=youtu.be>.

In the experiments, we investigate the basic gait pattern and the convergence property of the gait. In order to investigate the convergence property of the limb configuration according to the input voltage, we conducted 84 trials in total, each of which consisted of four trials from three different initial conditions under seven different input voltages ranging from 1.5 to 4.5 V. We set the initial states as follows:

- (a) $(\theta_{LF}, \theta_{RF}, \theta_{LH}, \theta_{RH}) = (\pi/2, \pi/2, \pi/2, \pi/2)$,
- (b) $(\theta_{LF}, \theta_{RF}, \theta_{LH}, \theta_{RH}) = (3\pi/2, \pi/2, 3\pi/2, \pi/2)$,
- (c) $(\theta_{LF}, \theta_{RF}, \theta_{LH}, \theta_{RH}) = (\pi/2, \pi/2, 3\pi/2, 3\pi/2)$.

Figure 6 shows the three initial conditions of motor phases.

4.1 Emerged Gaits

In order to investigate the convergence property of limb configuration, the authors visualized the sequence of phase differences of the limbs $(\theta_{RF} - \theta_{RH}, \theta_{LF} - \theta_{RH}, \theta_{LH} - \theta_{RH})$ on

⁴From $-\pi/2 \leq \theta(t) < \pi/2$ and Figure 4, we get $\sin(\phi) > 0$. Moreover, we get $\cos(\phi) > 0$ from a constraint of the slider crank mechanism $-\pi/2 < \phi(t) < \pi/2$. Therefore, $\sin(2\phi) = 2\sin(\phi)\cos(\phi) > 0$.

⁵At the equilibrium point $\dot{\theta}(t) = 0$, the limb angle satisfies $\phi(t) = 1/2 \arcsin(2\omega/\varepsilon b N(t))$. Therefore, when $N(t) \gg 0$, the limb angle becomes $\phi(t) \approx 0$. Moreover, when $\phi(t) \approx 0$, from the geometric constraint in Figure 4, the motor angle becomes $\theta(t) = \pi/2$ or $3\pi/2$. Finally, from the discussion so far, we found a stable equilibrium point $\theta = \pi/2$ and an unstable equilibrium point $\theta = 3\pi/2$.

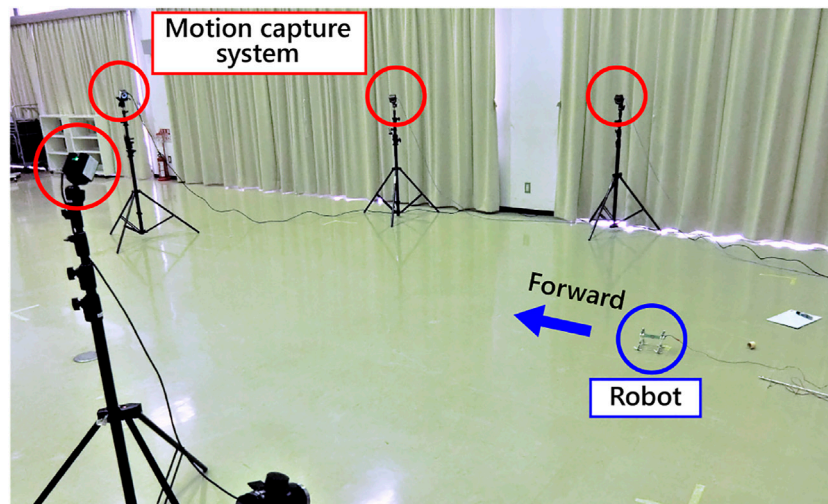


FIGURE 5 | Experimental setting.

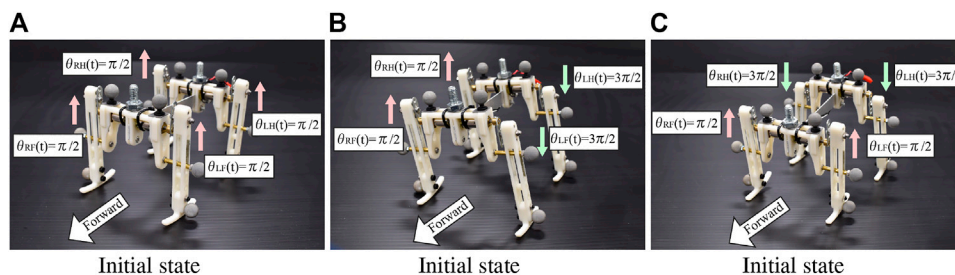


FIGURE 6 | Initial states of the robot. The motor phases are illustrated in the figures.

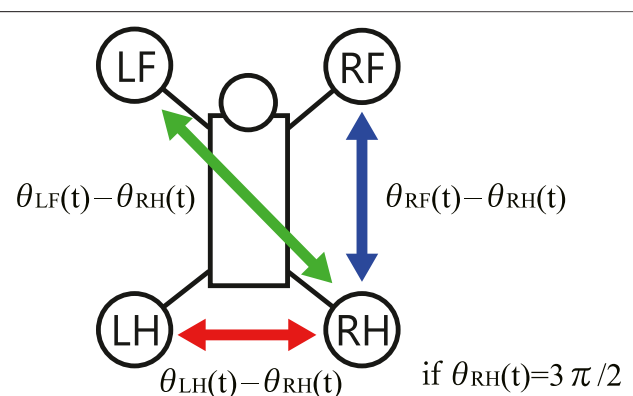


FIGURE 7 | The phase differences between the limbs on the Poincaré section.

Poincaré section when the RH limb are fully extended, namely, when the RH phase is $\theta_{RH} = (2n + 3/2)\pi$, ($n = 0, 1, 2, \dots$) as shown in Figure 7. We show the values ranging from $-3\pi/2$ to $\pi/2$ in a cyclic manner.

Figure 8 illustrates the sequences of phase differences of the limbs. The red points denote $\theta_{RF} - \theta_{RH}$, the green points are $\theta_{LF} - \theta_{RH}$, and the blue points are $\theta_{LH} - \theta_{RH}$. The authors qualitatively decided the stability of the limb configuration at each voltage as to whether or not it converged to a constant value with high repeatability. The authors qualitatively determined the gait name in the figure by comparing the typical gait pattern with the limb configuration in the figures and videos.

As shown in Figure 8, when we applied 2.5 V, the limb configuration converged to a pace gait in which the phase difference of front and hind limbs be zero, and with 4.5 V the half-bound gait emerged in which the phase difference of LH and RH limbs be zero. With low voltages such as 1.5 V and 2.0 V, we observed a bi-stable structure in which the convergence point changes depending on the initial value. Furthermore, note that when 1.5 V is applied, the robot generated a bound gait, in which the phase difference of left and right limbs was small and slightly different from the 4.5 V half-bound. In addition, although most of the gait was unstable from 3.0 to 4.0 V and a rotary gallop gait was observed in the initial state 1) at 4.0 V.

Figures 9–12 shows the gait diagram of the quadruped robot, roll, and pitch orientation. The robot has the circular foot to reduce

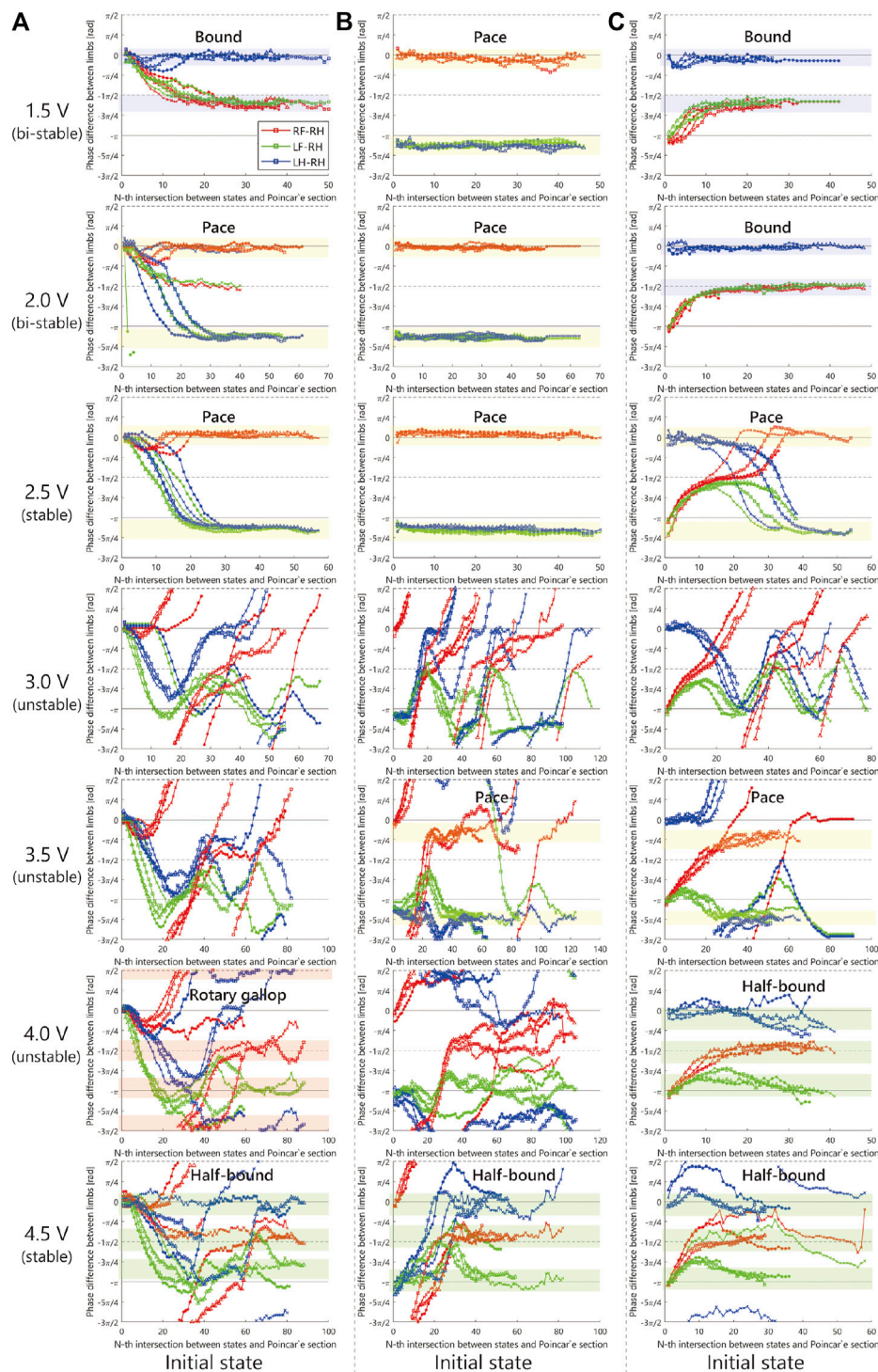


FIGURE 8 | Experimental result.

perturbation as much as possible and ground smoothly. Since the ground contact occurs at any point on the circular foot, it is difficult to detect the stance phase by the motion capture system. Therefore, in **Figures 9–12**, we illustrate the gait chart with a white region, when the leg is contracted $0 < \sin\theta$, and a black region, when the leg is

extended $\sin\theta \leq 0$. The numbers in the circle indicate the timing when each leg phase becomes $\theta = \pi/2$, assuming that the moment when $\theta_{LF} = \pi/2$ is 0 and the next $\theta_{LF} = \pi/2$ is 1.

As shown in **Figure 9**, when we applied 1.5 V to the robot, as the bound gait emerges, the side-to-side vibration in roll orientation

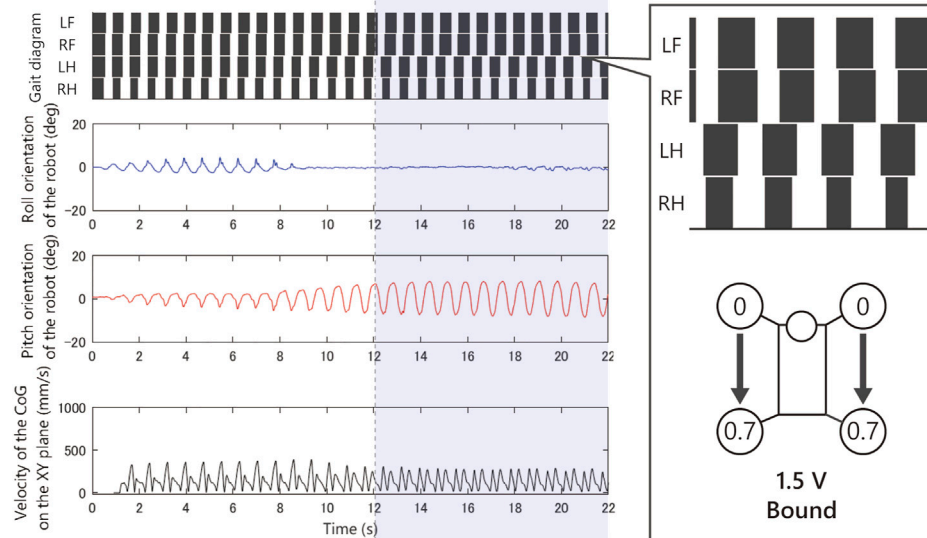


FIGURE 9 | Experimental result with an input voltage of 1.5 V. From the top: gait of the quadruped robot, roll, and pitch orientation. This bound gait emerged from only a few initial values.

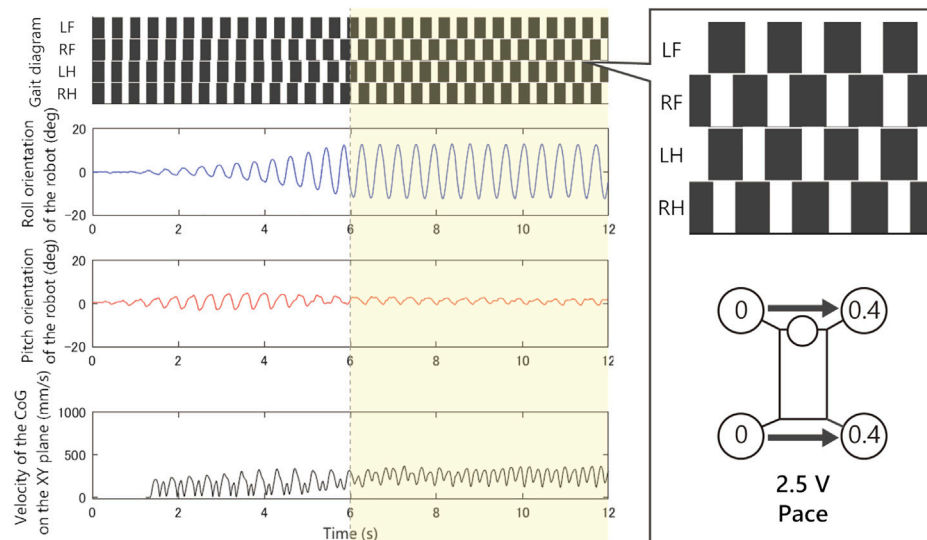


FIGURE 10 | Experimental result with an input voltage of 2.5 V. From the top: gait of the quadruped robot, roll, and pitch orientation. All the trials from the initial values converged to this pace gait.

decreases and the pitch vibration increases. On the contrary, in **Figure 10**, when we applied 2.5 V to the robot, as the pace gait emerges, the roll vibration increases and the pitch vibration decreases. On the rotary gallop gait in **Figure 11**, the vibrations increased in both roll and pitch, and on the half-bound-like transverse gallop in **Figure 11** keeps the vibration in the roll orientation to a low level.

5 DISCUSSION

5.1 Comparison With Previous Studies

The experimental results show that the brainless robot generated roughly four types of animal gaits depending on the running speed. These gaits were stabilized, exploiting only the physical

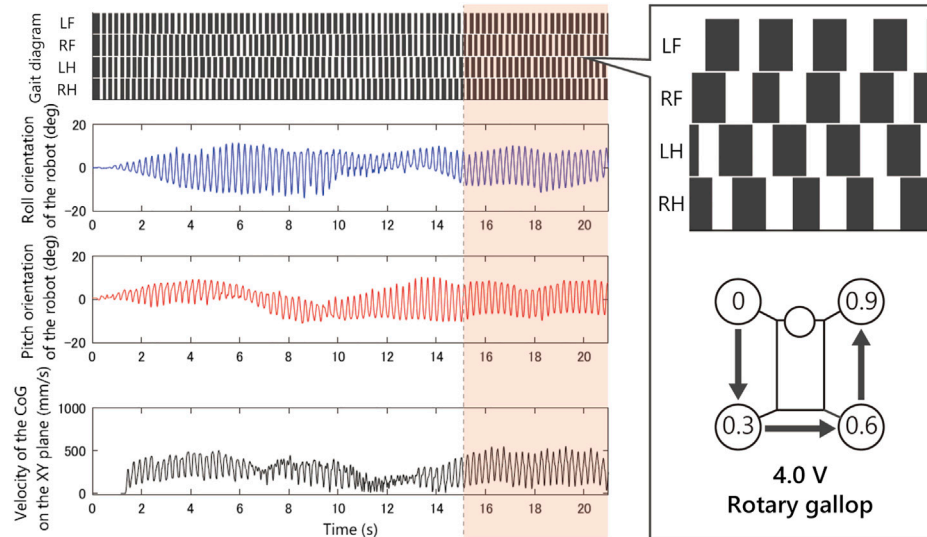


FIGURE 11 | Experimental result with an input voltage of 4.0 V. From the top: gait of the quadruped robot, roll, and pitch orientation. This rotary gallop gait emerged from only a few initial values.

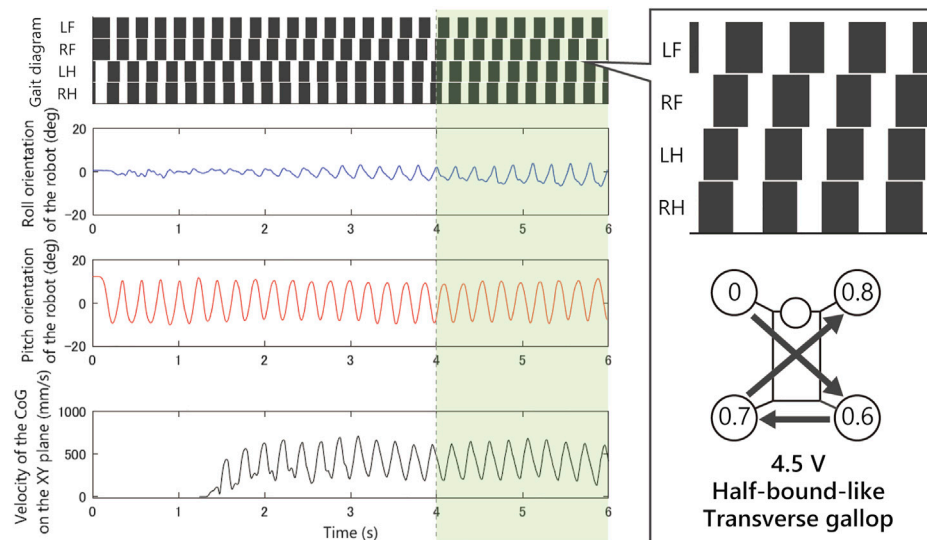


FIGURE 12 | Experimental result with an input voltage of 4.5 V. From the top: gait of the quadruped robot, roll, and pitch orientation. All the trials from the initial values converged to this half-bound-like transverse gallop gait.

interaction between the motor characteristics through the body–environment dynamics. Although some gait generation phenomena using nonneural interaction between the limbs were already reported (McGeer, 1990; Reis et al., 2013; Owaki and Ishiguro, 2017), there is no example of an active walking with multiple motors that can adaptively generate animal-like gait patterns without any sensors or controllers, to the best of the authors' knowledge. Our results provide a new example of how the actuator and body dynamics alone can generate a variety of gait.

The idea of utilizing the torque–velocity characteristics of a motor for robot control is not completely novel in itself. For example, the concept of back-drivability (Ishida and Takanishi, 2006), which allows a robot's motion to adapt to the environment, is already reported. The novelty of the phenomenon discovered in this study is that multiple motors interact and synchronize with each other through the physical body and the environment. In other words, the motor, which has been recognized as a mere actuator, actually has the function of a phase oscillator that adjusts the motion pattern of the whole robot body according

to the situation. The authors call this function as a phase oscillator, in such a motor the *compliant oscillator* (Masuda et al., 2017a).

Furthermore, the synchronization phenomenon between DC motors may be observed in other types of actuators, such as animal muscles and musculoskeletal robots. The animal muscles have force–velocity characteristics (Kandel et al., 2000), and the pneumatic artificial muscles have force–length characteristics (Klute et al., 1999). In fact, a musculoskeletal robot with pneumatic muscles (Masuda et al., 2020) generated alternating gait patterns of left and right limbs without any computer.

In addition, the motor model Eq. 6 has some interesting similarities with a CPG model proposed by (Owaki and Ishiguro, 2017). Their control law is described as follows:

$$\dot{\theta}(t) = \omega - \varepsilon N(t) \cos \theta(t). \quad (7)$$

Comparing the motor model Eq. 6 and the controller Eq. 7, the sign and the form of the function of the second term are different. Although the form of the functions are different, they share the same qualitative property of changing the phase speed in response to an external force $N(t)$. Moreover, the two formulas are symmetric because the motor Eq. 6 has the compliant property to external forces, and the controller Eq. 7 has the property of pushing back against external forces. The similarities between the emerged gait patterns of these two equations are interesting and we require further comparison and analysis.

5.2 Mechanism of Gait Generation

There are two important factors in understanding this phenomenon. The first factor is the torque–velocity characteristics of the actuator that functions as a feedback controller. The authors think that the dynamics of the motors through the linkage mechanisms Eq. 6 makes the robot generate an adaptive gait. This is because the structure of the robot is extremely simple, and there is no adaptive element other than the motor characteristics. When a limb is supporting the weight of the robot, the phase of the limb stays in place, and when the ground reaction force is decreased as the load is transferred to other limbs, the motor is driven to kick the ground. In other words, when a large external force is applied to the motor from the environment, the motor does not generate inefficient motion against the large external force. And after the peak of the external force has passed, the motor sends momentum to the body with a slight phase delay, and large-amplitude motion is effectively generated.

The second important factor of the phenomenon is the vibration mode intrinsic in the robot body. In the author's previous work (Masuda et al., 2017a), we have analyzed the synchronization mechanism of motors in more fundamental systems, such as spring–mass systems. The experiments and simulations in the article show that the synchronized DC motors converge to the resonant mode of the system and that the motors generate the resonant modes (primary, secondary, and tertiary modes) by increasing the input voltage. Although the system in this study has many nonlinearities, the basic

effects that the motor brings to the system are not very different from those of a linear system.

In the experiment Figures 8–12 with 1.5 V, at least two stable periodic solutions exist. As the voltage increased from 2.0 to 2.5 V, the bound gait was not observed, and the convergence property to the pace gait improved. And as the voltage was increased further, the pace gait disappeared from 4.0 to 4.5 V, and the gallop and half-bound gaits with a pitch oscillation emerged. From the results and analogy with phenomena observed in the previous study by Masuda et al. (2017a), we hypothesized that the phenomenon of the gait selection from pace to gallop could be interpreted as the frequency of the robot motion, which left the resonant frequency of the side-to-side motion and approached the resonant frequency of the gallop modes due to the increase in voltage. In other words, the robot body has a few vibration modes similar to the gait of an animal, and that these modes are entrained by the rotating motor with the force–velocity characteristics. We expect that a similar phenomenon may occur in the body of an animal.

5.3 Discussion of the Individual Gaits Emerged

Animals generally walk at slow speed and bound for high speed. However, the robot showed bound at slow speed. Although it is unclear why bound occurs when a low voltage is applied, we think that it is difficult to propel the body with the torque of one leg when the applied voltage is extremely low, so the leg stops until the phases of both legs become equal.

Moreover, the robot did not generate trot gait. The mechanism by which trot gait did not occur is also unclear. However, the previous study using a CPG with similar dynamics to our model (Owaki and Ishiguro, 2017) generated walk, trot, and gallop. Therefore, the authors think the first step to understanding the mechanism is to compare in detail the effects of this control law and the motor dynamics used in this study.

Notably, the asymmetric gaits appeared from the left–right symmetric robot. We expected that if the physical properties of the robot were perfectly symmetric, then either symmetric gaits would arise, or it would diverge into two types of gait (left-lead and right-lead). However, the robot generated asymmetric gaits (rotary gallop and half-bound-like transverse gallop) in the experiments. Although the mechanism that causes the convergence to asymmetric solutions is still unclear, we expect that the system is sensitive to small asymmetric errors such as individual differences of the motors, and these asymmetric errors cause the solution to converge to the asymmetric gaits.

5.4 Expected Application

We also expect synchronization between the motors to be applied as a novel control method for real-world robots. Modeling and controlling complex nonlinear systems, such as soft robots and legged robots, is very difficult. In the motion generation approach introduced in this study, some actuators embedded in the robots' whole body react immediately to stimuli from the outside world

and produce natural movement by harmonizing the body–environment dynamics. This idea would be a new approach to robot design, embedding a software-free controller throughout the body to generate adaptive whole-body movements without control.

6 CONCLUSION

In this study, we reported an example of how the actuator and body dynamics alone can generate a variety of animal gait. Although this robot does not have any sensors or microprocessors, the motors adjust their phases autonomously and finally converged to a steady gait pattern. Furthermore, by raising the input voltage from the power supply, various gaits (pace, bound, rotary gallop, and half-bound-like transverse gallop) were observed. We investigated the convergence property of the gaits for several initial states and input voltages, and described detailed experimental results of each gait observed. The analogy between the results and the previous analysis in the work by Masuda et al., 2017a suggested that the emerged gaits may be a kind of resonant mode intrinsic in the robot body.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material; further inquiries can be directed to the corresponding author.

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AUTHOR CONTRIBUTIONS

YM designed the study, contributed to experiment and analysis, and wrote the initial draft of the manuscript. KN contributed to data analysis and assisted in the preparation of the manuscript. MI contributed to the interpretation of data and assisted in the preparation of the manuscript. KO contributed to the interpretation of data and assisted in the preparation of the manuscript. All authors approved the final version of the manuscript and agree to be accountable for all aspects of the work, ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

FUNDING

This research is partially supported by JSPS KAKENHI (Grant-in-Aid for Scientific Research (S)) Grant Number JP17H06150, JSPS KAKENHI (Grant-in-Aid for Challenging Exploratory Research); Grant Number JP19K21974, JSPS KAKENHI (Grant-in-Aid for Young Scientists); Grant Number JP20K14695, and The Kyoto Technoscience Center Research and Development Grant.

ACKNOWLEDGMENTS

The authors would like to thank Kentaro Ito for fruitful discussion.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The handling editor declared a past co-authorship with one of the authors KO.

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Unified Approach to the Motion Design for a Snake Robot Negotiating Complicated Pipe Structures

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OPEN ACCESS

Edited by:

Dai Owaki,
Tohoku University, Japan

Reviewed by:

Takeshi Kano,
Tohoku University, Japan
Atsushi Kakogawa,
Ritsumeikan University, Japan

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Specialty section:

This article was submitted to
Computational Intelligence in
Robotics,
a section of the journal
Frontiers in Robotics and AI

Received: 14 November 2020

Accepted: 29 March 2021

Published: 03 May 2021

Citation:

Inazawa M, Takemori T, Tanaka M and
Matsuno F (2021) Unified Approach to
the Motion Design for a Snake Robot
Negotiating Complicated Pipe
Structures. *Front. Robot. AI* 8:629368.
doi: 10.3389/frobt.2021.629368

A unified method for designing the motion of a snake robot negotiating complicated pipe structures is presented. Such robots moving inside pipes must deal with various “obstacles,” such as junctions, bends, diameter changes, shears, and blockages. To surmount these obstacles, we propose a method that enables the robot to adapt to multiple pipe structures in a unified way. This method also applies to motion that is necessary to pass between the inside and the outside of a pipe. We designed the target form of the snake robot using two helices connected by an arbitrary shape. This method can be applied to various obstacles by designing a part of the target form specifically for given obstacles. The robot negotiates obstacles under shift control by employing a rolling motion. Considering the slip between the robot and the pipe, the model expands the method to cover cases where two helices have different properties. We demonstrated the effectiveness of the proposed method in various experiments.

Keywords: snake robots, pipe inspection, bio-inspired robots, redundant robots, motion design

1. INTRODUCTION

Despite their simple body configuration and lack of limbs, biological snakes move in a wide variety of environments, such as sandy and muddy places, in trees, and in narrow spaces. Inspired by biological snakes, snake robots with simple structures formed from repeating connecting modules have been developed and can perform various kinds of locomotion. They are expected to be used in dangerous situations, such as rescue work and infrastructure inspections, especially when spaces are narrow and inaccessible to humans, such as inside pipes. Controlling snake robots is a challenge because of their redundancy, and much research has been conducted to overcome this difficulty. The research that apply the motion observed in biological snakes, such as the undulation on the plane (Hirose, 1987) and the locomotion utilizing obstacles (Kano et al., 2018) into the engineering control of the snake robot has been done. Not only the motion but also the nervous system of biological snakes is utilized as the Central Pattern Generator (CPG) (Crespi and Ijspeert, 2008; Wu and Ma, 2013; Sartoretti et al., 2019).

Model-based control approach has also been studied. Several control methods have been developed that aid the convergence of control values toward reference values in modeling the interaction with snake robots and environments. These methods can be separated into two approaches. One considers the sideslip of the robot body (Saito et al., 2002; Mohammadi et al., 2015; Ariizumi et al., 2018), and the other considers non-holonomic constraints without sideslip

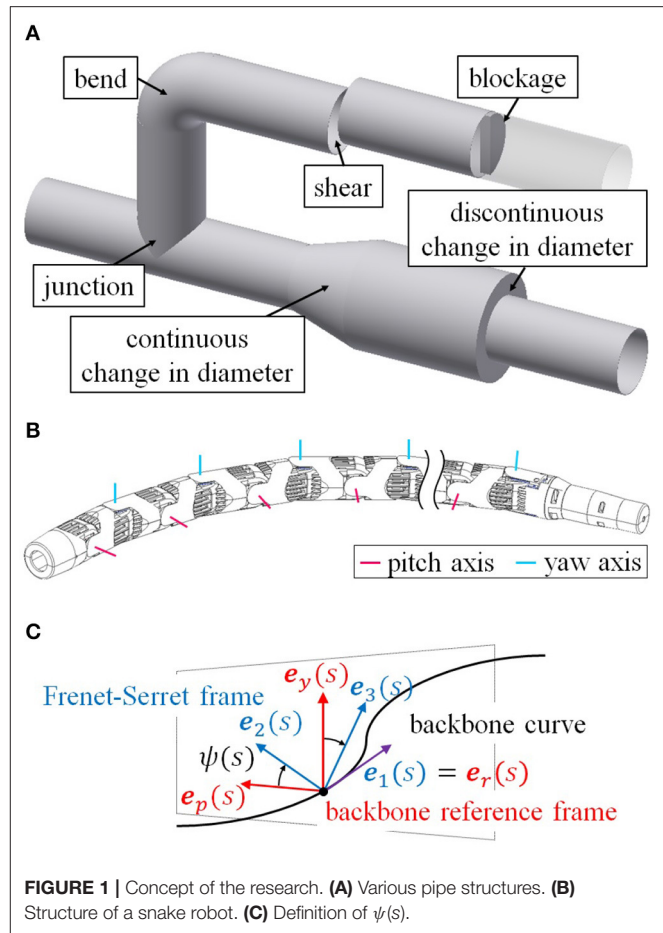
(Matsuno and Sato, 2005; Tanaka et al., 2015; Nakajima et al., 2019). These methods have the advantages of simple environments and essentially planar surfaces but are unsuitable for complex or unknown environments because it is difficult to construct the dynamic model including the interaction with such environments.

To fulfill locomotion in such complicated environments for modeling, various designs of the whole form of the robot for effective locomotion have been proposed. These methods without modeling are beneficial in challenging environments, such as in narrow spaces and pipes in which the robot makes multiple points of contact along its length. Several gaits, e.g., *lateral rolling* and *pipe crawling*, have been realized by formulating a trajectory of joint angles as a gait function and changing several gait parameters that possess clear physical characteristics (Tesch et al., 2009; Rollinson and Choset, 2016). For complicated target forms for a snake robot, however, this approach is not feasible because it is difficult to formulate target joint angles directly.

To realize locomotion based on more complex target curves, methods of designing gaits by fitting a snake robot configuration to a target curve, which is designed as a continuous curve, have been proposed (Yamada and Hirose, 2006, 2008; Andersson, 2008; Hatton and Choset, 2010; Liljebäck et al., 2014). These methods make it possible to consider snake robot configurations as continuous curves, thus making it easy to design complicated forms. Takemori et al. (2018a) expanded Yamada's method (Yamada and Hirose, 2006) and proposed a method involving the design of a target curve by connecting simple shapes. They used their proposed method to design a target form that required the robot to partially lift the body around a flange on a pipe and achieved movement over the flange. Movements over rough terrain and climbing up ladders (Takemori et al., 2018b) were also accomplished.

The research of the snake robot moving inside a pipe is on the way to the final goal of our research that is to be able to perform pipe inspections with snake robots. As shown in **Figure 1A**, there are likely to be many “obstacles” that a robot moving inside pipes will have to navigate, including junctions, bends, continuous and discontinuous changes in pipe diameter, shears, and blockages. Some of these obstacles, such as bends, junctions, and continuous changes in pipe diameter are overcome with the previous methods (Kamegawa et al., 2011; Rollinson and Choset, 2016), whereas it has been difficult to deal with discontinuous diameter changes, shears, and blockages. Also, the robot is likely to encounter various kinds of obstacles one after another in an actual pipeline system. Since previous methods are designed only for an individual obstacle, many different methods are needed to deal with many kinds of obstacles serially. However, it is impractical to seamlessly switch between disparate control methods depending on the obstacle.

To get one step closer to the final goal, we address the negotiation of the complicated pipe structures in this paper. We propose a “unified” method that enables a snake robot to deal with all obstacles in **Figure 1A**, some of which have not yet been overcome and the others of which have already been overcome, just by altering the target form of the robot partially depending on the obstacle. Consequently, we can realize the motion control



which serially negotiates various obstacles without switching to another method. In this method, the snake robot negotiates an obstacle by locally conforming to the shape of the obstacle while propelling itself forward through the pipe with a rolling motion. This method is improved by adjusting the rolling motion while considering the slip between the robot and a pipe, so as to make the method applicable to motion that includes two helices having different radii and pitches. Furthermore, this method creates a novel motion for entering and exiting a pipe. The entire motion of the robot is conducted remotely by an operator using simple inputs. We also demonstrate this unified motion, which is applicable to complicated pipe structures, to design target forms for junctions, bends, changes in pipe diameter, shears, blockages, and the inside-out motion as examples of its application. We also conduct experiments using this unified motion.

This research is based on Inazawa et al. (2020) and expands it by adding a model that considers the slip between pipe and robot in order to negotiate a change in diameter and to move from inside to outside a pipe. Finally, we carry out these experiments to verify the model.

2. PREVIOUS WORK

This section introduces the previous work mentioned in section 1 in detail.

2.1. Approximation to a Continuous Curve

Methods for calculating the joint angles of the snake robot to approximate to a continuous curve were proposed in Yamada and Hirose (2006, 2008), Andersson (2008), Hatton and Choset (2010), and Liljebäck et al. (2014). Andersson (2008) proposed a method of fitting each joint to a target curve from head to tail for an articulated robot with universal joints. Hatton and Choset (2010) proposed *annealed chain fitting*, where approximation was conducted from a head by minimizing a cost function about the distance between each joint and a target curve. Liljebäck et al. (2014) proposed a method of fitting to a continuous curve generated by connecting points in three-dimensional space. Yamada and Hirose (2008) modeled a target curve for a snake robot (Yamada and Hirose, 2006) and proposed a method of obtaining a target angle for each joint by the curvature and torsion of the curve (Yamada and Hirose, 2008).

This Yamada's method can be applied to a robot with any joint configuration and is computationally inexpensive. Various gaits employing this method have been proposed (Kamegawa et al., 2009, 2011; Baba et al., 2010; Zhen et al., 2015; Zhou et al., 2017; Qi et al., 2018; Yaqub et al., 2019). Kamegawa et al. designed a helical target form and proposed *helical rolling motion* for moving on a pipe (Kamegawa et al., 2009; Baba et al., 2010). They also proposed a *helical wave propagation motion* (Qi et al., 2018) to negotiate a branch on the pipe. By sending a waveform down the helix, this motion enabled movement in the tangential direction of the helix, which a rolling motion cannot realize. Zhen et al. (2015) designed a curve superimposing a hump onto an arc and proposed a *rolling hump* that enables movement over obstacles using a rolling motion. Zhou et al. (2017) designed a target form including two helices and a connecting curve; by expanding and contracting like a spring, the robot achieved a movement outside a pipe with a changing diameter. Yaqub et al. (2019) designed a spiral curve having a gradually changing diameter, which enables the snake robot to move outside a pipe with a discontinuous change in diameter.

When a target curve becomes more complicated, it is difficult to express the spatial curve analytically. Also, the target joint angle cannot be calculated with Yamada's method (Yamada and Hirose, 2008) when torsion at a point diverges as the curvature is zero (Yamada and Hirose, 2006). To solve these problems, Takemori et al. (2018a) expanded Yamada's method (Yamada and Hirose, 2006) and proposed a method to design a target curve by connecting simple shapes, such as straight lines, circular arcs, and helices. This method enables an intuitive design of connecting shapes with familiar properties. Also, there is no need to calculate the curvature or torsion of a curve that is already known.

2.2. Motion Inside a Complicated Pipe

Rollinson and Choset (2016) proposed a method of compliance control in which the present form of the robot can be estimated from the joint angles using an extended Kalman filter based on gait parameters. This enabled semi-autonomous adaptation to a changing environment and locomotion inside pipes having bends, junctions, and continuous changes in diameter. This method is thought to be difficult to apply to great and discontinuous changes in diameter because the whole part of the

robot winds around the pipe. Kamegawa et al. (2011) designed a target form by connecting a *bending helical curve* (Kamegawa et al., 2011) to a helix and realized movement inside a pipe with a bend. Some improvement is needed before these methods can be applied to shears and blockages, which require the robot to conform to obstacles elaborately.

3. GAIT DESIGN AND FITTING METHOD

3.1. Shape Fitting Using a Backbone Curve

The snake robot in this study consists of alternating connected pitch-axis and yaw-axis joints, as shown in **Figure 1B**. The link length is l , and the relative angle of the i -th joint is θ_i .

To start, we explain the approximation method with which we configure the snake robot to a target form (Yamada and Hirose, 2008). We begin with the representation of a spatial curve based on curvature and torsion. Let us consider the *Frenet-Serret frame*, which is an orthonormal basis ($e_1(s), e_2(s), e_3(s)$) that depends on a single parameter s associated with the length along the curve. Moreover, $e_1(s)$ is a vector tangential to the curve, $e_2(s)$ is an inward vector normal to the curve, and $e_3(s)$ is defined as $e_1(s) \times e_2(s)$. That is, the frame depends on the form of the curve. In addition, we need to consider the coordinate system that provides the orientation of the snake robot. We establish a *backbone reference frame* ($e_r(s), e_p(s), e_y(s)$) on the curve. $e_r(s)$ is the same vector as $e_1(s)$, whereas $e_p(s)$ and $e_y(s)$ are vectors in the direction of the pitch-axis and yaw-axis, respectively.

As in **Figure 1C**, $\psi(s)$ is defined as the twist angle between the Frenet-Serret frame and the backbone reference frame around $e_1(s)$ and expressed by torsion $\tau(s)$ as

$$\psi(s) = \int_0^s \tau(\hat{s}) d\hat{s} + \psi_0, \quad (1)$$

where ψ_0 is an arbitrary constant of integration corresponding to the initial value of the twist angle. Changing ψ_0 rotates the backbone reference frame around the curve and generates the *rolling motion*. The curvature around the pitch-axis and yaw-axis, denoted by $\kappa_p(s)$ and $\kappa_y(s)$, respectively, are expressible in terms of curvature $\kappa(s)$ and $\psi(s)$ as follows:

$$\kappa_p(s) = -\kappa(s) \sin \psi(s), \quad \kappa_y(s) = \kappa(s) \cos \psi(s). \quad (2)$$

Finally, we obtain the target angle of each joint as

$$\theta_i^d = \begin{cases} \int_{s_h-(i+1)l}^{s_h-(i-1)l} \kappa_p(s) ds & (i: \text{odd}) \\ \int_{s_h-(i+1)l}^{s_h-(i-1)l} \kappa_y(s) ds & (i: \text{even}) \end{cases}, \quad (3)$$

where s_h is the head position of the snake robot on the target curve. The robot transforms itself smoothly under *shift control*, by which the change in s_h shifts the range corresponding to the robot's body within a target curve.

3.2. Backbone Curve Connecting Simple Shapes

Next, we explain the method of representing the target form as connected simple shapes for which the curvature and torsion

are constant, such as straight lines, circular arcs, and helices (Takemori et al., 2018a). This method expands Yamada's method (Yamada and Hirose, 2008) to address the Frenet–Serret frames that are discontinuous at *connection-parts*, where simple shapes are brought together.

A connected simple shape is called a *segment*, and the j -th segment is referred to as *segment- j* ($j \in \mathbb{Z}$). The connection-part between segment- j and segment- $(j + 1)$ is referred to as *connection-part- j* at point $s = s_j$. Points infinitesimally before and after the connection-part- j are denoted by s_{j-} and s_{j+} , respectively. The curvature and torsion of segment- j are represented as κ_j and τ_j , respectively. Using κ_j and τ_j , the curvature $\kappa(s)$ and torsion $\tau(s)$ of the target curve at $s_{j-1} < s \leq s_j$, which is equivalent to the point on segment- j within the connected segments, are defined as

$$\kappa(s) = \kappa_j(s - s_{j-1}), \quad \tau(s) = \tau_j(s - s_{j-1}) \quad (s_{j-1} < s \leq s_j). \quad (4)$$

Let us next consider twists at the connection-part. The twist angle between $\mathbf{e}_2(s_{j-})$ and $\mathbf{e}_2(s_{j+})$ around $\mathbf{e}_1(s_{j-})$ is denoted by $\hat{\psi}_j$. To incorporate this twist angle into the calculation of shape fitting, (1) is replaced by

$$\psi(s) = \int_0^s \tau(\hat{s})d\hat{s} + \psi_0 + \sum_j \hat{\psi}_j u(s - s_j), \quad (5)$$

where $u(s)$ is the step function, for which its value is 0 if $s < 0$ and 1 if $s \geq 0$.

In this study, we use straight lines, circular arcs, and helices as segments. For a straight line, the Frenet–Serret frame and the torsion cannot be determined; in this instance, we define the torsion as 0. An arc has a constant curvature and zero torsion and is defined by its radius r_j and central angle ϕ_j . A helix has curvature and torsion that are both non-zero and constant and is defined by its radius a_j , b_j , and central angle ϕ_j . Here, $b_j = p_j/2\pi$ is satisfied, where p_j is the pitch of the helix. Let us call the angle between the tangent of the helix and the plane perpendicular to the axis of the helix the *lead angle*, expressed as $\alpha = \arctan(p_j/2\pi r_j)$. On the helix, $\mathbf{e}_2(s)$ is a vector directed vertically from the helix to the axis of the helix.

3.3. Shape Constraints

We consider the shape constraints for a target form resulting from the limits imposed on the joint angles. The maximum bending angle of a joint is represented as $\theta_{\max}$. Whereas it is difficult to consider constraints in all states, here we only consider instances where the integration range in (3) includes separately only a circular arc and only a helix.

For the first instance, we let κ_c denote the curvature of the circular arc. From (3), the condition imposed to limit the target joint angle is given by

$$\begin{aligned} |\theta_i^d| &= \begin{cases} \left| \int_{s_{h-(i+1)l}^{s_h-(i-1)l} -\kappa(s) \sin \psi(s) ds \right| & (i: \text{odd}) \\ \left| \int_{s_{h-(i+1)l}^{s_h-(i-1)l} \kappa(s) \cos \psi(s) ds \right| & (i: \text{even}) \end{cases} \\ &\leq \int_{-l}^l \kappa_c ds = 2l\kappa_c \leq \theta_{\max}. \end{aligned} \quad (6)$$

In the second instance, the curvature and torsion of the helix is denoted by κ_h and τ_h , respectively. By substituting these into (5), $\psi(s)$ is represented as

$$\psi(s) = \tau_h s + \psi_0. \quad (7)$$

Substituting this into (2), the equation is represented as

$$\kappa_p(s) = -\kappa_h \sin(\tau_h s + \psi_0), \quad \kappa_y(s) = \kappa_h \cos(\tau_h s + \psi_0). \quad (8)$$

By substituting these into (3), the condition limiting the target joint angle is expressed as,

$$\begin{aligned} |\theta_i^d| &= \begin{cases} \left| \int_{s_{h-(i+1)l}^{s_h-(i-1)l} -\kappa_h \sin(\tau_h s + \psi_0) ds \right| & (i: \text{odd}) \\ \left| \int_{s_{h-(i+1)l}^{s_h-(i-1)l} \kappa_h \cos(\tau_h s + \psi_0) ds \right| & (i: \text{even}) \end{cases} \\ &\leq \max \left[\left| \int_{-l}^l \kappa_h \sin(\tau_h \bar{s} + x) d\bar{s} \right| \quad (0 \leq x < 2\pi) \right] \\ &= \max \left[2 \left| \frac{\kappa_h}{\tau_h} \sin(\tau_h l) \sin(x) \right| \quad (0 \leq x < 2\pi) \right] \\ &\leq 2 \left| \frac{\kappa_h}{\tau_h} \sin(\tau_h l) \right| \leq \theta_{\max}, \end{aligned} \quad (9)$$

where

$$\bar{s} = s - (s_h - il), \quad (10)$$

$$x = \tau_h(s_h - il) + \psi_0. \quad (11)$$

4. MOTION DESIGN

We now discuss the target form of the proposed motion. As shown in **Figure 2A**, the target form consists of two helices on straight pipes, called the *head winding part* near the head and the *tail winding part* near the tail; an axis for each winding part, called the *head axis* and *tail axis*; a guiding part from each winding part to its respective axis, called the *head guiding part* and *tail guiding part*; and a *dodging part*, which connects two guiding parts and dodges obstacles. Tailoring this dodging part to obstacles enables the robot to adapt to various obstacles. The robot negotiates an obstacle under shift control while moving its whole body from the tail winding part to the head winding part.

We mention the purpose of guiding each end of the dodging part from the winding part to its axis. First, consider an instance where each end of the dodging part (black dotted ellipse) is not on the axis of a pipe, as shown in the left panel of the **Figure 2B**. Although discussed in detail in section 4.2.1, here we remark that each winding part rotates around its axis according to commands from the shift control, and the relative position of the two end points of the dodging part changes. It is difficult to deform the dodging part (blue line) adequately in response to this change in the relative position of two end points. To solve this, we design guiding parts to guide each end of the dodging part (black dotted ellipse) onto each axis. Although each guiding part rotates around its axis, the relative position of the two ends of the dodging part no longer changes as shown in the right panel of **Figure 2B**.

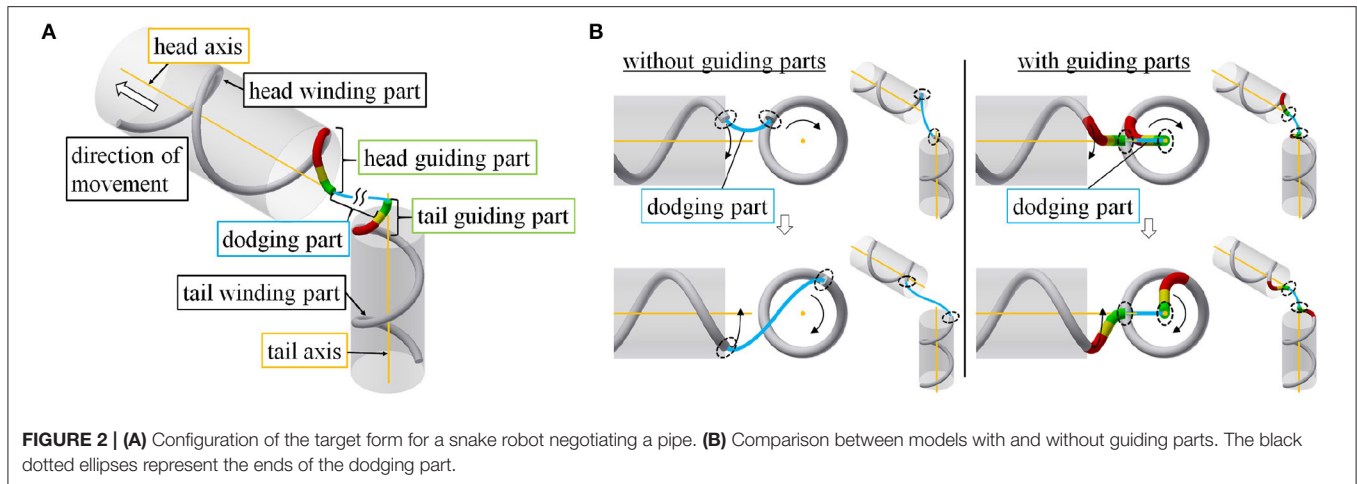


TABLE 1 | Parameters describing segments that compose the form for pipe negotiation.

Part	Seg no. j	Type	Parameter	$\hat{\psi}_j$
Tail winding part	1	Helix	$(a_j, b_j, \phi_j) = ({}^t r_w, {}^t p_w/2\pi, {}^t \beta_w)$	0
Tail guiding part	2	Helix	$(a_j, b_j, \phi_j) = ({}^t r_{in}, {}^t p_{in}/2\pi, {}^t \beta_{in})$	0
	3	Straight line	$l_j = {}^t l_s$	$\frac{\pi}{2}$
	4	Circular arc	$(r_j, \phi_j) = (r_c, \frac{\pi}{2} - {}^t \alpha)$	$\phi_{offset} + {}^t \phi_{rot}$
Dodging part	–	–	–	–
Head guiding part	$5 + n_d$	Circular arc	$(r_j, \phi_j) = (r_c, \frac{\pi}{2} - {}^h \alpha)$	0
	$6 + n_d$	Straight line	$l_j = {}^h l_s$	$\frac{\pi}{2}$
	$7 + n_d$	Helix	$(a_j, b_j, \phi_j) = ({}^h r_{in}, {}^h p_{in}/2\pi, {}^h \beta_{in})$	0
Head winding part	$8 + n_d$	Helix	$(a_j, b_j, \phi_j) = ({}^h r_w, {}^h p_w/2\pi, {}^h \beta_w)$	0

Therefore, the dodging part (blue line) easily adapts to an obstacle without deforming itself.

The winding and guiding parts are designed independently of an obstacle, whereas the dodging part is designed for it. In the following sections, we discuss the form design and the movement to realize the motion described above.

4.1. Form Design

We discuss the design of common parts regardless of obstacles. The parameters for these parts are shown in Table 1. We continue to describe each of these parts.

4.1.1. Winding Part

The radius of the tail winding part ${}^t r_w$ is given by $({}^t d_{pipe}/2) - r_{link}$, where ${}^t d_{pipe}$ is the inner diameter of the pipe on the tail side and r_{link} is the link radius of the snake robot. The pitch of the tail winding part ${}^t p_w$ is designed along with the tail guiding part, to which we turn next. The tail winding part is designed to be long enough to cover the whole body of the robot. Using the equation to obtain the length of the helix, the central angle of the

tail winding part ${}^t \beta_w$ is determined to satisfy

$$l_{robot} \leq l_1 = {}^t \beta_w \sqrt{{}^t r_w^2 + \left(\frac{{}^t p_w}{2\pi}\right)^2}, \quad (12)$$

where l_{robot} is the total length of the snake robot. The radius, pitch, and central angle of the head winding part are denoted by ${}^h r_w$, ${}^h p_w$, and ${}^h \beta_w$, respectively, and defined in a similar way to those of the tail winding part.

4.1.2. Guiding Part

Figure 3A shows the segment configuration of the guiding parts. In Table 1, n_d is the number of segments comprising the dodging part. The head and tail guiding parts have similar shapes and parameters depending on the head and tail winding parts, respectively. For this reason, we treat only the tail guiding part, whose shape is determined by ${}^t p_w$, the radius of segment-2 ${}^t r_{in}$, and the radius of segment-4 r_c .

A projection of the tail guiding part onto the xy plane in the absolute coordinate system $O - xyz$, where the z axis is equivalent to the axis of the pipe, is shown in Figure 3B. The points P, Q, R, O_w on the top of the figure are the connection-parts and have corresponding points on the bottom of the figure. O_w represents the center point of the gray circle in Figure 3B, which is the projection of segment-1 on the xy plane. Segment-2 is a helix, which changes the direction of the target curve toward the tail axis. The axis of segment-2 is designed to be parallel to the tail axis in order to simplify the geometrical calculation by turning all helices into a circle and an arc on the xy plane, as in Figure 3B. O_{in} represents the center point of the red circular arc in Figure 3B, which is the projection of segment-2 on the xy plane.

To realize this segment configuration, ${}^t p_{in}$ and ${}^t \beta_{in}$, and ${}^t l_s$ are determined after the following calculation. Since segment-1 and segment-2 are connected continuously, the angle between the xy plane and the target curve at connection-part-1 is equal to the lead angle of segment-1. If the lead angle of segment-2 is equal to that of segment-1, the axis of segment-2 is perpendicular to the xy plane and parallel to that of segment-1. To ensure that the axes

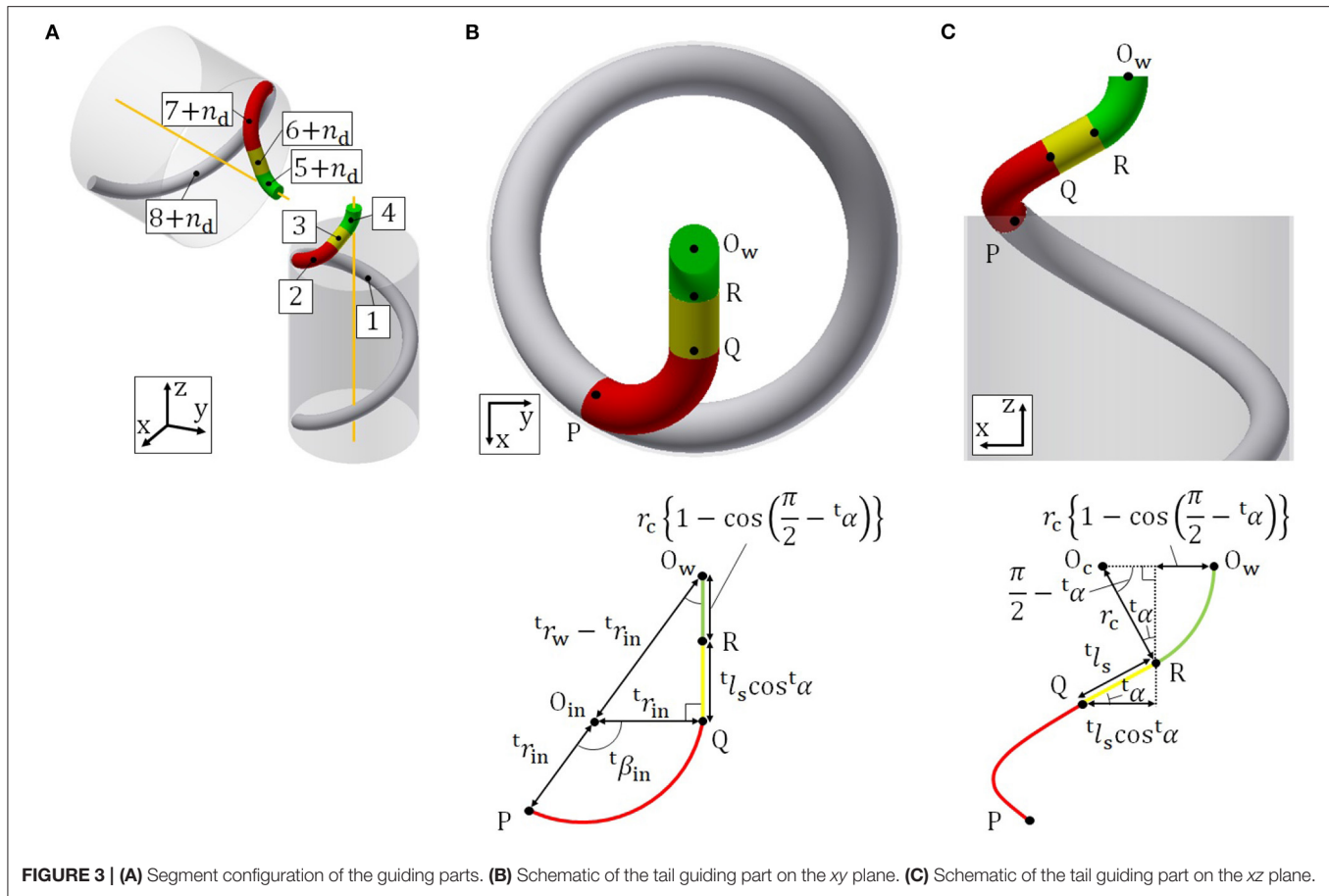


FIGURE 3 | (A) Segment configuration of the guiding parts. (B) Schematic of the tail guiding part on the xy plane. (C) Schematic of the tail guiding part on the xz plane.

of segment-2 and the tail winding part are parallel to each other, the lead angle $^t\alpha$ must satisfy

$$^t\alpha = \arctan \frac{^tp_w}{2\pi ^tr_w} = \arctan \frac{^tp_{in}}{2\pi ^tr_{in}}. \quad (13)$$

Then, we obtain $^tp_{in}$ as

$$^tp_{in} = \frac{^tr_{in}}{^tr_w} ^tp_w. \quad (14)$$

A projection of the tail guiding part onto the xz plane is also shown in **Figure 3C**. The points P, Q, R, O_w on the top of the figure are the connection-parts and have corresponding points on the bottom of the figure. O_c represents the center point of the green circular arc in **Figure 3C**, which is the projection of segment-4 on the xz plane. $^t\beta_{in}$ is derived by the geometric relationship shown in **Figure 3B** as

$$^t\beta_{in} = \angle O_{in}QO_w + \angle O_{in}O_wQ = \frac{\pi}{2} + \arcsin \frac{^tr_{in}}{^tr_w - ^tr_{in}}. \quad (15)$$

To obtain tl_s , we firstly derive O_wR and RQ in **Figure 3B** by the geometric relationship shown in **Figure 3C** as

$$RQ = ^tl_s \cos ^t\alpha, \quad (16)$$

$$O_wR = r_c \left\{ 1 - \cos \left(\frac{\pi}{2} - ^t\alpha \right) \right\}. \quad (17)$$

Then, tl_s is given by (16), (17), and the geometric relationship shown in **Figure 3B** as

$$\begin{aligned} ^tl_s &= \frac{RQ}{\cos ^t\alpha} = \frac{O_wQ - O_wR}{\cos ^t\alpha} \\ &= \frac{\sqrt{(^tr_w - ^tr_{in})^2 - ^tr_{in}^2} - r_c \left\{ 1 - \cos \left(\frac{\pi}{2} - ^t\alpha \right) \right\}}{\cos ^t\alpha}. \end{aligned} \quad (18)$$

Note that tp_w and $^tr_{in}$ should be determined while satisfying $^tl_s \geq 0$ for this segment configuration. In addition, the shape constraints described in section 3.3 also should be satisfied.

We introduce a parameter, ϕ_{offset} , that is tuned by an operator and used to adjust the direction of the dodging part appropriately to the shape of the pipe.

4.1.3. Dodging Part

The dodging part can be designed for a specific pipe structure. Section 5 provides examples relevant to a junction, bend, shear, blockage, and change in pipe diameter.

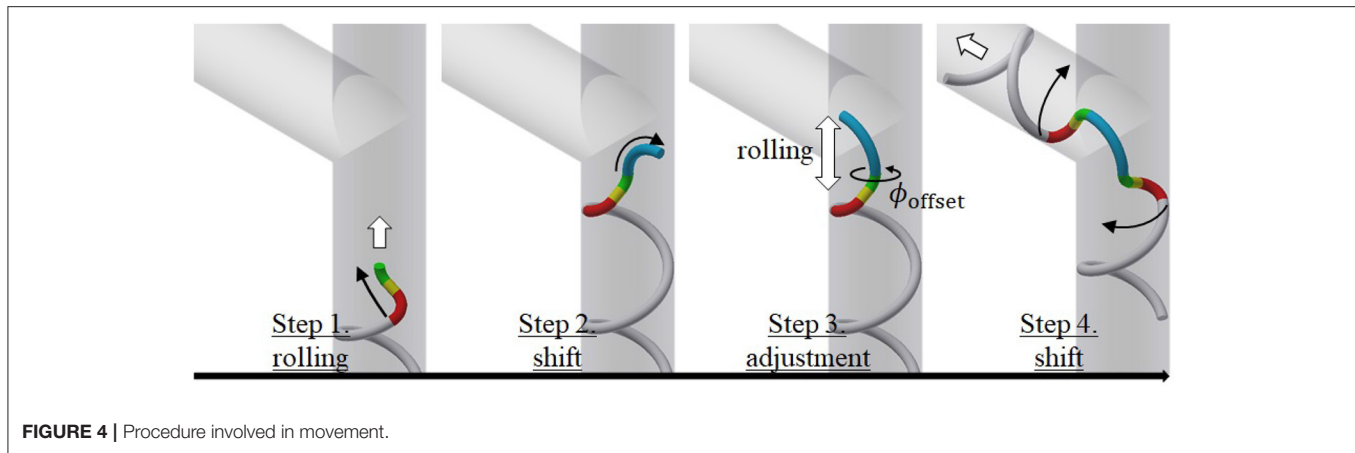


FIGURE 4 | Procedure involved in movement.

4.2. Procedure of Movement

We next explain the movement for the proposed motion. **Figure 4** shows the procedural steps involved in negotiating an obstacle. Here, we use the target form for the junction presented in section 5. The four steps in **Figure 4** are described as follows:

- Step 1: Approach the obstacle using a rolling motion (rolling angle).
- Step 2: Shift the head position to the dodging part under shift control (shift length).
- Step 3: Adjust the position of the dodging part in the axial direction with a rolling motion and the direction using ϕ_{offset} (rolling angle and ϕ_{offset}).
- Step 4: Negotiate the obstacle under shift control (shift length).

Here, an operator commands the value in parentheses in each step. The operator can recognize the dodging part with Step 2 and adjust its position and direction with Step 3. The appropriate position and direction of the dodging part in Step 3 are different for each obstacle, as described in section 5.

4.2.1. Fixing of Dodging Part

The position of the dodging part should be fixed to an environment while the robot is negotiating the pipe without colliding with the pipe in Step 4. The following figures illustrate instances for a junction. Here, no slip is assumed between the robot and pipe.

First, consider the displacement in the axial direction. As shown in the left panel of **Figure 5A**, just executing a shift control leads to the collapse of the target form because of the displacement of the dodging part in the axial direction. Therefore, this displacement caused by the shift control is canceled with a rolling motion, as shown in the right panel of **Figure 5A**. To this end, as shown in **Figure 5B**, the rolling velocity at connection-part-1 ${}^t\dot{\psi}_{\text{roll}}$ is determined by the velocity of the shift control $\dot{s}_h$,

$${}^t\dot{\psi}_{\text{roll}} = -\frac{\dot{s}_h \sin {}^t\alpha}{{}^t k_{\text{axis}}}, \quad (19)$$

where ${}^t k_{\text{axis}}$ is the displacement in the axial direction per unit rolling angle.

Second, consider the rotation around the axis. The rotation of the dodging part also breaks the target form because the direction of the dodging part becomes ill suited to the obstacle, as shown in **Figure 5C**. ${}^t\phi_{\text{rot}}$, the term in $\hat{\psi}_4$ in **Table 1**, is changed so as to cancel out the rotation of the dodging part (see **Figure 5D**). For this purpose, as shown in **Figure 5E**, ${}^t\phi_{\text{rot}}$, the time derivative of ${}^t\phi_{\text{rot}}$ is determined using $\dot{s}_h$ and ${}^t\dot{\psi}_{\text{roll}}$ by

$${}^t\dot{\phi}_{\text{rot}} = -{}^t k_{\text{rot}} {}^t\dot{\psi}_{\text{roll}} + \frac{2\dot{s}_h \cos {}^t\alpha}{{}^t d_{\text{pipe}}}, \quad (20)$$

where ${}^t k_{\text{rot}}$ is the rotation angle around the tail axis per unit rolling angle. ${}^t k_{\text{axis}}$ and ${}^t k_{\text{rot}}$ depend on the parameters of the tail winding part. It is difficult to analytically derive these values because of the fitting error of the robot and the slippage between robot and pipe. Therefore, these are actually measured in experiments in which only the rolling motion is performed.

4.2.2. Derivation for Fixing the Dodging Part

We derive the appropriate value of $\dot{\psi}_0$, the time derivative of the initial twist angle ψ_0 , to realize ${}^t\dot{\psi}_{\text{roll}}$ and ${}^h\dot{\psi}_{\text{roll}}$ in the previous section.

The point a away from the head of the robot is $s_r = s_h - a$ ($0 \leq a \leq l_{\text{robot}}$) on the target curve. From (5), $\dot{\psi}(s_r)$, the rolling velocity at $s = s_r$, is expressed as

$$\dot{\psi}(s_r) = \dot{s}_r \frac{d}{ds_r} \int_0^{s_r} \tau(\hat{s}) d\hat{s} + \dot{\psi}_0 + \frac{d}{dt} \sum_j \hat{\psi}_j u(s_r - s_j). \quad (21)$$

After substituting $s_r = s_h - a$ and rearranging the equation, this equation is expressed as

$$\begin{aligned} \dot{\psi}(s_h - a) = & \tau(s_h - a) \dot{s}_h + \dot{\psi}_0 + \sum_j \hat{\psi}_j u(s_h - a - s_j) \\ & + \sum_j \hat{\psi}_j \delta(s_h - a - s_j) \dot{s}_h, \end{aligned} \quad (22)$$

where δ is the impulse function. The impulse function has zero value except at the connection-part, where $s_h - a - s_j = 0$. On the other hand, the impulse function has non-zero value at the connection-part. However, it doesn't have any effect on

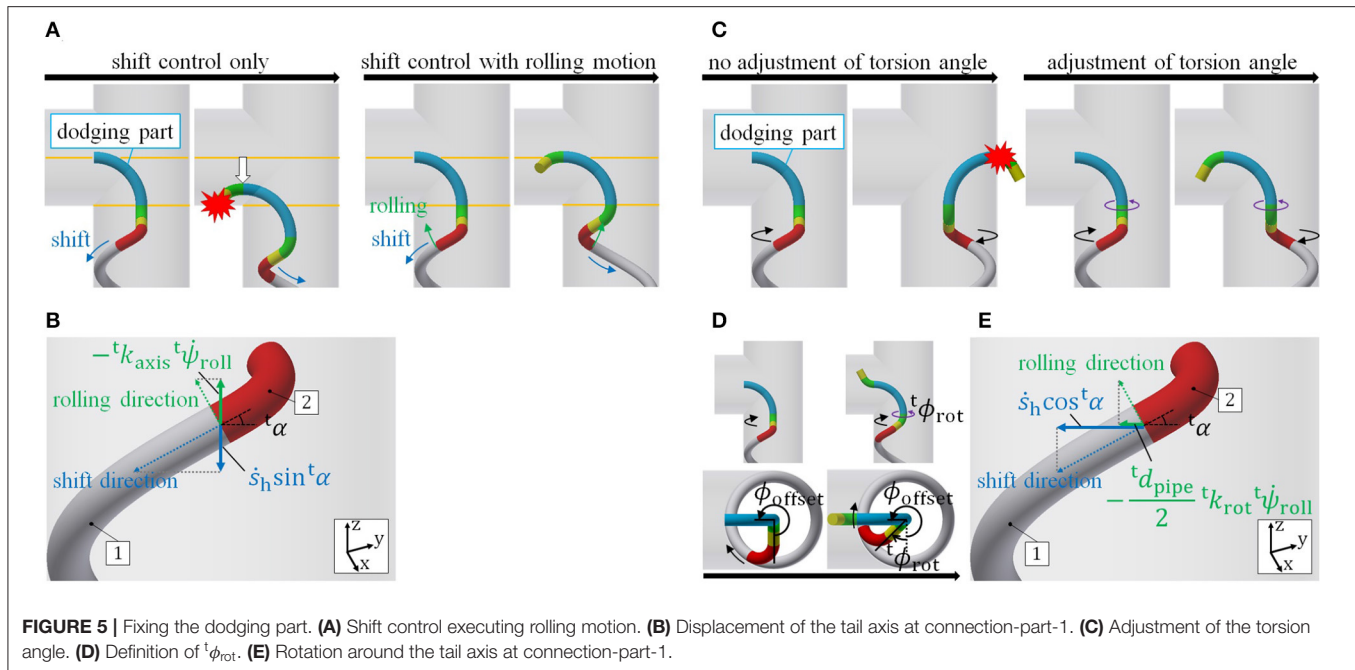


FIGURE 5 | Fixing the dodging part. **(A)** Shift control executing rolling motion. **(B)** Displacement of the tail axis at connection-part-1. **(C)** Adjustment of the torsion angle. **(D)** Definition of ${}^t\phi_{rot}$. **(E)** Rotation around the tail axis at connection-part-1.

the overall movement of the robot because the length of the connection-part is zero. Therefore, the last term on the right-hand side is negligible. The points on the tail winding part and on the head winding part in the target curve are represented as $s_r = s_h - {}^t a$ and $s_r = s_h - {}^h a$, respectively. To realize $\dot{\psi}(s_h - {}^t a) = {}^t \dot{\psi}_{roll}$ on the tail winding part and $\dot{\psi}(s_h - {}^h a) = {}^h \dot{\psi}_{roll}$ on the head winding part, the desired values of $\dot{\psi}_0$ on the tail winding part and on the head winding part are given by

$${}^t \dot{\psi}_{roll} = \dot{\psi}_0 + {}^t \tau_w \dot{s}_h, \quad (23)$$

$${}^h \dot{\psi}_{roll} = \dot{\psi}_0 + {}^h \tau_w \dot{s}_h + {}^t \dot{\phi}_{rot} - {}^h \dot{\phi}_{rot}, \quad (24)$$

where ${}^t \tau_w$ and ${}^h \tau_w$ denote the torsions of the tail and head winding parts, respectively.

When both of these winding parts have the same radius, ${}^t \dot{\psi}_{roll} = {}^h \dot{\psi}_{roll}$, ${}^t \tau_w = {}^h \tau_w$, and ${}^t \dot{\phi}_{rot} = {}^h \dot{\phi}_{rot}$. Therefore, (23) and (24) are satisfied simultaneously. This means that the fixing of the dodging part can be realized rigidly without the slip between the robot and pipe, which depends on the frictional condition and model.

However, when both winding parts have different radii, ${}^t \dot{\psi}_{roll} \neq {}^h \dot{\psi}_{roll}$, ${}^t \tau_w \neq {}^h \tau_w$ and ${}^t \dot{\phi}_{rot} \neq {}^h \dot{\phi}_{rot}$. Therefore, there is no $\dot{\psi}_0$ that satisfies (23) and (24) at the same time. For any value of $\dot{\psi}_0$, the slip occurs between the robot and pipe on one or both of the head and tail winding parts. This slip is possible to prevent the fixing of the dodging part which is based on the assumption of no slip. Hence, the model including the slip between the robot and pipe is required to realize the fixing of the dodging part.

4.2.3. Model Including Slip Between Robot and Pipe

We next consider a model that includes the slip between the robot and pipe, and aim to derive the relationship between the shift velocity, $\dot{\psi}_0$, and $\dot{\phi}_{diff}$ to fix the dodging part against the

pipe, where

$$\dot{\phi}_{diff} = {}^t \dot{\phi}_{rot} - {}^h \dot{\phi}_{rot} + \omega_{slip}. \quad (25)$$

Here, ω_{slip} is the sum of the slip angular velocity around the axis on the tail and head winding parts.

Let us assume viscous friction between robot and pipe as in Saito et al. (2002), Liljebäck et al. (2010), Ariizumi and Matsuno (2017), and Ariizumi et al. (2018). The friction is assumed to be proportional to the normal force from the pipe as in Hicks and Ito (2005) and Ariizumi and Matsuno (2017). The normal force is considered to work equally along the body of the robot and is represented as $T = \rho l_{cont}$, which is proportional to the contact length l_{cont} . ρ is the coefficient of pressure per unit contact length. Here, the equilibrium of force in the axial direction is represented as

$$\mu {}^t v_{slip} \rho {}^t l_w + \mu {}^h v_{slip} \rho {}^h l_w = 0, \quad (26)$$

where μ is the coefficient of friction, and ${}^t v_{slip}$ and ${}^h v_{slip}$ are the slip velocities in the axial direction on the tail and head winding parts, respectively. Also, ${}^t l_w$ and ${}^h l_w$ are respectively the lengths of the tail and head winding parts within the range corresponding to the robot's body in the target curve. We next consider the velocity of the dodging part against the pipe. In order to fix the dodging part against the pipe, we consider the velocity occurring by shift control, rolling motion, and slip, and make its value zero. Since the target form is connected continuously, the two ends of the dodging part have the same velocity against the pipe v_{dod} . Our purpose is to make v_{dod} zero.

4.2.3.1. Change in Pipe Diameter

In the case of a change in diameter, the velocity of the dodging part in the axial direction, as shown in **Figure 6A**, is

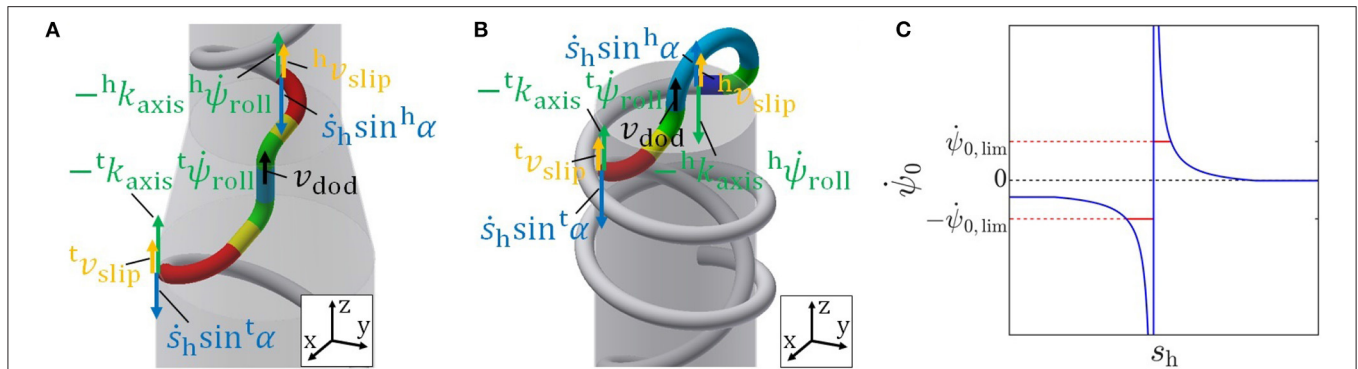


FIGURE 6 | (A) Velocity of the dodging part in the axial direction in the case of a change in diameter. **(B)** Velocity of the dodging part in the axial direction in the case of inside-out motion. **(C)** $\dot{\psi}_0$ for the inside-out motion obtained by (42).

represented as

$$\begin{aligned} v_{dod} &= -^t k_{axis} ^t \dot{\psi}_{roll} - \dot{s}_h \sin^t \alpha + ^t v_{slip} \\ &= -^h k_{axis} ^h \dot{\psi}_{roll} - \dot{s}_h \sin^h \alpha + ^h v_{slip}. \end{aligned} \quad (27)$$

Using (23), (24), and (26), (27) is rewritten as

$$v_{dod} = -^t k_{axis} \dot{\psi}_0 - (^t k_{axis} ^t \tau_w + \sin^t \alpha) \dot{s}_h + ^t v_{slip} \quad (28)$$

$$\begin{aligned} &= -^h k_{axis} \dot{\psi}_0 - (^h k_{axis} ^h \tau_w + \sin^h \alpha) \dot{s}_h - \frac{^t l_w}{^h l_w} ^t v_{slip} \\ &\quad - ^h k_{axis} \dot{\phi}_{diff}. \end{aligned} \quad (29)$$

Moreover, $\dot{\phi}_{diff}$ is expressed using $\dot{\psi}_0$, $\dot{s}_h$, and ω_{slip} by substituting (20) into (25) as

$$\dot{\phi}_{diff} = A \dot{\psi}_0 + B \dot{s}_h + \omega_{slip}, \quad (30)$$

where

$$\begin{aligned} A &= -\frac{^t k_{rot} - ^h k_{rot}}{1 - ^h k_{rot}}, \\ B &= \frac{-^t k_{rot} ^t \tau_w + \frac{2 \cos^t \alpha}{^t d_{pipe}} + ^h k_{rot} ^h \tau_w - \frac{2 \cos^h \alpha}{^h d_{pipe}}}{1 - ^h k_{rot}}. \end{aligned} \quad (31)$$

Eventually, by substituting (30) into (29), (27) is expressed as

$$v_{dod} = -^t k_{axis} \dot{\psi}_0 - (^t k_{axis} ^t \tau_w + \sin^t \alpha) \dot{s}_h + ^t v_{slip} \quad (32)$$

$$\begin{aligned} &= -^h k_{axis} (1 + A) \dot{\psi}_0 - \{^h k_{axis} (^h \tau_w + B) + \sin^h \alpha\} \dot{s}_h \\ &\quad - \frac{^t l_w}{^h l_w} ^t v_{slip} - ^h k_{axis} \omega_{slip}. \end{aligned} \quad (33)$$

As mentioned initially, our purpose is to derive $\dot{\psi}_0$ and $\dot{\phi}_{diff}$ as functions of the input value in Step 4 $\dot{s}_h$, to realize the fixing of the dodging part, i.e., $v_{dod} = 0$. In addition to three equations, (30), (32), and (33), another equation is needed to designate four variables, $\dot{\psi}_0$, $\dot{\phi}_{diff}$, $^t v_{slip}$, and ω_{slip} . We introduce the control of the balance between the slip in the axial direction $^t v_{slip}$ and slip

around the axis ω_{slip} as another equation. There is a trade-off relationship between $^t v_{slip}$ and ω_{slip} , and cannot be zero at the same time in the case of the different radii of the head and tail winding parts. Here, we deal with two extreme instances: (A) a motion that no slip occurs around the axis but slip occurs in the axial direction ($^t v_{slip} \neq 0$, $\omega_{slip} = 0$) and (B) a motion that where no slip occurs in the axial direction but slip occurs around the axis ($^t v_{slip} = 0$, $\omega_{slip} \neq 0$). In (A), the slip in the axial direction $^t v_{slip}$ should be derived based on the slip model to fix the dodging part, whereas the slip around the axis ω_{slip} is determined to be zero. In (B), the slip around the axis ω_{slip} should be derived based on the slip model to fix the dodging part, whereas the slip in the axial direction $^t v_{slip}$ is determined to be zero.

(A) No slip around the axis but slip in the axial direction:

We discuss the motion of no slip around the axis but slip in the axial direction ($^t v_{slip} \neq 0$, $\omega_{slip} = 0$) first. Since the position of the dodging part in the axial direction is designed to be fixed relying on the slip in the axial direction $^t v_{slip}$, the position is possible to be moved if there is the modeling error of the slip in the axial direction. On the other hand, the direction of the dodging part is able to be fixed precisely because there is no slip around the axis. Therefore, this motion is suitable for navigating around an obstacle for which the direction of the dodging part should be neatly fixed. In this motion, from (32), (33), and $\omega_{slip} = 0$, the velocity of the dodging part is represented as

$$v_{dod} = -\frac{^t F ^t l_w + ^h F ^h l_w}{^t l_w + ^h l_w} \dot{\psi}_0 - \frac{^t G ^t l_w + ^h G ^h l_w}{(1 - ^h k_{rot})(^t l_w + ^h l_w)} \dot{s}_h, \quad (34)$$

where

$$\begin{aligned} ^t F &= ^t k_{axis}, \\ ^h F &= \frac{1 - ^t k_{rot} ^h k_{axis}}{1 - ^h k_{rot}}, \\ ^t G &= ^t k_{axis} ^t \tau_w + \sin^t \alpha, \\ ^h G &= \frac{^h k_{axis}}{1 - ^h k_{rot}} \left(-^t k_{rot} ^t \tau_w + \frac{2 \cos^t \alpha}{^t d_{pipe}} + ^h \tau_w - \frac{2 \cos^h \alpha}{^h d_{pipe}} \right) \\ &\quad + \sin^h \alpha. \end{aligned} \quad (35)$$

Therefore, $\dot{\psi}_0$ to fix the dodging part in the axial direction, i.e., to realize $v_{\text{dod}} = 0$, is obtained by

$$\dot{\psi}_0 = -\frac{{}^tG^t l_w + {}^hG^h l_w}{{}^tF^t l_w + {}^hF^h l_w} \dot{s}_h. \quad (36)$$

Then, $\dot{\phi}_{\text{diff}}$ is calculated by substituting $\omega_{\text{slip}} = 0$ and (36) into (30) as

$$\begin{aligned} \dot{\phi}_{\text{diff}} &= A\dot{\psi}_0 + B\dot{s}_h, \\ &= \left(-\frac{{}^tG^t l_w + {}^hG^h l_w}{{}^tF^t l_w + {}^hF^h l_w} A + B \right) \dot{s}_h. \end{aligned} \quad (37)$$

(B) No slip in the axial direction but slip around the axis:

Next, let us consider the motion of no slip in the axial direction but slip around the axis (${}^t v_{\text{slip}} = 0$, $\omega_{\text{slip}} \neq 0$). Since the direction of the dodging part is designed to be fixed relying on the slip around the axis ω_{slip} , the direction is possible to be moved if there is the modeling error of the slip around the axis. On the other hand, the position of the dodging part in the axial direction is able to be fixed precisely because there is no slip in the axial direction. Hence, this motion is effective when the position of the dodging part in the axial direction has to be maintained primarily, e.g., a change in diameter whose target form is axially symmetric as described later. Using (28), (29), and ${}^t v_{\text{slip}} = 0$, $\dot{\psi}_0$ and ω_{slip} to fix the dodging part are obtained by

$$\dot{\psi}_0 = -\left({}^t\tau_w + \frac{\sin {}^t\alpha}{{}^t k_{\text{axis}}} \right) \dot{s}_h, \quad (38)$$

$$\dot{\phi}_{\text{diff}} = \left({}^t\tau_w + \frac{\sin {}^t\alpha}{{}^t k_{\text{axis}}} - {}^h\tau_w - \frac{\sin {}^h\alpha}{{}^h k_{\text{axis}}} \right) \dot{s}_h. \quad (39)$$

Note that these two motions (A) and (B) are equal to each other in the junction, bend, shear, and blockage, which can be negotiated without any slip in the axial direction and around the axis. For these cases, ${}^t v_{\text{slip}}$ and $\dot{\phi}_{\text{diff}}$ become zero, and the same result is derived as in section 4.2.1.

4.2.3.2. Motion Between Inside and Outside

We next consider a case of inside-out motion. As in the case of a change in diameter, the equilibrium of force in the axial direction is described as (26). Then, the velocity of the two ends of the dodging part, as shown in **Figure 6B**, is represented as

$$\begin{aligned} v_{\text{dod}} &= -{}^t k_{\text{axis}} {}^t \dot{\psi}_{\text{roll}} - \dot{s}_h \sin {}^t\alpha + {}^t v_{\text{slip}} = {}^h k_{\text{axis}} {}^h \dot{\psi}_{\text{roll}} \\ &\quad + \dot{s}_h \sin {}^h\alpha + {}^h v_{\text{slip}}. \end{aligned} \quad (40)$$

(A) No slip around the axis but slip in the axial direction:

We begin, as before, with the motion of no slip around the axis but slip in the axial direction (${}^t v_{\text{slip}} \neq 0$, $\omega_{\text{slip}} = 0$). From (26), (40), and $\omega_{\text{slip}} = 0$, the velocity of the dodging part is represented as

$$v_{\text{dod}} = -\frac{{}^tF^t l_w - {}^hF^h l_w}{{}^t l_w + {}^h l_w} \dot{\psi}_0 - \frac{{}^tG^t l_w - {}^hG^h l_w}{{}^t l_w + {}^h l_w} \dot{s}_h. \quad (41)$$

Therefore, $\dot{\psi}_0$ and $\dot{\phi}_{\text{diff}}$ to realize $v_{\text{dod}} = 0$ is derived by

$$\dot{\psi}_0 = -\frac{{}^tG^t l_w - {}^hG^h l_w}{{}^tF^t l_w - {}^hF^h l_w} \dot{s}_h, \quad (42)$$

$$\dot{\phi}_{\text{diff}} = \left(-\frac{{}^tG^t l_w - {}^hG^h l_w}{{}^tF^t l_w - {}^hF^h l_w} A + B \right) \dot{s}_h. \quad (43)$$

Here, $\dot{\psi}_0$ ends up diverging when the denominator ${}^tF^t l_w - {}^hF^h l_w$ becomes zero, as shown in **Figure 6C**. Therefore, we introduce the limitations $-\dot{\psi}_{0,\text{lim}}$ and $\dot{\psi}_{0,\text{lim}}$ for $\dot{\psi}_0$ so as not to require a rapid change in the joint angle that the actuator cannot realize. The effect of this limitation must be considered. Since v_{dod} is a linear function of $\dot{\psi}_0$, the sign of v_{dod} is determined by the coefficient of $\dot{\psi}_0$ and whether $\dot{\psi}_0$ is larger or smaller than $\dot{\psi}_{0,\text{lim}}$ to realize $v_{\text{dod}} = 0$ (42). Before the divergence, ${}^tF^t l_w - {}^hF^h l_w$ is positive and the coefficient of $\dot{\psi}_0$ in (41) becomes positive. Here, ${}^t l_w + {}^h l_w > 0$ satisfies because ${}^t l_w$ and ${}^h l_w$ are the lengths of the winding parts within the approximation range of the robot. $-\dot{\psi}_{0,\text{lim}}$ is smaller than $\dot{\psi}_0$ obtained by (42), as shown in **Figure 6C**. After the divergence, ${}^tF^t l_w - {}^hF^h l_w$ is negative, the coefficient of $\dot{\psi}_0$ in (41) becomes negative. $\dot{\psi}_{0,\text{lim}}$ is larger than $\dot{\psi}_0$ obtained by (42), as shown in **Figure 6C**. Therefore, v_{dod} becomes negative while the limitation is imposed on $\dot{\psi}_0$. This $v_{\text{dod}} < 0$ indicates that both the head and tail winding parts move to the side of the pipe until segment-5 contacts the pipe's edge. This phenomenon only fixes the dodging part and doesn't interfere with overall motions, such as the robot falling out of the pipe.

(B) No slip in the axial direction but slip around the axis:

We next consider the motion of no slip in the axial direction but slip around the axis (${}^t v_{\text{slip}} = 0$, $\omega_{\text{slip}} \neq 0$). This motion is also suitable for the inside-out motion because its target form is axially symmetric, as described later, and the displacement of the dodging part in the axial direction has to be maintained more appropriately than the rotation of the dodging part around the axis. Using (40), $\dot{\psi}_0$ and $\dot{\phi}_{\text{diff}}$ to fix the dodging part, i.e., to realize $v_{\text{dod}} = 0$, are obtained by (38) and (39), the same equations as in the case of the change in diameter.

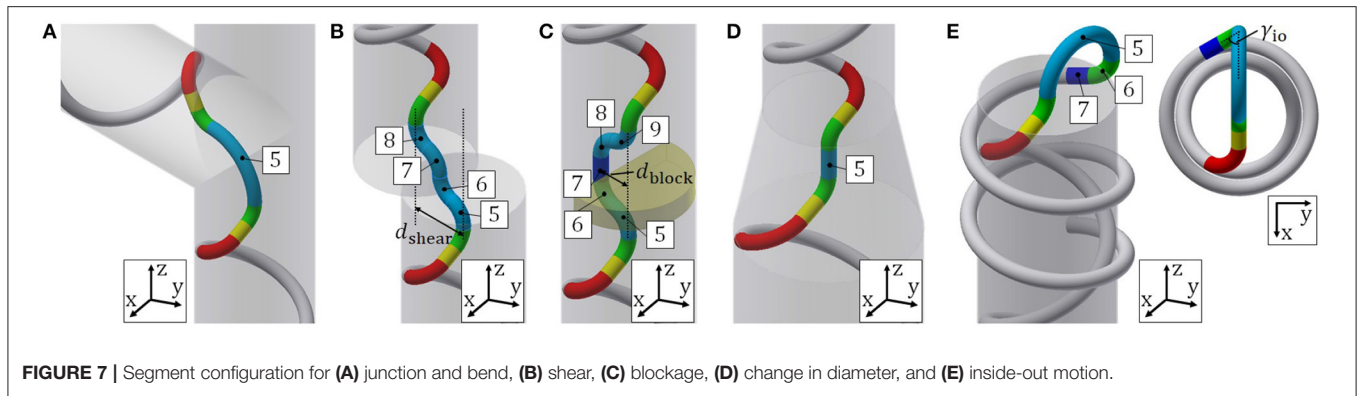
Note that the position in the axial direction of the dodging part can be compensated by the rolling motion, and the direction of the dodging part can be compensated by ϕ_{offset} if the dodging part deviates from the appropriate position and direction during movement.

5. FORM DESIGN FOR APPLICATION

In this section, we present the design of the dodging parts for a junction, bend, shear, blockage, and change in pipe diameter and the design of a guiding part for outside the pipe for the motion between the inside and outside of a pipe as examples of applications of the proposed motion.

5.1. Junction and Bend

The target form for a junction and bend is presented in **Figure 7A**. The dodging part is composed of segment-5, an arc segment, whose parameters are $(r_j, \phi_j) = (r_{\text{bend}}, \phi_{\text{bend}})$ and $\hat{\psi}_5 = \pi - {}^h\phi_{\text{rot}}$. For a junction, r_{bend} is the outer radius of a pipe and



ϕ_{bend} is the bending angle of the junction. For a bend, r_{bend} is the radius and ϕ_{bend} is the bending angle of the bend.

5.2. Shear

The target form for shear is shown in **Figure 7B**. The dodging part is composed of segments-5–8, which are arc segments whose parameters are $(r_j, \phi_j) = (r_c, \gamma_s)$, $\hat{\psi}_5 = \hat{\psi}_6 = \hat{\psi}_7 = \pi$, and $\hat{\psi}_8 = \pi - {}^h\phi_{\text{rot}}$. The dodging part is defined by the distance between the two axes of pipes d_{shear} . γ_s is calculated from,

$$\gamma_s = \arccos \left(1 - \frac{d_{\text{shear}}}{4r_c} \right). \quad (44)$$

5.3. Blockage

The target form for a blockage is illustrated in **Figure 7C**. The dodging part is composed of four arc segments-5, 6, 8, 9, whose parameters are $(r_j, \phi_j) = (r_c, \gamma_{\text{block}})$ and $(\hat{\psi}_5, \hat{\psi}_6, \hat{\psi}_8, \hat{\psi}_9) = (\pi, 0, 0, \pi, -\frac{\pi}{2} - {}^h\phi_{\text{rot}})$, and a straight line segment-7, whose parameters are $l_j = l_{\text{block}}$ and $\hat{\psi}_7 = 0$. The dodging part is determined by its width d_{block} , which is defined as the length between the axis of the pipe and the straight line segment parallel to the axis, and $l_7 = l_{\text{block}}$, depending on the shape of the blockage. The geometric parameter γ_{block} is calculated from,

$$\gamma_{\text{block}} = \arccos \left(1 - \frac{d_{\text{block}}}{2r_c} \right). \quad (45)$$

5.4. Change in Pipe Diameter

The target form for a change in pipe diameter is shown in **Figure 7D**. The dodging part is composed of segment-5, a straight line segment, whose parameters are $l_5 = l_{\text{dc}}$ and $\hat{\psi}_5 = 0$. Since the dodging part is the straight line segment and $\hat{\psi}_5 = 0$, $\hat{\psi}_4$ is determined by $\hat{\psi}_4 = \pi + \phi_{\text{offset}} + \phi_{\text{diff}}$ instead, where ϕ_{diff} is the time integral of $\dot{\phi}_{\text{diff}}$. The determination of the dodging part depends on the length of the part of the pipe where the diameter changes. This form is axisymmetric, and the direction of the dodging part does not matter. Hence we set $\phi_{\text{offset}} = 0$. Eventually, $\hat{\psi}_4$ is determined by $\hat{\psi}_4 = \pi + \phi_{\text{diff}}$.

5.5. Motion Between Inside and Outside

Expanding on the proposed motion, we propose a motion that corresponds to passing between the inside and outside of a pipe.

TABLE 2 | Parameters of the segments comprising the head guiding part for the outside of a pipe.

Seg. no. j	Type	Parameter	$\hat{\psi}_j$
5	Circular arc	$(r_j, \phi_j) = (r_{\text{io}}, \pi)$	γ_{io}
6	Circular arc	$(r_j, \phi_j) = (r_c, \frac{\pi}{2} - {}^h\alpha)$	0
7	Straight line	$l_j = l_{\text{io}}$	$-\frac{\pi}{2}$

This motion is useful when a pipe opening is difficult to approach directly or when a pipe needs to be inspected from both inside and outside. The target form for this motion is illustrated in **Figure 7E**, and the parameters for each segment are shown in **Table 2**. To begin, we design the guiding part for outside the pipe. Here segments-5–7 comprise the head guiding part, which is fixed by the radius of segment-5 r_{io} . γ_{io} and l_{io} are given by

$$\gamma_{\text{io}} = \arcsin \frac{{}^h r_w}{2r_{\text{io}}}, \quad (46)$$

$$l_{\text{io}} = \frac{\sqrt{(2r_{\text{io}})^2 - {}^h r_w^2} - r_c \left\{ 1 - \cos \left(\frac{\pi}{2} - {}^h\alpha \right) \right\}}{\cos {}^h\alpha}. \quad (47)$$

Here, r_{io} should be determined so that $l_{\text{io}} \geq 0$ holds. In this way, the proposed motion available for an arbitrary dodging part can be expanded to outside the pipe by designing guiding part for the outside. This target form does not have a dodging part, and the tail guiding part is directly connected to the head guiding part. Therefore, this motion can also be realized in the same way as for inside the pipe, by determining $\hat{\psi}_4 = \pi + \phi_{\text{diff}}$. For the motion from outside to inside a pipe, the tail guiding parts are composed of segments listed in the opposite order in **Table 2**.

6. EXPERIMENTAL RESULTS

We performed experiments to verify the effectiveness of the proposed method. The system configuration of a snake robot is illustrated in **Figure 8**. We used the snake robot developed in Takemori et al. (2018b). The snake robot has a module configuration, which has a joint and link covered by an exterior. This exterior has a pectinate shape, providing a smooth surface

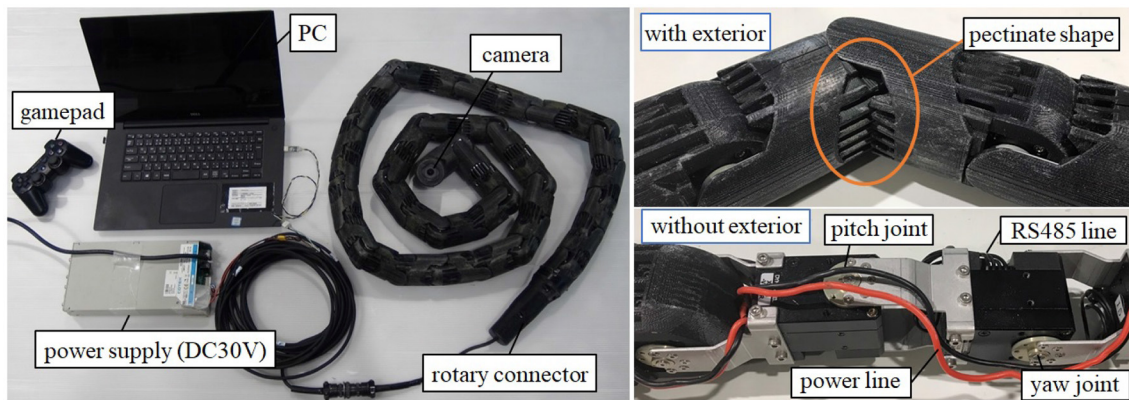


FIGURE 8 | System configuration of a snake robot developed in Takemori et al. (2018b).

TABLE 3 | Parameters used in experiments.

Pipe diameter	${}^m r_w$ mm	${}^m p_w$ mm	${}^m r_{in}$ mm	${}^m k_{axis}$ mm/rad	${}^m k_{rot}$ –
194 mm (inside)	69	501	31	24.2	0.348
194 mm (inside)	69	600	31	17.2	0.343
200 mm (outside)	128	150	–	37.8	0.0111
290 mm (inside)	117	556	53	27.1	0.187

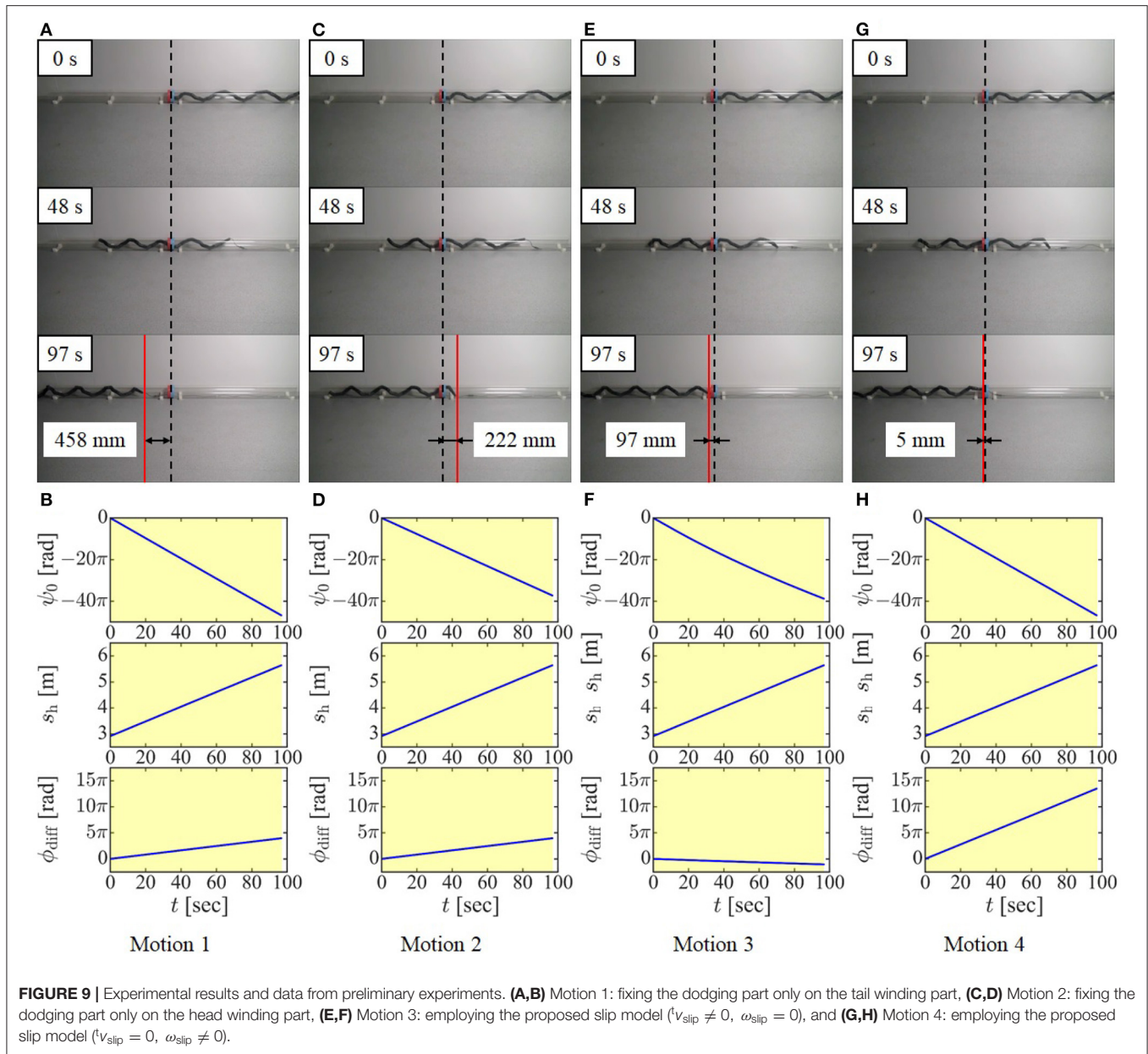
without affecting the bending of the joint. The number of joints is 36, the link length is 70 mm, the diameter of the link is 56 mm, the weight per link is 150 g, the maximum torque of a joint is 4.0 Nm, and the maximum bending angle of a joint is 90° . The motor was driven by the position control with the limitation of the current (0.3 A) to allow the compliance of the joint, and the PID gains are set as (P, I, D) = (800, 0, 100). The snake robot is powered via a cable, and the target angle for each joint is sent from a computer via an RS485 interface. The camera is mounted on the head to inspect the pipe and to help the operator control the robot remotely. The operator uses a gamepad to perform an operation.

The pipes used must have an inner diameter of 194 mm and an outer diameter of 200 mm. The only pipe used in the experiments involving a change in pipe diameter had an inner diameter of 290 mm. The parameters used in the experiments are listed in **Table 3**. Here, index m means t or h. ${}^m k_{axis}$ and ${}^m k_{rot}$ for each pipe were measured in the preliminary experiments in which only the rolling motion was performed. We determined $r_c = 90$ mm for all subsequent cases.

We measured the static coefficient between the robot surface and inner wall of the pipe. We put one unit of the robot, which is composed of one link and one joint, on the pipe and measured the tilted angle of the pipe when the unit started sliding. The unit started sliding when the tilted angle was about 16° , and then, the measured static coefficient was $\arctan 16^\circ = 0.27$. This value is the reference value because it seems to be easily changed according to the condition of contact.

6.1. Evaluation of Proposed Slip Model

First, we conducted experiments to verify the model considering the slip in cases where the head and tail winding parts have different radii based on the displacement of the dodging part in the axial direction. If two pipes have different radii, it is physically impossible for a winding part having a larger radius to enter the smaller pipe. In this case, the displacement of the dodging part toward the smaller pipe is altered constrainedly and cannot be observed correctly. Therefore, two pipes having the same diameter, 194 mm, were used instead, and the tail winding part, for this experiment only, had a larger pitch (${}^t p_w = 600$ mm) than the head winding part (${}^h p_w = 501$ mm). To clearly show the displacement of the dodging part, the head of the robot was located between the ends of two pipes at the beginning of the experiment, as indicated by the dotted line in **Figure 7**. Then, the shift control, combined with the rolling motion and the change in $\hat{\psi}_4$ calculated in Motions 1–4 [(Motion 1) considering the displacement only on the tail winding part (23), (Motion 2) considering the displacement only on the head winding part (24), (Motion 3) considering the displacement with the slip between the robot and pipe in the motion of no slip around the axis but slip in the axial direction (${}^t v_{slip} \neq 0$, $\omega_{slip} = 0$), and (Motion 4) considering the displacement with the slip in the motion of no slip in the axial direction but slip around the axis (${}^t v_{slip} = 0$, $\omega_{slip} \neq 0$)], was conducted in Step 4 until the tail of the robot reached the head guiding part. Considering the target form of the robot as shown in **Figure 7D** when $l_{dc} = 0$ mm, the tail of the robot is located just between the ends of two pipes at the end of the experiment if the dodging part is fixed properly. Therefore, we measured the position of the tail of the robot at the end of each experiment, as indicated by the red line in the image, and compared it under four conditions. Note that this experiment is focused on the fixing of the position of the dodging part only in the axial direction since it is difficult to observe the change of the direction of the dodging part in the axially symmetric target form. The results and data of these experiments are shown in **Figure 9**. When the displacement of the dodging part was considered on either the tail winding part or the head winding part (Motion 1 and Motion 2), the error was



458 or 222 mm, respectively. On the other hand, the proposed model ($\dot{v}_{slip} \neq 0$, $\omega_{slip} = 0$) (Motion 3) produced less error, 97 mm. Furthermore, the proposed model considering the slip ($\dot{v}_{slip} = 0$, $\omega_{slip} \neq 0$) (Motion 4) produced the smallest error, 5 mm. These results indicated that Motion 1 and Motion 2 produces the large errors because they ignore the effect of the slip. Motion 3 reduced the error compared with the first two motions by fixing the dodging part in consideration of the slip. However, a small error was left due to the modeling error caused by the viscous friction model or the condition of the contact in the axial direction because Motion 3 is relying on the slip in the axial direction. In contrast, Motion 4 successfully realized the fixing of the dodging part in the axial direction as expected because it did not require the slip in the axial direction and

was not affected by the modeling error of the slip in the axial direction. Consequently, the proposed motions based on the slip model both in the cases of ($\dot{v}_{slip} \neq 0$, $\omega_{slip} = 0$) and ($\dot{v}_{slip} = 0$, $\omega_{slip} \neq 0$) are regarded as effective for fixing the dodging part. The reduction of the modeling error of the slip is left as our future task.

6.2. Experiments for Various Pipe Structures

We then performed four experiments in which the robot negotiated a junction, a shear, a blockage, and a discontinuous change in diameter. As mentioned in section 5, the target form for a bend is similar to that for a junction, and the target form for a continuous change in pipe diameter is similar to that for

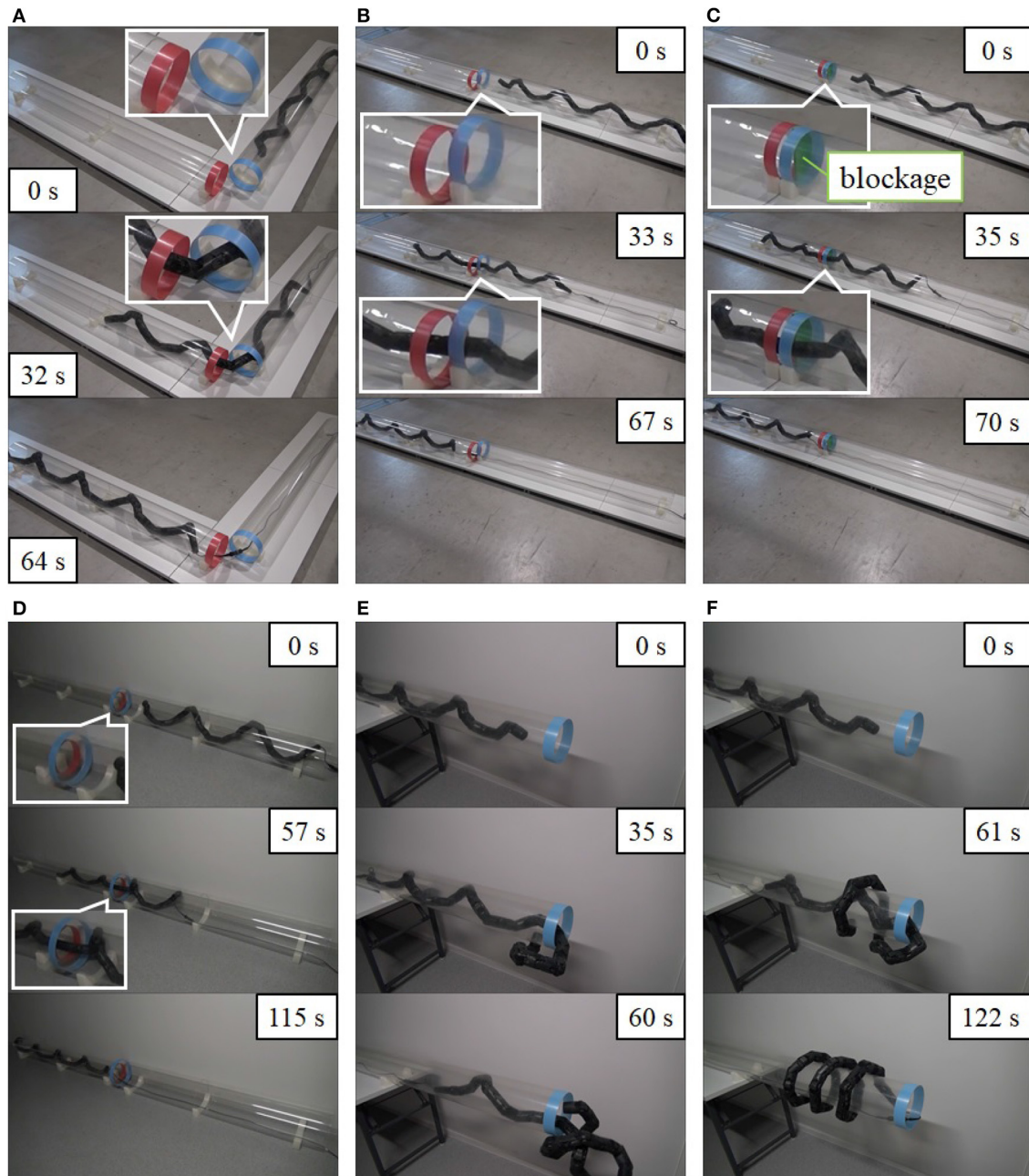
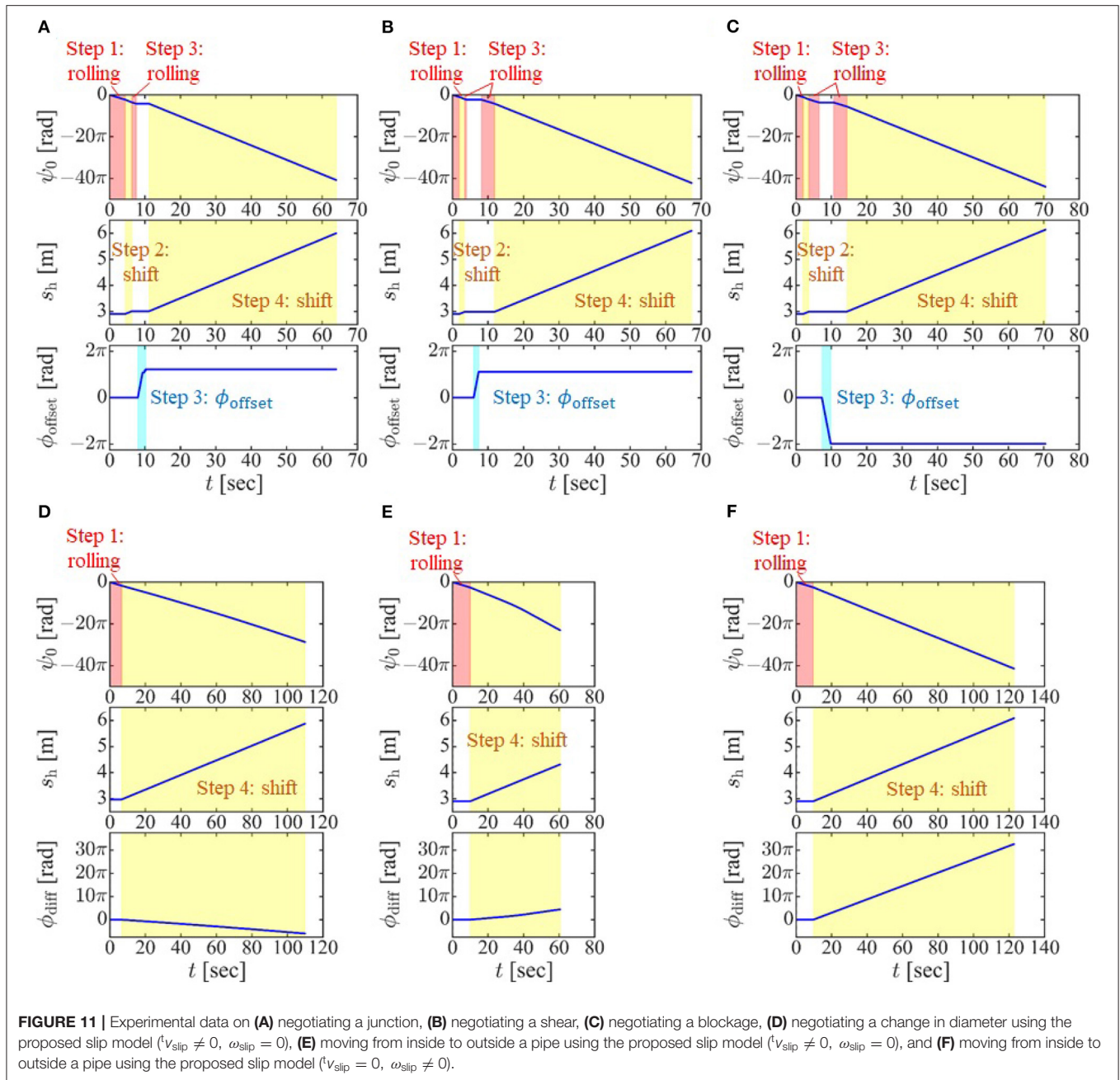


FIGURE 10 | Experimental results of **(A)** negotiating a junction ($r_{\text{bend}} = 100$ mm and $r_{\text{bend}} = 90^\circ$), **(B)** negotiating shear ($d_{\text{shear}} = 100$ mm), **(C)** negotiating a blockage (the right half of the pipe is blocked in width by 10 mm, and $d_{\text{block}} = 48.5$ mm, $l_{\text{block}} = 30$ mm), **(D)** negotiating a change in diameter (pipe inner diameter changes from 290 to 194 mm, and $l_{\text{dc}} = 0$ mm) using the proposed slip model ($\dot{v}_{\text{slip}} \neq 0$, $\omega_{\text{slip}} = 0$), **(E)** moving from inside to outside a pipe using the proposed slip model ($\dot{v}_{\text{slip}} \neq 0$, $\omega_{\text{slip}} = 0$, $r_{\text{io}} = 90$ mm, $\psi_{0,\text{limit}} = 0.03$ rad/s), and **(F)** moving from inside to outside a pipe using the proposed slip model ($\dot{v}_{\text{slip}} = 0$, $\omega_{\text{slip}} \neq 0$, $r_{\text{io}} = 90$ mm).

a discontinuous change in pipe diameter. Therefore, these four experiments can demonstrate the effectiveness of the proposed method for all pipe structures in **Figure 1A**. Also, we performed an experiment in which the movement is from inside to outside a pipe. The operator looked at the snake robot directly and performed the operation according to the procedure described in the first part of section 4.2.

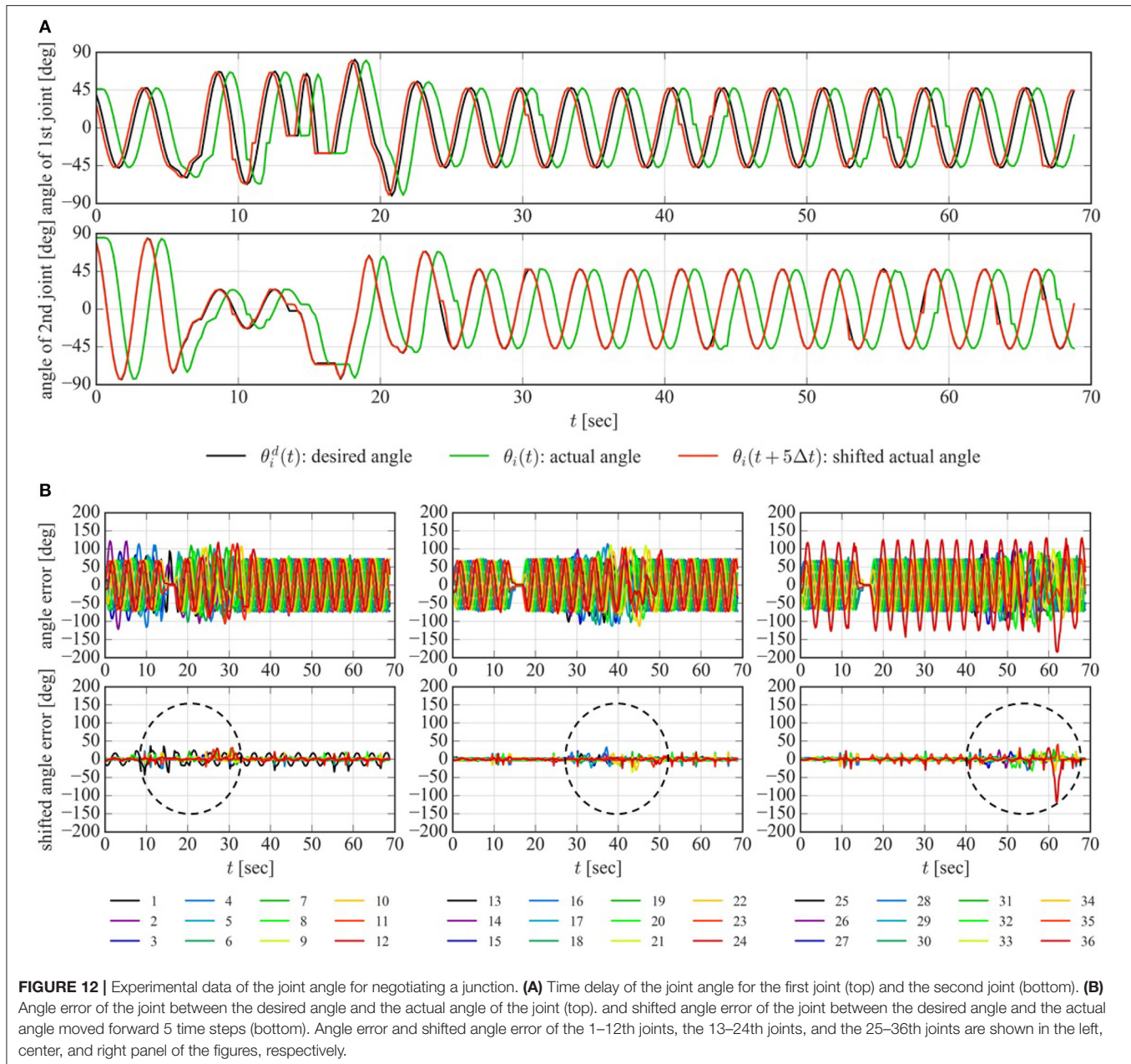
As shown in **Figures 10A–D**, the snake robot successfully negotiated the junction, shear, blockage, and change in pipe diameter. The snake robot was also able to move from the inside to the outside of the pipe, as shown in **Figure 10F**. Please also see the **Supplementary Video 1** for details. **Figure 11** indicates the values of ψ_0 , s_h , and ϕ_{offset} for each experiment. For the experiments involving a junction, shear, and blockage, the robot



was able to negotiate the pipe under shift control and rolling motion, as described in section 4.2, with only the first adjustment by the operator of the position and direction of the dodging part in Step 3.

Since the junction is the severest obstacle that does not allow the slightest deviation of the position and direction of the dodging part, the experiment to verify the angle error of the joint between the desired angle and the actual angle was also conducted for negotiating a junction. Due to the limitation of the communication speed, the time step of this experiment ($\Delta t = 0.2$ s) is 10 times as large as that of the other experiments to obtain the joint angle. As shown in Figure 12B, the actual angle

of the joint $\theta_i(t)$ (green line) lagged behind the desired angle $\theta_i^d(t)$ (black line). This steady delay is thought to be caused by the communication delay to send the desired angle to each joint and receive the actual angle from each joint and the time delay needed to change the angle of each joint from the actual angle to the desired angle due to the limitation of the speed of the motor. The length of the time delay was about five steps for every joint except the first joint, which responded one time step earlier than the others. The actual angle moved forward five steps $\theta_i(t + 5\Delta t)$ (red line) matched the desired angle well for the second joint as shown in the bottom of the Figure 12A, although the error about one time step was left only for the first joint. The angle error



between the desired and actual angle for each joint ($\theta_i(t) - \theta_i^d(t)$) is depicted in the top of the **Figure 12B**. To eliminate the effect of the time delay, the angle error between the desired and shifted actual angle for five time steps for each joint ($\theta_i(t) - \theta_i^d(t + 5\Delta t)$) is depicted in the bottom of the **Figure 12B**. As shown in the bottom of the **Figure 12B**, the comparatively large angle error of the joint was moved from head to tail with the passage of time. This indicates that the angle error was observed near the dodging part as enclosed with dotted lines in **Figure 12B** and the dodging part deviates from the appropriate position and direction to some extent. In addition, the error of the last joint, 36th joint, is quite large at $t = 62$ s. This is because the tail link is longer than the other links and was caught by the pipe when it passed through the

junction. The error of the position and direction of the dodging part is thought to be compensated by two factors caused by the robot's geometric constraints: the compliant adaptation to the environment at the joint thanks to the position control of the motor with the limitation of the torque, and the slippage between the robot and the pipe.

Also, the robot was able to negotiate the change in diameter with the proposed model considering the slip between the robot and the pipe even when the radii of the head and tail winding parts differed. **Figure 10D** shows only the result of the proposed model ($\tau_{\text{slip}} \neq 0$, $\omega_{\text{slip}} = 0$), but the model ($\tau_{\text{slip}} = 0$, $\omega_{\text{slip}} \neq 0$) also worked successfully; see **Supplementary Video 1**. In contrast, the robot failed to move from inside to outside the pipe

using the proposed slip model ($v_{\text{slip}} \neq 0$, $\omega_{\text{slip}} = 0$), as in **Figure 10E**, and succeeded to do so only with the proposed slip model ($v_{\text{slip}} = 0$, $\omega_{\text{slip}} \neq 0$) **Figure 10F**. As shown in the middle panel of **Figure 10E**, the robot was unable to support the part of itself that was below the pipe due to the torque limitation of the motor, and the head winding part did not contact the pipe and receive the friction force, contrary to what we had expected. Hence, the dodging part moved the right side of the image, although in theory it was expected to move to the left side of the image after $\dot{\psi}_0$ reached $-\dot{\psi}_{0,\text{limit}}$. This effect led the robot to fall out of the pipe. On the other hand, since the experiment shown in **Figure 10F** was conducted using the proposed slip model ($v_{\text{slip}} = 0$, $\omega_{\text{slip}} \neq 0$), the dodging part did not deviate from the proper position in the axial direction even though the robot was not always able to press its body against the pipe. Instead, the rotation of the robot around the axis was found to be caused by the slip around the axis. In addition, due to the torque limitation of the motor, the robot is likely to failed to support the head winding part for both **Figures 10E,F** of the revised paper depending on the initial orientation of the robot and the protective function of the motor, which made the motor output torque zero when the motor detects the persistent load that exceeds maximum output.

7. CONCLUSION

A unified approach was proposed for designing the motion that enables a snake robot to negotiate complicated pipe structures. The proposed method enables the robot to overcome various obstacles by designing the dodging part, which is part of the target form, specifically for the obstacle. To realize this, both ends of the dodging part are arranged on the axes of the pipes with guiding parts. In addition, we developed a method of fixing the dodging part to an obstacle during obstacle negotiation that involved an appropriate combination of rolling motion and shift control. Also, we constructed a model considering slippage between robot and pipe, and expanded the proposed method to make it applicable to motions that require two helices having different radii, i.e., the motion for change in diameter and the motion between inside and outside of a pipe. We conducted experiments to verify the effectiveness of these methods and demonstrated that the snake robot successfully negotiated not only a junction, which was already realized, but also a shear, a blockage, and a discontinuous change in pipe diameter, which were impossible previously. We also realized movement from inside to outside a pipe in an experiment.

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We shall in a future study consider a way to conduct remote operations more easily. Currently, the operator has to adjust appropriately the relative position of the dodging part to the environment. Also, experiments are now conducted in the ideal situation where the operator can recognize the state of the robot by directly looking at the robot through the transparent pipe. We also leave as a future task the realization of autonomous movement by detecting a pipe structure using sensors given no parameter values. Finally, another task for the future is a kinematic/dynamic analysis of the motion to keep the appropriate contact with the pipe.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

MI: writing the paper, developing the theory, and running experiments. TT: developing the theory, running experiments, providing feedback to theoretical and experimental results, and providing feedback on drafts of the report. MT and FM: developing the theory, providing feedback to theoretical and experimental results, and providing feedback on drafts of the report. All authors contributed to the article and approved the submitted version.

FUNDING

This work was partially supported by the ImPACT Program of the Council for Science, Technology and Innovation (Cabinet Office, Government of Japan).

ACKNOWLEDGMENTS

The content of this manuscript has been presented in part at the IEEE International Conference on Robotics and Automation (Inazawa et al., 2020).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frobt.2021.629368/full#supplementary-material>

Supplementary Video 1 | Pipe negotiation.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Tegotae-Based Control Produces Adaptive Inter- and Intra-limb Coordination in Bipedal Walking

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Despite the appealing concept of central pattern generator (CPG)-based control for bipedal walking robots, there is currently no systematic methodology for designing a CPG-based controller. To remedy this oversight, we attempted to apply the Tegotae approach, a Japanese concept describing how well a perceived reaction, i.e., sensory information, matches an expectation, i.e., an intended motor command, in designing localised controllers in the CPG-based bipedal walking model. To this end, we developed a Tegotae function that quantifies the Tegotae concept. This function allowed incorporating decentralised controllers into the proposed bipedal walking model systematically. We designed a two-dimensional bipedal walking model using Tegotae functions and subsequently implemented it in simulations to validate the proposed design scheme. We found that our model can walk on both flat and uneven terrains and confirmed that the application of the Tegotae functions in all joint controllers results in excellent adaptability to environmental changes.

OPEN ACCESS

Edited by:

Zlatko Matjacic,
University Rehabilitation Institute,
Slovenia

Reviewed by:

Andrej Olenšek,
University Rehabilitation Institute,
Slovenia

Patrick Henaff,
Université de Lorraine, France

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Received: 27 November 2020

Accepted: 07 April 2021

Published: 12 May 2021

Citation:

Owaki D, Horikiri S, Nishii J and
Ishiguro A (2021) Tegotae-Based
Control Produces Adaptive Inter- and
Intra-limb Coordination in Bipedal
Walking.
Front. Neurobot. 15:629595.
doi: 10.3389/fnbot.2021.629595

Keywords: bipedal walking, central pattern generator, inter- and intra-limb coordination, Tegotae, adaptability

1. INTRODUCTION

The human body is capable of astoundingly adaptive and versatile locomotion when faced with real-world constraints. For robots to possess similar capabilities, their bodies must have comparable degrees of freedom (DOFs) more significant than those implemented in existing designs. Most previously developed centralised approaches to improving humanoid locomotion (Hirai et al., 1998; Sakagami et al., 2002; Hirukawa et al., 2004; Kaneko et al., 2004; Hirose and Ogawa, 2007), where one centralised controller regulates each DOF to continually track the desired trajectory of each point in the robot's body. However, this centralised approach is not suitable for systems with relatively large DOFs, leading to increased computational cost and reduced adaptability to unpredictable environmental changes.

Alternatively, autonomous decentralised control has received considerable attention because it offers the flexibility required for a robot with many DOFs to coordinate its movement successfully. In fact, animals deftly coordinate the many DOFs of their bodies using distributed neural networks called central pattern generators (CPGs), which are responsible for generating rhythmic movements, particularly locomotion (Shik et al., 1966; Grillner, 1975, 1985). Such knowledge about animal locomotion has been referenced by various researchers to incorporate artificial CPGs into legged robots for generating highly adaptive locomotion (Taga et al., 1991; Taga, 1994, 1995; Kimura et al., 1999, 2007; Fukuoka et al., 2003; Tsujita et al., 2003; Aoi and Tsuchiya, 2005, 2006; Buchli et al., 2006; Ijspeert, 2008; Righetti and Ijspeert, 2008).

CPG-based bipedal walking control originated in the pioneering work done by Taga et al. (1991) and Taga (1994, 1995). In these studies, sensory information from the environment was fed back to a nervous system model to generate walking from the interaction between the nervous system model, musculoskeletal model, and environment (“Global Entrainment”). Aoi and Tsuchiya (2005) and Aoi and Tsuchiya (2006) focused on “phase resetting” (Schomburg et al., 1998), a feedback mechanism found in animals, to add gait stabilisation in CPG-based control models. Furthermore, the feedback law based on phase resetting is suitable for musculoskeletal models (Aoi et al., 2010), which are more similar to humans. For generating stable motion in a bipedal robot through entrainment between a controller and robot motion, Morimoto et al. (2006) modelled the controller of the robot as an oscillator and the motion phase based on the position and velocity information of the centre of pressure (CoP) in the lateral direction of the robot, to achieve stepping and walking motions. Nassour et al. (2014) developed a two-layer CPG model for walking control in a humanoid robot: a rhythm generator layer and pattern formation layer (Rybak et al., 2006; McCrea and Rybak, 2008). They also attempted to generate non-periodic motions using neuron models that generate various signals such as periodic and non-periodic signals as components. Quadrupedal robots have been studied more intensively due to their dynamic stability and variety of walking patterns: Kimura et al. (1999) and Fukuoka et al. (2003) proposed a model integrating CPG and reflex mechanisms to realise uneven terrain walking; Tsujita et al. (2003) implemented the phase resetting in a quadrupedal walking model to actualise a stable walking pattern; Buchli et al. (2006) proposed an adaptive frequency oscillator that learns the motion frequency adaptively and verified the generation of gait according to the body characteristics; In addition, a model that employs load information as sensory information and generates adaptive and diverse walking patterns has been proposed thus far (Maufroy et al., 2010; Fukuoka et al., 2015; Owaki and Ishiguro, 2017). However, there is currently no systematic methodology for designing a CPG-based controller, as each CPG-based model has been custom-designed for a specific practical situation.

To address this oversight, we attempted to construct a CPG-based bipedal walking model with a localised joint-controller design based on the Tegotae approach (Owaki et al., 2017; Kano et al., 2019), which is a Japanese concept that focuses on how well a perceived reaction matches an expectation. We quantified the Tegotae concept by creating the Tegotae function, which is the quantified product of what a localised controller wants to achieve and its resulting reaction. The Tegotae function allows the systematic design of decentralised controllers with localised sensory feedback. The feedback scheme allows the operation of each localised controller based on consistency between the generated action and perceived reaction. Specifically, the Tegotae function increases in the case of consistency and decreases in the case of inconsistency. Here, we show how the Tegotae approach can be implemented in a decentralised control scheme for bipedal walking robots and validates the system by evaluating its adaptability to environmental changes.

2. BIPEDAL WALKING MODEL

2.1. Musculoskeletal Structure

To validate the Tegotae-based control scheme, we conducted simulations using a two-dimensional bipedal walking model. **Figure 1A** shows the musculoskeletal structure of the bipedal walking model, the movements of which were constrained in the sagittal plane for simplicity. The structure consists of 13 mass points (i.e., the trunk, waist, hip, knees, ankles, heels, metatarsals, and toes) and 14 rigid links that connect these mass points. For simplicity and ease of modelling the musculoskeletal system, we employed a model with masses located in the joints. The body parameters, e.g., link length, mass distribution, were set to approximately match the corresponding human body parameters in Ogihara and Yamazaki (2001). The model includes seven actuators at the waist, hip joints, knee joints, and ankle joints; each actuator was designed to generate joint torque based on proportional-derivative (PD) control, as explained in section 2.2. Passive springs and dampers have been integrated into the toe joints to passively generate an effective push-off force at the end of the stance phase. Based on human and animal locomotion research, that show the role of cutaneous receptors in the foot in controlling the gait (Nurse and Nigg, 1999, 2001; Dietz and Duysens, 2000; Duysens et al., 2000; Eils et al., 2002; Elis et al., 2004), we modelled plantar sensation by incorporating sensors to detect the vertical and horizontal ground reaction forces (GRFs) ($N_{x,i}^V$ and $N_{x,i}^H$, respectively) exerted at heel ($x = h$), metatarsal ($x = m$), and toe ($x = t$) points. Here, the suffix i denotes leg ($i = 0$: left and $i = 1$: right). In this study, the equations of motion were constructed as dynamics of mass points. For each mass point, the following forces were applied: force due to gravity, force applied by the links modelled with a rigid spring and damper, force applied by the actuators of each joint, and force applied by the passive spring and damper at toe joints. The details are described in the **Supplementary Material**.

2.2. Implementation of Tegotae Approach in a Systematic CPG-Based Control Scheme

The proposed control system for adaptive bipedal walking consists of four components (**Figure 1B**): (1) hip controllers, (2) knee controllers, (3) ankle controllers, and (4) a posture controller. The first three components utilise Tegotae functions to coordinate the inter- and intra-limb movements to enable adaptive walking, whereas the fourth component stabilises the upper body using the waist actuator and vestibular sensor.

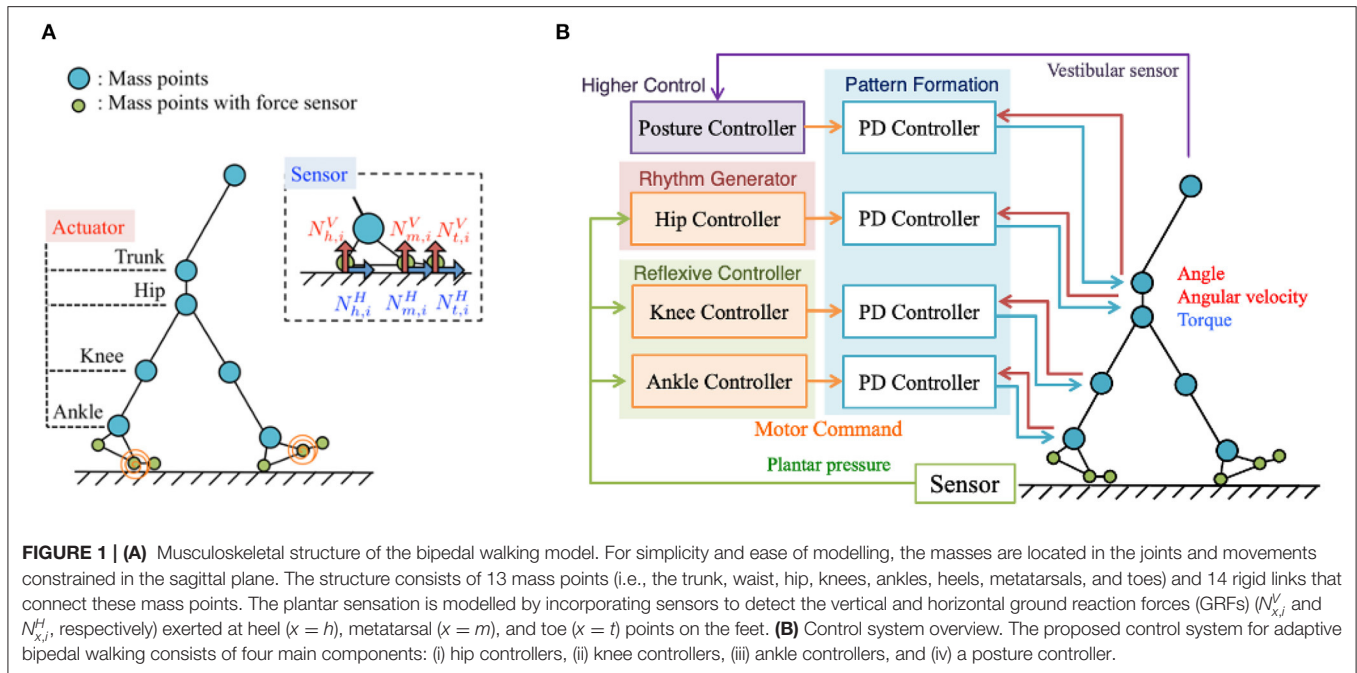
The hip, knee, ankle, trunk joint torques $\tau_{y,i}$ in each i th leg (y indicates one of the joints) are generated by the PD control mechanism, which is dependent on the target angles determined by the hip, knee, ankle, and posture controllers. These torques are calculated as follows:

$$\tau_{hip,i} = -K_{hip}(\theta_{hip,i} - \bar{\theta}_{hip,i}) - D_{hip}\dot{\theta}_{hip,i}, \quad (1)$$

$$\tau_{knee,i} = -K_{knee,i}(\theta_{knee,i} - \bar{\theta}_{knee,i}) - D_{knee}\dot{\theta}_{knee,i}, \quad (2)$$

$$\tau_{ankle,i} = -K_{ankle}(\theta_{ankle,i} - \bar{\theta}_{ankle,i}) - D_{ankle}\dot{\theta}_{ankle,i}, \quad (3)$$

$$\tau_{trunk} = -K_{trunk}(\theta_{trunk} - \bar{\theta}_{trunk}) - D_{trunk}\dot{\theta}_{trunk}, \quad (4)$$



where $\theta_{y,i}$ and $\bar{\theta}_{y,i}$ represent the actual and target angles, respectively, for Joint y in the i th leg, and K_y and D_y represent the proportional and derivative gains of the PD controller for Joint y , respectively. The hip, knee, and ankle joint controllers use the Tegotae function to modulate the target angles $\bar{\theta}_{y,i}$ or proportional gains K_y for adaptive walking. The parameters for PD gains are shown in **Supplementary Tables 1, 2**. The remaining section describes the Tegotae function and concept of Tegotae-based control, including a comprehensive explanation of each controller.

2.2.1. Tegotae Functions

As explained in section 1, Tegotae is a Japanese concept centred around the extent to which a generated action matches a perceived reaction. In robotics, it is the consistency between the intended motor command from a controller and received sensory information based on the motion generated by the controller. Thus, quantification of the Tegotae concept yielded a Tegotae function that can be described as the product of the (i) intended motor command of a controller $f(x)$, where x denotes the control variable, and (ii) resulting sensory information $g(S)$ obtained in the form of sensor values, S , as follows:

$$T(x, S) = f(x)g(S). \quad (5)$$

The Tegotae function was created such that the positive/negative values output by the function indicate consistency/inconsistency between the intended motor command and resulting sensory information.

2.2.2. Tegotae-Based Control

Using the Tegotae function $T(x, S)$, we can modulate the localised control variable x as follows:

$$\dot{x} = h(x) + \frac{\partial T(x, S)}{\partial x}, \quad (6)$$

where the first term on the right represents the intrinsic dynamics of the localised controller, and second term represents the Tegotae-based localised sensory feedback for the control variable x . Using the sensory feedback determined by the partial differential form of the Tegotae function, the controller can modulate its control variable x such that it maximises the Tegotae-based consistency with the expectation. Thus, we can design a systematic control scheme for many components by creating Tegotae functions for each controller. We next describe the localised hip, knee, and ankle joint controllers with Tegotae function-based designs.

2.3. Design of Joint Controllers

2.3.1. Hip Control

The role of the hip joints in human gait is to generate rhythmic forward and backward leg-swinging movements (Perry and Burnfield, 2010). To enable such rhythmic movements, we incorporated phase oscillators as a component of the CPG-based model to generate the target angle for the hip actuators (Equation 1) as follows:

$$\bar{\theta}_{hip,i} = -C_{1,hip} \cos \phi_i + C_{2,hip}, \quad (7)$$

where $C_{1,hip}$ and $C_{2,hip}$ [rad], respectively, represent the amplitude and offset components of the hip target angle. When implementing the oscillator phases, legs are controlled to remain

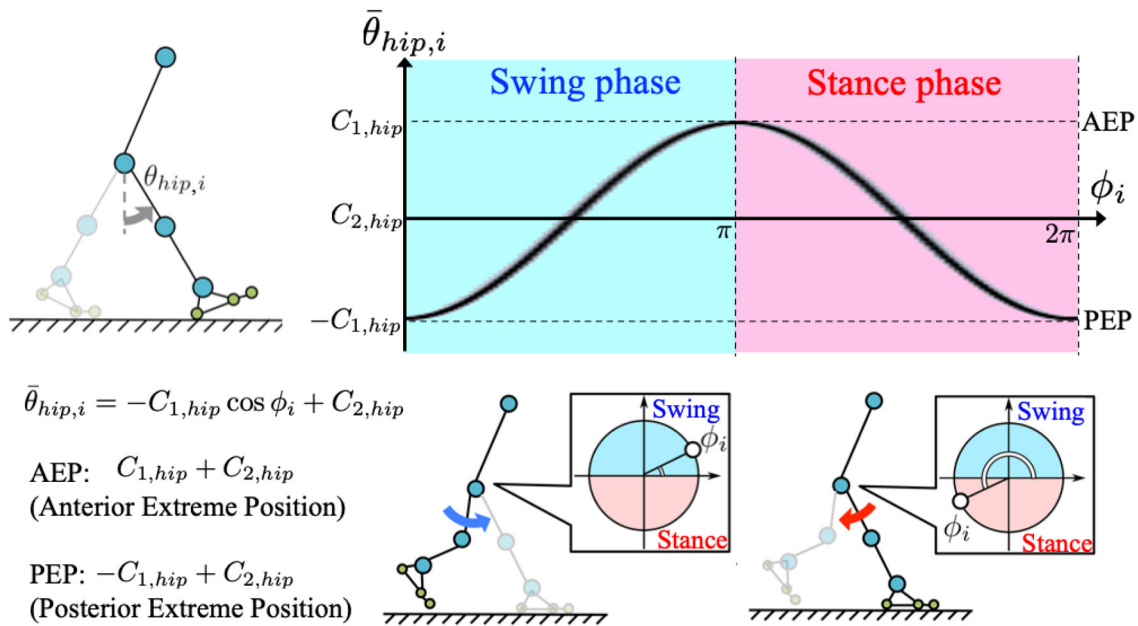


FIGURE 2 | Generation of target angle in hip joint control: we incorporated a phase oscillator as a component of the CPG-based model to generate target angle for the corresponding hip actuator. The target angle is described by $\bar{\theta}_{hip,i} = -C_{1,hip} \cos \phi_i + C_{2,hip}$, where $C_{1,hip}$, and $C_{2,hip}$ are amplitude and offset angles of the hip target angle, respectively. According to the equation, posterior and anterior extreme positions (PEP and AEP, respectively) of the target angle result in $-C_{1,hip} + C_{2,hip}$ ($\phi_i = 0, 2\pi$) and $C_{1,hip} + C_{2,hip}$ ($\phi_i = \pi$), respectively. Therefore, legs are controlled to be in the swing phase for $0 \leq \phi_i < \pi$, and in the stance phase for $\pi \leq \phi_i < 2\pi$.

in the swing phase for $0 \leq \phi_i < \pi$, and stance phase for $\pi \leq \phi_i < 2\pi$ (Figure 2).

The dynamics of the phase oscillators with the localised Tegotae function-based sensory feedback can be described as follows:

$$\dot{\phi}_i = \omega + \frac{\partial T_{hip,i}(\phi_i, \mathbf{N})}{\partial \phi_i}, \quad (8)$$

where ω [rad/s] represents the intrinsic angular velocity of the oscillators. The Tegotae function for hip control has been defined as follows:

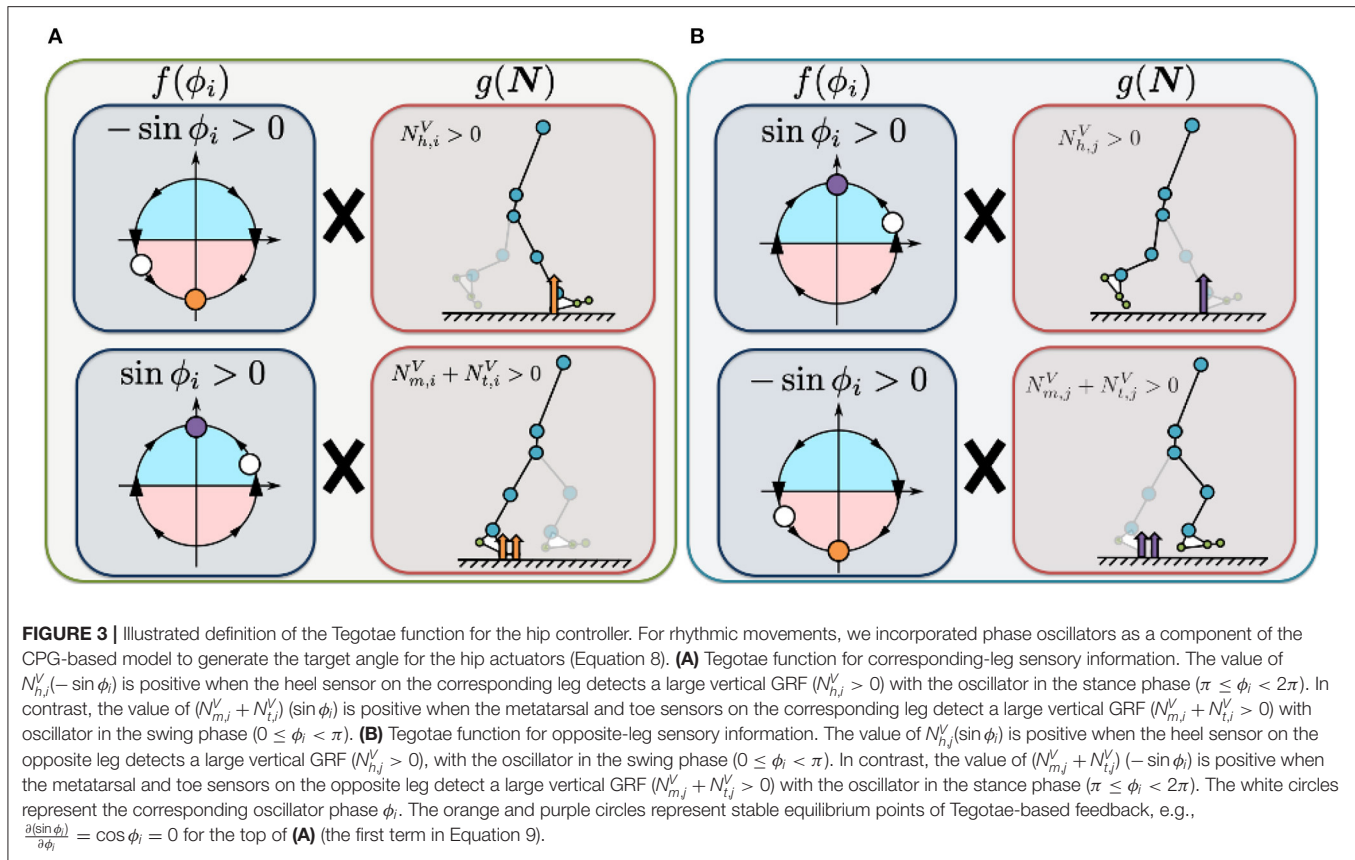
$$T_{hip,i}(\phi_i, \mathbf{N}) = \sigma_{hip,1} \{N_{h,i}^V(-\sin \phi_i) + (N_{m,i}^V + N_{t,i}^V)(\sin \phi_i)\} \\ + \sigma_{hip,2} \{N_{h,j}^V(\sin \phi_i) + (N_{m,j}^V + N_{t,j}^V)(-\sin \phi_i)\}, \quad (9)$$

where $\sigma_{hip,1}$ and $\sigma_{hip,2}$ [rad/Ns] represent the feedback gains. The suffixes i and j denote the corresponding leg and other leg, respectively.

The first term on the right describes how the Tegotae function is applied in the case of sensory information for the corresponding leg (Figure 3A). The value of $N_{h,i}^V(-\sin \phi_i)$ is positive when the heel sensor on the corresponding leg detects a large vertical GRF ($N_{h,i}^V > 0$) with the oscillator in the stance phase ($\pi \leq \phi_i < 2\pi$). Increasing this Tegotae term allows the leg to remain in the stance phase as it supports the body ($N_{h,i}^V > 0$). In contrast, the value of $(N_{m,i}^V + N_{t,i}^V)(\sin \phi_i)$ is positive when the metatarsal and toe sensors on the corresponding leg detect a large

vertical GRF ($N_{m,i}^V + N_{t,i}^V > 0$) with the oscillator in the swing phase ($0 \leq \phi_i < \pi$). In this case, increasing the Tegotae term results in the leg transitioning from the stance to swing phase ($N_{m,i}^V + N_{t,i}^V > 0$), propelling the body forward.

The second term describes how the Tegotae function is applied in the case of sensory information for the opposite leg (Figure 3B). The value of $N_{h,j}^V(\sin \phi_i)$ is positive when the heel sensor on the opposite leg detects a large vertical GRF ($N_{h,j}^V > 0$), with the oscillator in the swing phase ($0 \leq \phi_i < \pi$). Increasing this Tegotae term allows the corresponding leg to remain in the swing phase as the opposite leg supports the body ($N_{h,j}^V > 0$); this support allows the corresponding leg to complete the swing phase successfully. In contrast, the value of $(N_{m,j}^V + N_{t,j}^V)(-\sin \phi_i)$ is positive when the metatarsal and toe sensors on the opposite leg detect a large vertical GRF ($N_{m,j}^V + N_{t,j}^V > 0$) with the oscillator in the stance phase ($\pi \leq \phi_i < 2\pi$). Under these conditions, an increase in the Tegotae term results in the corresponding leg initiating a smooth transition from the swing to stance phase ($N_{m,j}^V + N_{t,j}^V > 0$). Here, we do not use any neural synaptic connections between the hip oscillators; previous studies achieved the desired rhythmic walking motion by manually setting the neural synaptic connectivity parameters in advance (e.g., Taga et al., 1991; Nassour et al., 2014). Implementation of the Tegotae-based localised feedback scheme described by Equation (8) allows the hip controllers to achieve interlimb coordination in the absence of any neural communication between oscillators.



2.3.2. Knee Control

The roles of a knee joint in human gait (Perry and Burnfield, 2010) are as follows: (1) support the body by increasing its stiffness in the stance phase (2) increase the effective flexion by reducing its stiffness in the swing phase. Thus, we established the control variable χ_i , representing the control command that increases/decreases the knee joint stiffness. To implement this stiffness control mechanism, we use χ_i to adjust the gain $K_{knee,i}$ in the knee controllers, as follows:

$$\tau_{knee,i} = -K_{knee,i}(\theta_{knee,i} - \bar{\theta}_{knee,i}) - D_{knee}\dot{\theta}_{knee,i}, \quad (10)$$

$$K_{knee,i} = \max[C_{1,knee} \tanh \chi_i, 0] + C_{2,knee}, \quad (11)$$

where $C_{1,knee}$ and $C_{2,knee}$ [Nm/rad] represent the variable range and offset value of the gain $K_{knee,i}$, respectively. We used tanh function to model continuous on/off-like function (scaled from -1.0 to 1.0) according to the control variable χ_i . In Equation (2), the target angle θ_{knee} for the knee controllers was set to 0 [rad]; this angle indicates the degree of knee extension and determines whether the stiffness should be increased/decreased to extend/flex the knee joint.

The dynamics of the control variable χ_i for the localised Tegotae function-based sensory feedback scheme can be described as follows:

$$\dot{\chi}_i = -c_{knee}\chi_i + \frac{\partial T_{knee,i}(\chi_i, \mathbf{N})}{\partial \chi_i}, \quad (12)$$

where c_{knee} represents the parameter related to its response time for the first-order dynamical model of the knee controller. The reason for choosing a first-order model was its simplicity (only one parameter c_{knee}) and non-rhythmic behaviour, meaning that it stays at an equilibrium point ($\dot{\chi}_i = 0$) without feedback. The Tegotae function for knee control is defined as follows:

$$T_{knee,i}(\chi_i, \mathbf{N}) = \sigma_{knee,1}N_i^V\chi_i + \sigma_{knee,2}N_j^V(-\chi_i), \quad (13)$$

$$N_i^V = N_{h,i}^V + N_{m,i}^V + N_{t,i}^V, \quad (14)$$

$$N_j^V = N_{h,j}^V + N_{m,j}^V + N_{t,j}^V, \quad (15)$$

where N_i^V and N_j^V [N] represent the sums of the vertical force sensor values corresponding to the heel, metatarsal, and toe joints of the corresponding and opposite legs, respectively. The parameters $\sigma_{knee,1}$ and $\sigma_{knee,2}$ [1/N] represent the feedback gains. The first term on the right represents the Tegotae function for the corresponding leg (Figure 4A). The value of $N_i^V\chi_i$ is positive when the foot sensors on the corresponding leg detect a large vertical GRF ($N_i^V > 0$) and the control command for the knee is to increase the stiffness (i.e., $\chi_i > 0$). Increasing this Tegotae term causes the knee stiffness to remain high to ensure that the body is supported ($N_i^V > 0$). The second term represents the Tegotae function for the opposite leg (Figure 4B). The value of $N_j^V(-\chi_i)$ is positive when the foot sensors on the opposite leg detect a large vertical GRF ($N_j^V > 0$) and the control command for the knee

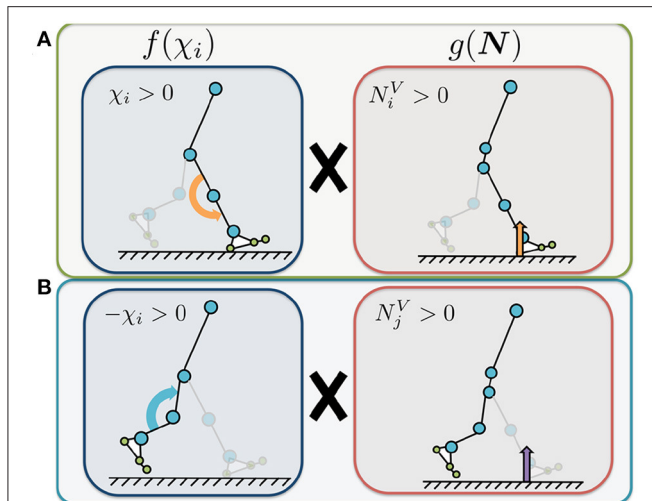


FIGURE 4 | Illustrated definition of the Tegotae function for the knee controller. The control variable χ_i represents the control command that increases or decreases the knee joint stiffness (Equation 9). We use χ_i to adjust the P-gain $K_{knee,i}$ in the knee controllers for the implementation of stiffness control mechanism, in Equation (10). N_i^V and N_j^V represent the sums of the vertical force sensor values corresponding to the heel, metatarsal, and toe joints of the corresponding (i) and opposite (j) legs, respectively. **(A)** Tegotae function for corresponding-leg sensory information. The value of $N_i^V \chi_i$ is positive when the foot sensors on the corresponding leg detect a large vertical GRF ($N_i^V > 0$) and the control command for the knee is to increase the stiffness (i.e., $\chi_i > 0$). **(B)** Tegotae function for opposite-leg sensory information. The value of $N_j^V (-\chi_i)$ is positive when the foot sensors on the opposite leg detect a large vertical GRF ($N_j^V > 0$) and the control command for the knee is to decrease the stiffness (i.e., $\chi_i < 0$).

is to decrease the stiffness (i.e., $\chi_i < 0$). Increasing this Tegotae term ensures that the knee stiffness remains low to allow the knee to bend during the swing phase as the opposite leg supports the body ($N_j^V > 0$); this state allows the corresponding leg to swing forward in the swing phase.

2.3.3. Ankle Control

The role of an ankle joint in human gait (Perry and Burnfield, 2010) is to generate the propulsive forces necessary for the leg to transition from the stance to swing phase while avoiding a collision between the foot and ground. Therefore, we established the control variable ψ_i for the ankle controllers, which represents the control command that increases or decreases the target angle of the ankle joints as follows:

$$\bar{\theta}_{ankle,i} = C_{1,ankle} \tanh \psi_i + C_{2,ankle}, \quad (16)$$

where $C_{1,ankle}$ and $C_{2,ankle}$ [rad] represent the variable range and offset value of the ankle target angle, respectively. We used tanh function to model continuous on/off-like function (scaled from -1.0 to 1.0) according to the control variable ψ_i . A positive/negative value of ψ_i represents the plantar/dorsal flexion of an ankle joint.

The dynamics of the control variable ψ_i for the localised Tegotae function-based sensory feedback method can be

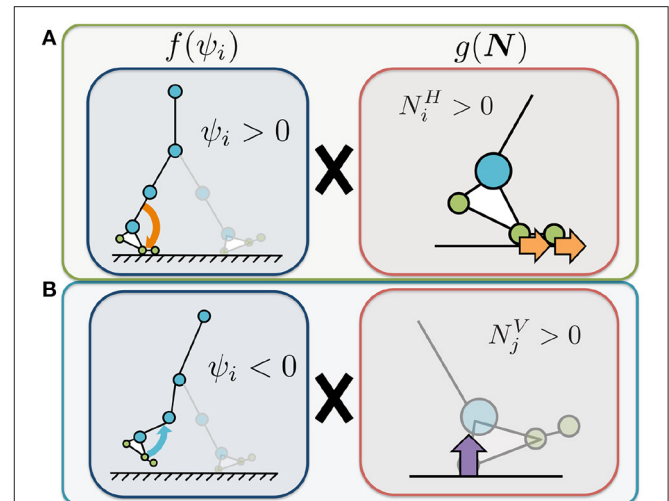


FIGURE 5 | Illustrated definition of the Tegotae function for the ankle controller. The control variable ψ_i represents the control command that increases or decreases the target angle of the ankle joints. We use ψ_i to adjust the target angle for the ankle controllers. N_i^H represents the sum of the horizontal force sensor values corresponding to the heel, metatarsal, and toe joints of the corresponding leg. N_j^V represents the sum of the vertical force sensor values corresponding to the opposite leg. **(A)** Tegotae function for corresponding-leg sensory information. The value of $N_i^H \psi_i$ is positive when the foot sensors on the corresponding leg detect a large horizontal GRF ($N_i^H > 0$) and the command for the ankle is plantar flexion (i.e., $\psi_i > 0$). **(B)** Tegotae function for opposite-leg sensory information. The value of $N_j^V (-\psi_i)$ is positive when the foot sensors on the opposite leg detect a large vertical GRF ($N_j^V > 0$) and the command for the ankle is dorsal flexion ($\psi_i < 0$).

described as follows:

$$\dot{\psi}_i = -c_{ankle} \psi_i + \frac{\partial T_{ankle,i}(\psi_i, N)}{\partial \psi_i}, \quad (17)$$

where c_{ankle} represents the parameter related to its response time for the first-order dynamical model of the ankle controller. The Tegotae function for ankle control is defined as follows:

$$T_{ankle,i}(\psi_i, N) = \sigma_{ankle,1} N_i^H \psi_i + \sigma_{ankle,2} N_j^V (-\psi_i), \quad (18)$$

$$N_i^H = N_{h,i}^H + N_{m,i}^H + N_{t,i}^H, \quad (19)$$

$$N_j^V = N_{h,j}^V + N_{m,j}^V + N_{t,j}^V, \quad (20)$$

where N_i^H [N] represents the sum of the horizontal force sensor values corresponding to the heel, metatarsal, and toe joints of the corresponding leg; Similarly, N_j^V [N] represents the sum of the vertical force sensor values corresponding to the opposite leg; The parameters $\sigma_{ankle,1}$ and $\sigma_{ankle,2}$ [1/N] represent the feedback gains. The first term on the right represents the Tegotae function for the corresponding leg (Figure 5A). The value of $N_i^H \psi_i$ is positive when the foot sensors on the corresponding leg detect a large horizontal GRF ($N_i^H > 0$) and the command for the ankle is plantar flexion (i.e., $\psi_i > 0$). Increasing this Tegotae term results in stronger plantar flexion at the end of the stance phase ($N_i^H > 0$), thus generating a larger propulsive force. The

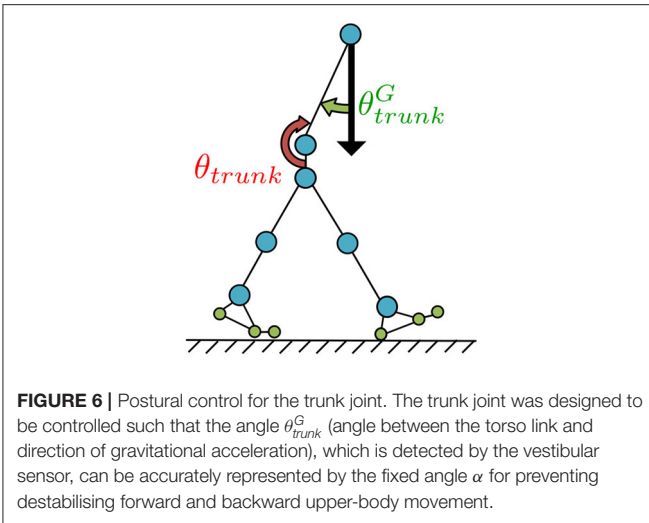


FIGURE 6 | Postural control for the trunk joint. The trunk joint was designed to be controlled such that the angle θ_{trunk}^G (angle between the torso link and direction of gravitational acceleration), which is detected by the vestibular sensor, can be accurately represented by the fixed angle α for preventing destabilising forward and backward upper-body movement.

second term represents the Tegotae function for the opposite leg (**Figure 5B**). The value of $N_j^V(-\psi_i)$ is positive when the foot sensors on the opposite leg detect a large vertical GRF ($N_j^V > 0$) and the command for the ankle is dorsal flexion ($\psi_i < 0$). Increasing this Tegotae term allows the ankle joint controller to effectively generate the dorsal flexion strength necessary for ground clearance during the swing phase as the opposite leg supports the body ($N_j^V > 0$).

To reiterate, the dynamics of each of the joint controller designs can be described as follows:

$$\begin{aligned} \dot{\phi}_i &= \omega + \sigma_{hip,1}(-N_{h,i}^V + N_{m,i}^V + N_{t,i}^V) \cos \phi_i \\ &+ \sigma_{hip,2}(N_{h,j}^V - N_{m,j}^V - N_{t,j}^V) \cos \phi_i, \end{aligned} \quad (21)$$

$$\begin{aligned} \dot{\chi}_i &= -c_{knee} \chi_i + \sigma_{knee,1}(N_{h,i}^V + N_{m,i}^V + N_{t,i}^V) \\ &- \sigma_{knee,2}(N_{h,j}^V + N_{m,j}^V + N_{t,j}^V), \end{aligned} \quad (22)$$

$$\begin{aligned} \dot{\psi}_i &= -c_{ankle} \psi_i + \sigma_{ankle,1}(N_{h,i}^H + N_{m,i}^H + N_{t,i}^H) \\ &- \sigma_{ankle,2}(N_{h,j}^V + N_{m,j}^V + N_{t,j}^V), \end{aligned} \quad (23)$$

The advantage of implementing the Tegotae functions is that it allows us to systematically design controllers for various joint types for the robot to perform the target movements. Furthermore, we expect that the sensory information (i.e., GRFs) utilised by the Tegotae-based hip, knee, and ankle joint controllers will enable spontaneous and adaptive inter- and intra-limb coordination.

2.3.4. Postural Control for the Trunk

To prevent destabilising forward and backward upper-body movement, the trunk joint was designed to be controlled such that the angle θ_{trunk}^G between the torso link and direction of gravitational acceleration, which is detected by the vestibular sensor, can be accurately represented by the fixed angle α

(**Figure 6**), as described by the following equations:

$$\tau_{trunk} = -K_{trunk}(\theta_{trunk} - \bar{\theta}_{trunk}) - D_{trunk}\dot{\theta}_{trunk}, \quad (24)$$

$$\bar{\theta}_{trunk} = \alpha - \theta_{trunk}^G, \quad (25)$$

where $\bar{\theta}_{trunk}$ represents the target angle for the PD controller at the trunk joint, and K_{trunk} and D_{trunk} are the proportional and derivative gains of the PD controller, respectively.

3. SIMULATION RESULTS

3.1. Steady Walking

In this section, we present the results of the numerical simulations performed in this study to validate our proposed design scheme. We set the body and control parameters in our bipedal model as shown in Supplementary Table 2 (**Supplementary Material**). In this study, we derived the control parameters through the trial and error method. **Figure 7A** is a screenshot of the steady-walking simulation (**Supplementary Movie 1**), with Tegotae-based controls for the hip, knee, and ankle joints and posture control for the trunk joint. **Figure 7B** shows the body, trunk, and CoM (Center of Mass) trajectories during the steady walking. **Figure 7C** presents the steady-walking time-series data in Model 3 with PC for the angle of each joint (including trunk angle), target angles of the hip and ankle joints, knee joint gain, vertical and horizontal GRFs, generated torque at each joint, and stance phase duration. By adjusting the target angles of the hip and ankle joints and the knee gain based on Tegotae control, the appropriate timing and magnitude of torques were generated for steady walking. Furthermore, the time-series pattern reproduced in the model was remarkably similar to that of a human steady-state walking time series (**Supplementary Figure 3**), except for the trunk angle, demonstrating the ability of Tegotae control in extracting the essential aspects of human walking control. We also compared walking speed and Froude numbers with human and other robots in Supplementary Table 3 (**Supplementary Material**).

3.2. Adaptability to Uneven Terrain

Here, we present examples of the simulated results that were subsequently analysed to evaluate the adaptability of the proposed model to environmental changes. To verify the adaptability, we modelled uneven terrains in the simulations by embedding circle obstacles into the ground, as shown in **Figure 8A**. Here, we again used Tegotae-based controls for the hip, knee, and ankle joints and posture control for the trunk joint. The radii of the circle obstacles and distances between the obstacles were randomly selected from values within the range of 10–50% of the body height of the model. The height of each obstacle was also randomly selected from values within the range of 0.5–2.0% of the body height. **Figure 8B** shows a screenshot of the uneven-terrain simulation. The results obtained via this simulation indicate that the Tegotae-based control scheme can

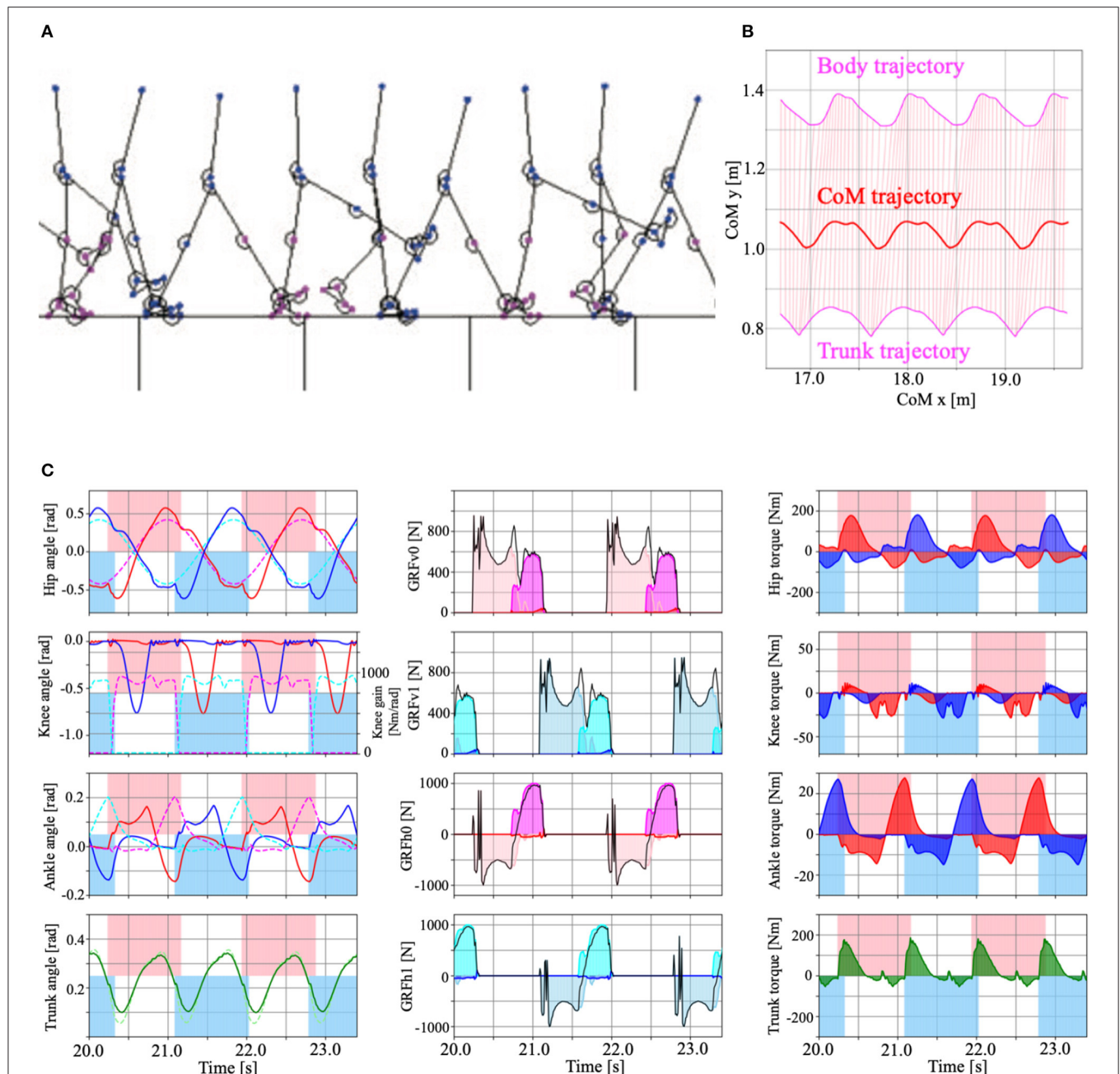
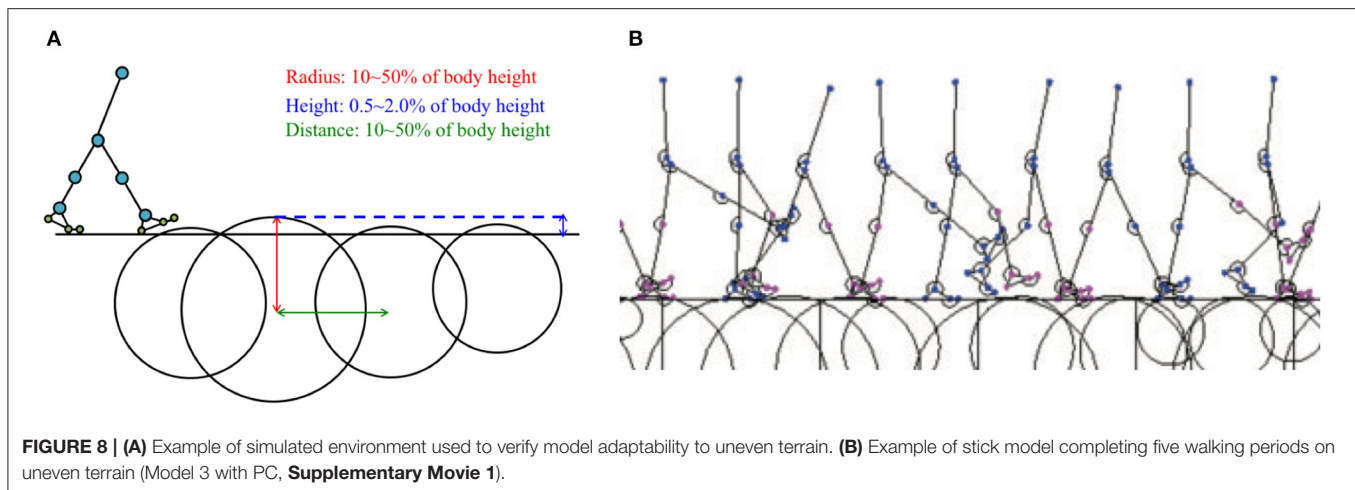


FIGURE 7 | (A) Example of the model walking in steady-state (Model 3 with PC, **Supplementary Movie 1**). **(B)** Body, trunk (magenta), and CoM (Centre of Mass, red) trajectories during the steady walking. Pink lines represent the torso link that connects the body and trunk mass. **(C)** Time series data of the steady walking in Model 3 with PC. Left panels show the hip, knee, ankle, and trunk angle from top to bottom. The red and blue lines show the left and right legs, respectively. The dotted magenta (left leg), cyan (right leg), and light green (trunk) lines represent the target angle of the hip, ankle and trunk, and the knee gain that determined by Tegotae-based control. The centre panels show vertical (top, second) and horizontal (third, bottom) ground reaction forces (GRFs). The pink, magenta, and red coloured regions represent the vertical forces applied to the heel, metatarsals, and toe masses on the left leg. The sky blue, cyan, and blue coloured regions represent the horizontal forces applied to the heel, metatarsals, and toe masses on the right leg. The right panels represent the torque applied to the hip, knee, ankle, and trunk joints by the PD control. The red, blue, and green colour regions represent the left, right legs, and trunk, respectively. For the left and right panels, the pink and sky blue coloured regions represent the stance phase of the left and right legs, determined by the vertical GRFs ($N_i^V > 0$), respectively.



be successfully implemented to allow a bipedal walking robot to adapt to environmental changes.

To investigate the extent of the contributions of the joint controllers to the observed adaptability, we tested the adaptability of the walking model under the following conditions:

- Model 1: Tegotae-based knee controller ($\sigma_{knee,k} \neq 0$, $\sigma_{hip,k} = \sigma_{ankle,k} = 0$)
- Model 2: Tegotae-based knee and ankle controllers ($\sigma_{knee,k}, \sigma_{ankle,k} \neq 0$, $\sigma_{hip,k} = 0$)
- Model 3: Tegotae-based hip, knee, and ankle controllers ($\sigma_{hip,k}, \sigma_{knee,k}, \sigma_{ankle,k} \neq 0$)

All the models include posture control. We simulated a test environment that consisted of 10 m of flat ground, followed by 20 m of uneven terrain (refer to the above-described method), and another 10 m of flat ground (**Supplementary Movie 1**). We verified the walking performance for 100 randomly generated uneven-terrain patterns. **Figure 9A** presents a comparison of the success rates of these three models for different oscillator angular velocities. We judged the success case as the condition in which the bipedal model successfully walked 40 m ground in total. These results indicated that Model 3 showed higher adaptability in a wide range of ω from low speed to high speed, whereas Model 2 and Model 3 showed almost the same adaptability on the uneven terrain in high speed walking ($\omega = 4.5$ rad/s) (**Figures 9A,B**). However, for ω exceeding 4.5, the walking speed decreases along with the increase of ω . One possible reason is that the model used in this study cannot reproduce the running motion.

3.3. Effects of Postural Control

To investigate the extent of the contribution of the posture controller to the observed adaptability, we conducted tests to evaluate the adaptability of the walking model with and without postural control explained in section 2.3.4. For the condition without postural control, we set the target angle of the trunk to be $\bar{\theta}_{trunk} = \alpha$. **Figure 9B** shows the effects of postural control on the adaptability of Models 1, 2, and 3. The results shown in this plot suggest that the posture controller implemented in this

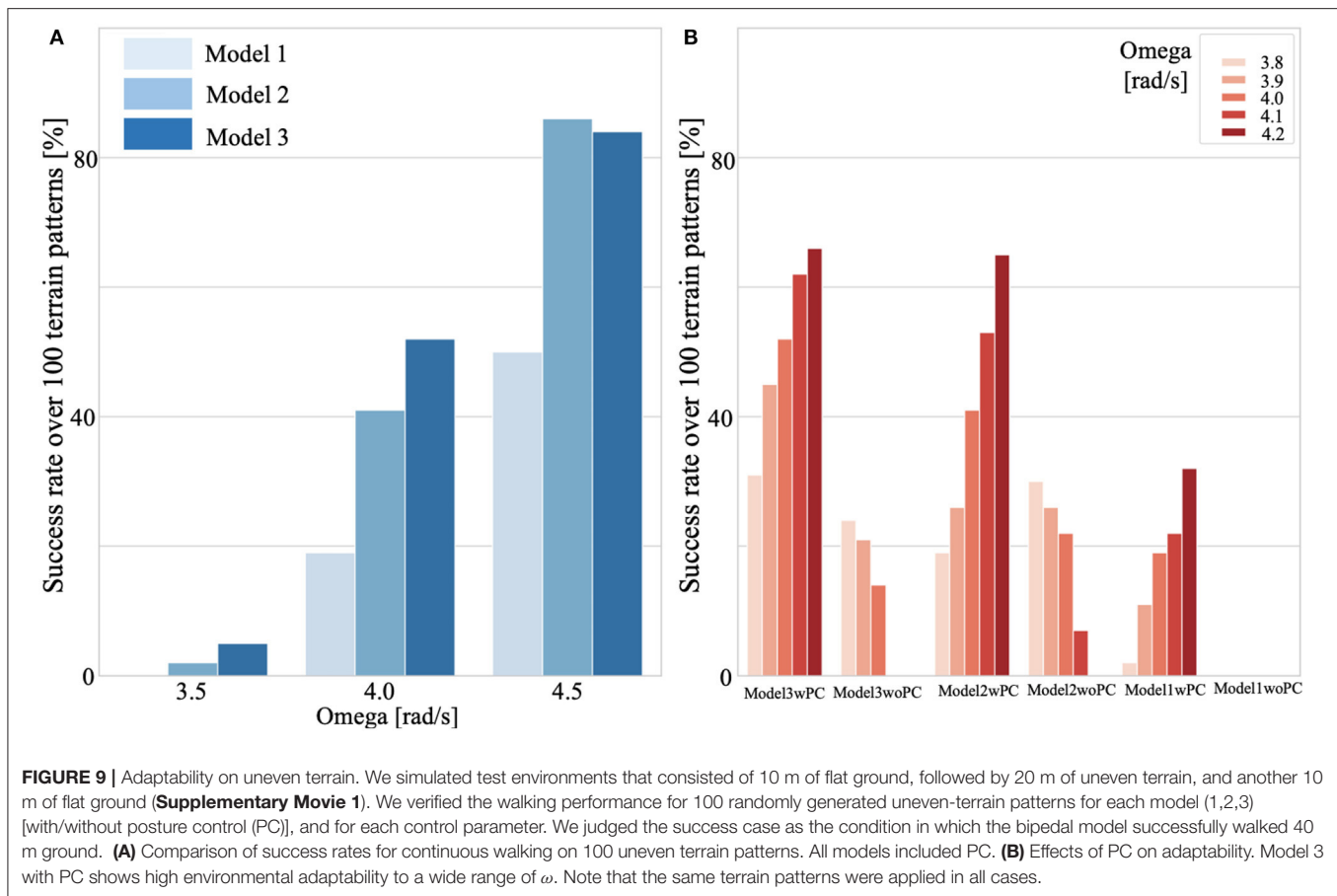
study can improve the adaptability of any bipedal walking model. Note that, under some of the simulated no-postural-control conditions (**Supplementary Movie 2**), particularly for Models 1 and 2, steady walking could not be achieved.

3.4. Effect of Control Parameters on Walking

Here, we verified the effect of the control parameters on walking performance (adaptability to environmental changes) when using the Tegotae-based control.

First, to verify the effect of the controller dynamics on walking, we tested c_{knee} and c_{ankle} , which define the dynamics of the knee (Equation 12) and ankle control variables (Equation 17). **Figure 10A** shows the effect of c_{knee} on the knee gain $K_{knee,i}$ and walking adaptability (left), and the effect of c_{ankle} on the ankle target angle and adaptability (right). The results showed that (i) when c_{knee} was 20 (reaction time is fast), the Tegotae feedback (the 2nd term of Equation 12) weakened relative to the first term, the gain $K_{knee,i}$ was fastly modified toward 0 via $-c_{knee}\chi_i$, which improves gait adaptability. When c_{knee} was small ($c_{knee}=5$), the effect of feedback was large and the gain K_{knee} was almost constant in higher value. (ii) When c_{ankle} was 5 (reaction time is slow), the target angle of the ankle joint changes significantly due to the effect of the Tegotae feedback term (the 2nd term in Equation 17), thus generating sufficient ankle joint torque and improving walking adaptability. When the c_{ankle} was large, the change in the target angle of the ankle joint was small, resulting in insufficient ankle joint torque. In sum, the first order equations exhibit non-rhythmic behaviour, where the control variable stays at an equilibrium point without feedback: the parameters c_{knee} and c_{ankle} determine the strength of staying at the equilibrium point ($\chi_i = 0$, $\psi_i = 0$).

Next, we examined the effects of $C_{1,hip}$, $C_{1,knee}$, and $C_{1,ankle}$, the parameters that set amplitude in Equations (7), (11), and (16), which determine the target angle $\bar{\theta}_{hip,i}$, $\bar{\theta}_{ankle,i}$ and gain $K_{knee,i}$ of the PD control. The results are shown in **Figure 10B**; (i) Because $C_{1,hip}$ is a parameter that determines the amplitude of the target angle $\bar{\theta}_{hip,i}$ of the hip joint, setting $C_{1,hip}$ to a large value increased



the amplitude of the hip joint angle $\theta_{hip,i}$ (**Figure 10B**, lower left), resulting in an increase in gait stability; (ii) $C_{1,knee}$ is a parameter that sets the maximum value of the knee P-gain $K_{knee,i}$ (middle of **Figure 10B**); changes in the upper limit of the P-gain $K_{knee,i}$ resulted in an increase in the small oscillations of the knee joint, but there was no significant difference in adaptability; and (iii) $C_{1,ankle}$ is a parameter that determines the maximum amplitude of the target angle $\bar{\theta}_{ankle,i}$ of the ankle joint. Therefore, increasing this parameter increased the range of changes in the ankle joint $\theta_{ankle,i}$, but had a negative effect on walking adaptability. The reason for this may be that the larger the ankle joint change, the easier it is to trip during walking, leading to falls.

3.5. Stability Analysis

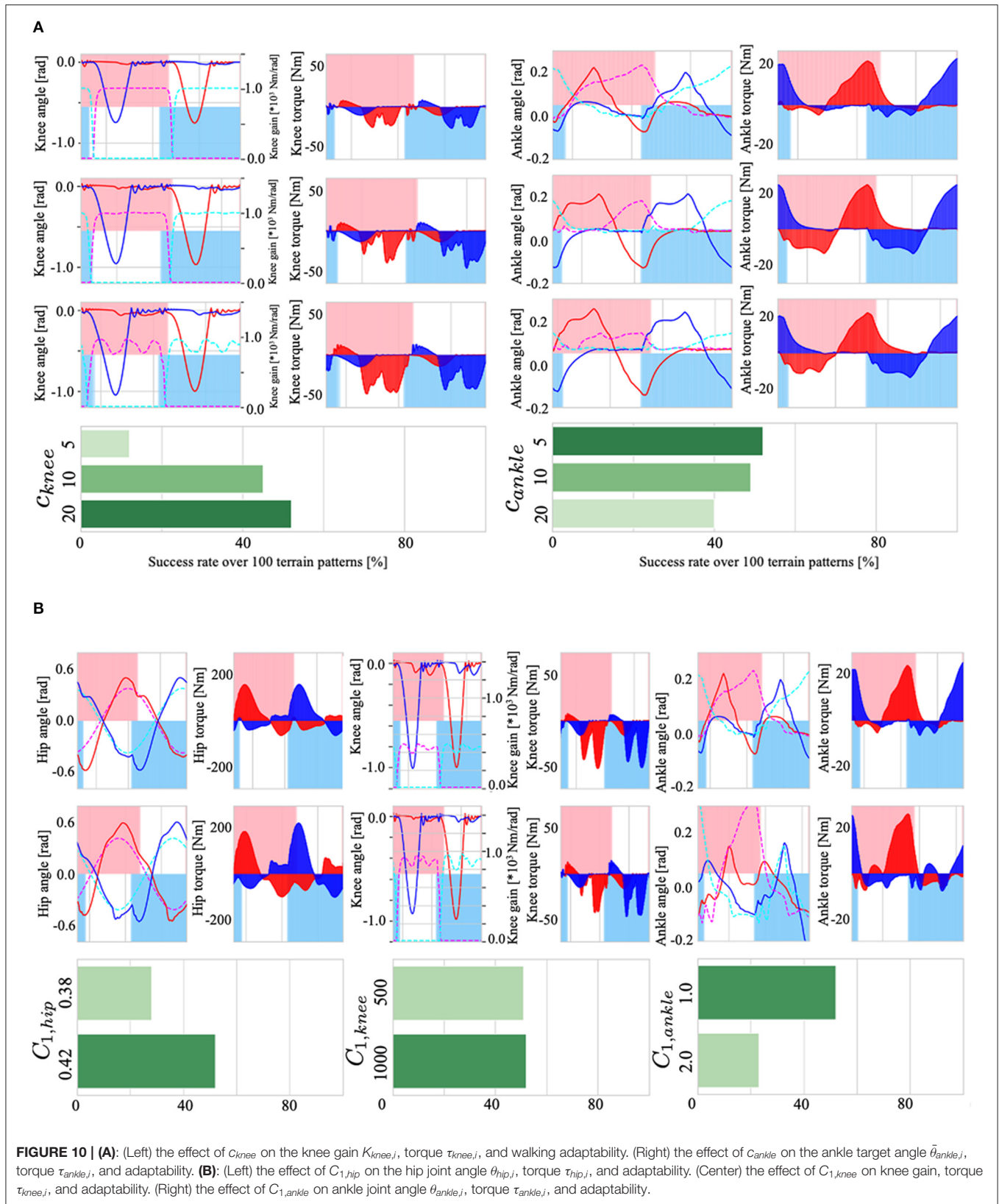
To numerically verify the stability of the walking motion generated by the Tegotae-based control, we plotted the phase diagram consisting of the trunk angle θ_{trunk} and angular velocity $\dot{\theta}_{trunk}$. For testing the adaptability to environmental changes, mentioned in section 3.2 ($\omega = 4.5$ rad/s), we compared the gait that could (**Figure 11A**) and could not (**Figure 11B**) move over uneven terrain. The lower graphs of **Figures 11A,B** show the time evolution of the trunk angle θ_{trunk} . In both cases (**Figures 11A,B**), the walking quickly converges from the initial state to the steady state (0 s to around 8 s). The red trajectories in the upper figures show the limit cycle trajectory from 8 s to the beginning of uneven

terrain (pink area in the figure below), which is defined as the steady-state trajectories. The black border points in the phase diagrams indicate the minimum trunk angle ($\dot{\theta}_{trunk} = 0$) during each walking cycle. We defined this state (minimum angle θ_{trunk} and $\dot{\theta}_{trunk} = 0$) as the Poincaré section Σ (Nassour et al., 2014), then, we can confirm the convergence of the walking to the steady state from the transition process (bottom of **Figures 11A,B**).

The grey areas in the lower figures of **Figures 11A,B** indicate the period during uneven terrain walking. The upper right figures in **Figures 11A,B** show the phase diagram during uneven terrain walking. In case A, the trajectory was disturbed by the uneven terrain, but the trajectory was within the basin of attraction of walking, so the biped model can continue to walk on the uneven terrain. In contrast, in case B, the trajectory goes out of the basin of attraction due to uneven terrain, making it impossible to converge to the limit cycle, and the model falls down. This analysis confirms existence of the basin of attraction in walking based on Tegotae control and the destabilisation that caused it to fall over when walking on uneven terrain.

4. DISCUSSION

In this paper, we proposed a systematic CPG-based control design scheme for bipedal walking robots based on the Japanese concept of Tegotae in Owaki et al. (2017) and Kano et al.



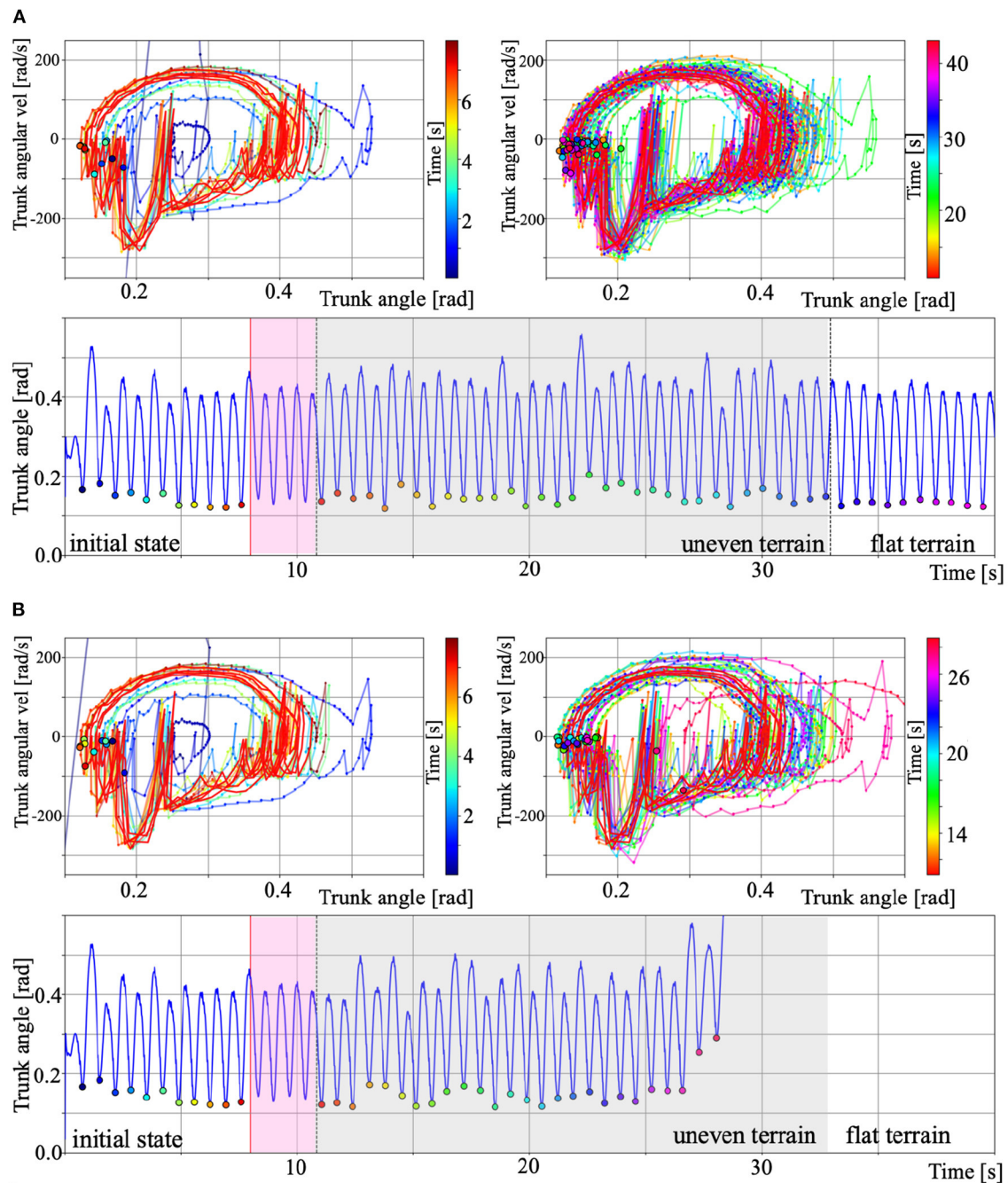


FIGURE 11 | Phase diagram of the trunk angle θ_{trunk} and angular velocity $\dot{\theta}_{trunk}$ for the results of section 3.2. **(A)** Gait over uneven terrain. **(B)** Gait that could not move over uneven terrain. For A and B, the upper left and right panels show the period from initial to steady state and during uneven terrain walking. The colour legend for each panel indicate the time [s]. The red trajectories show the limit cycles from 8 s to the beginning of uneven terrain (pink area in the lower panels), which is defined as the steady-state trajectories. The black border points in the phase diagrams indicate the minimum trunk angle ($\theta_{trunk} = 0$) during each walking cycle. We defined this point as the Poincaré section Σ (Nassour et al., 2014). We can then confirm the convergence of the walking to the steady state from the transition process. The lower graphs show the time evolution of the trunk angle θ_{trunk} . The pink and grey area show the steady-state and period during uneven terrain walking, and the other areas show period during walking on flat terrain.

(2019). To validate the proposed method, we designed hip, knee, and ankle joint controllers for a two-dimensional bipedal walking model. The results of dynamic simulations with the

proposed bipedal walking model design have demonstrated that steady walking, stability, and spontaneous inter- and intra-limb coordination can be achieved. Furthermore, we found the model

with three types of joint controllers to be highly adaptable to environmental changes during walking tasks. These findings imply that the systematic nature of the proposed control scheme can improve the motor function, i.e., adaptability, of bipedal walking robots.

We have previously shown the potential of the *Tegotae* approach in reproducing animals' locomotion and understanding the underlying mechanism based on the synthetic approaches. The *Tegotae* approach was first used by Owaki et al. (2017) to develop a minimal model for interlimb coordination on hexapod robot locomotion with CPG-based control, where all controllers were uniform for all elements. Kano et al. (2018) demonstrated gait transition between the concertina and scaffold-based locomotion on snake model simulation with reflex-like control, where all controllers were uniform, but generated non-rhythmic control signals. Kano et al. (2019) proposed detailed design of the *Tegotae* function, especially for motor command, using genetic algorithm (GA) to simulate a simple 1-D earthworm model with CPG-based control (uniform controllers for all elements). Compared to these approaches, here, we showed adaptive walking control on biped model with CPG and reflex-based control (non-uniform controllers, i.e., hip has CPG-based control, but the knee, and ankle have reflex-like controllers with no rhythmic signals). The novel attempts of this study can be summarised as follows: (i) First application of the *Tegotae* approach for the non-homogeneous system of animals' body, i.e., bipedal model with the hip, knee, and ankle joint, which need individual controllers for the generation of walking motion; (ii) combination between CPG-based rhythmic control for the hip joint and reflex-like non-rhythmic control for knee and ankle joints; finally, (iii) verification of adaptability against unknown environmental changes during bipedal walking.

The detail design guidelines of the *Tegotae* function for a local joint controller are as follows. The hips have periodic motions in which the swing leg descends forward and the stance leg kicks the ground alternately. For generating this motion, a phase oscillator is used as a controller for the hip joint (Equation 8). We used a heel load sensor, which reflects ground contact and load information during walking, and metatarsal and toe load sensors, for obtaining load information just before pushing-off the ground, as sensory information for the hip controllers. The feature of the *Tegotae* function of the hip joint is that we used the sensory information of not only the corresponding leg but also that of the other leg in designing the function. A mechanism called "Crossed Inhibitory Response," which contributes to interlimb coordination in bipedal walking, was reported in Stubbs and Mrachacz-Kersting (2009) and Gervasio et al. (2017). We also designed a *Tegotae* function using the load information of neighbouring legs in our hexapod model (Owaki et al., 2017). Based on the above considerations, we designed the *Tegotae* function of hips in Equation (9); when an action, e.g., $-\sin \phi_i > 0$ for stance phase, and a reaction, e.g., $N_{h,i}^V > 0$ for heel feels load, are highly consistent, the *Tegotae* function of the hip shows high value. See more details for the other three cases in Table 1.

The role of the knee joint during walking is important for stabilising the gait. During the stance phase, the knee joint stiffness is increased to support the body. In the swing phase,

TABLE 1 | Design for Tegotae function.

Joint	State	Action $f(x)$	Reaction $g(S)$	$T(x, S)$
Hip	Stance phase	$-\sin \phi_i > 0$	$N_{h,i}^V > 0$	$(-\sin \phi_i)N_{h,i}^V$
		$-\sin \phi_i > 0$	$N_{m,i}^V + N_{t,i}^V > 0$	$(-\sin \phi_i)(N_{m,i}^V + N_{t,i}^V)$
	Swing phase	$\sin \phi_i > 0$	$N_{m,i}^V + N_{t,i}^V > 0$	$\sin \phi_i(N_{m,i}^V + N_{t,i}^V)$
		$\sin \phi_i > 0$	$N_{h,i}^V > 0$	$\sin \phi_i N_{h,i}^V$
Knee	Stiff	$\chi_i > 0$	$N_i^V > 0$	$\chi_i N_i^V$
	Soft	$-\chi_i > 0$	$N_i^V > 0$	$(-\chi_i)N_i^V$
Ankle	Plantarflexion	$\psi_i > 0$	$N_i^H > 0$	$\psi_i N_i^H$
	Dorsiflexion	$-\psi_i > 0$	$N_i^V > 0$	$(-\psi_i)N_i^V$

the knee joint stiffness must be dramatically reduced to realise efficient swinging of the swing leg. Therefore, the knee joint stiffness was adopted as a control variable. The sum of the heel, metatarsal, and toe loads at planter sensation was used as sensory information. The knee stiffness is switched ON and OFF to switch between the stance and swing phases. The conversion from the control variable to the joint stiffness was set up using the tanh and max function (Equation 11). As the dynamics of the control variable, a reflexive stiffness change based on non-periodic dynamics was modelled by the first order equation (Equation 12). The *Tegotae* function was designed as the product of the knee stiffness control variable and load on foot (heel, metatarsal, and toe). When the consistency between the action, e.g., $\chi_i > 0$ for stiff knee, and reaction, e.g., $N_i^V > 0$ for foot heels load, is high, the *Tegotae* function of the knee joint also takes a high value. The details for the other case are shown in Table 1.

The important functions of the ankle joint for gait stabilisation are to "push-off" (Lipfert et al., 2014; Zelik and Adamczyk, 2016) in the late stance phase and to suppress stumbling of the toe during the swing phase. Therefore, the control variables were set to indicate the non-periodic degree of plantar flexion and dorsiflexion of the ankle joint using the first order equation of Equation (17). The target angle of the ankle joint was set using the tanh function for the control variables (Equation 16). The horizontal GRFs of the foot N_i^H were used as sensory information to generate propulsive force as the *Tegotae* function to express the push-off function in the first right-hand term of Equation (18). The *Tegotae* function for the dorsiflexion motion of the ankle joint during the swing phase was designed to adjust the degree of dorsiflexion according to the load of the foot of the other leg N_j^V (see the details in Table 1).

In this research, various *Tegotae* functions have been selected and verified by trial and error in the design process. The *Tegotae* function used in this study is one of the examples that realised stable and adaptive walking. We can easily imagine that an inappropriate *Tegotae* function clearly does not lead to gait stabilisation. For example, consider a *Tegotae* function at the hip joint, where $f(x) = \sin \phi_i > 0$, meaning swing phase, and $g(S) = N_i^V > 0$ (foot feels load). This *Tegotae* function does not lead to a stable walking because of the inconsistency between action $f(x)$ and reaction $g(S)$. Thus, the point of designing the *Tegotae* function is to consider the physical consistency of the

action and reaction for the desired motion, and to design the *Tegotae* function so that its value becomes large in such cases. Once such a *Tegotae* function is designed, it is possible to modify the control variables in a situation-dependent manner by modifying the control variables by increasing the *Tegotae* function as a feedback term $\partial T(x, S)/\partial x$. Thus, the *Tegotae* approach enables the design of an autonomous decentralised controller in a systematic manner, by designing *Tegotae* function in line with the desired motions.

For the results of environmental adaptability on uneven terrain, Model 3, which has hip, knee, and ankle control, showed higher adaptability in a wide range of ω from low speed to high speed. However, in high speed walking, such as $\omega = 4.5$ rad/s, Model 2 and Model 3 showed almost the same adaptability on the uneven terrain. The difference between Model 2 and Model 3 is the presence or absence of the hip controller based on *Tegotae*. In other words, Model 2 is a non-periodic reflex-based walking model without feedback for hip CPG (only feedforward CPG), whereas Model 3 implements *Tegotae*-based feedback for periodic CPG. Thus, when ω is small, i.e., slow speed walking, *Tegotae* feedback on CPG contributes to the adaptability of walking, whereas when ω is large, i.e., fast speed walking, the presence or absence of feedback to CPG does not affect the adaptability of walking. Manoonpong et al. (2007) showed that a walking controller based on a reflex model could achieve stable and fast walking, suggesting that the role of reflex-based control becomes salient in high-speed walking motions because the response time of feedback to CPG is not fast enough for the modification of the rhythmic control signals. In our model, *Tegotae*-based feedback to CPG at the hip joint and *Tegotae*-based feedback to reflex-based control at the knee and ankle joints were implemented. Therefore, the role of the feedback in the periodic and non-periodic controllers may have resulted in a high degree of adaptability to a wide range of ω . As shown in **Figure 9B**, Model 3 with PC shows high environmental adaptability to a wide range of ω .

In this study, we used plantar sensation (i.e., GRFs) as sensory information for feedback to CPG-based controllers. Past studies with humans and animals have shown that cutaneous receptors in the foot play an essential role in the control of gait (Dietz and Duysens, 2000; Duysens et al., 2000) and posture (Magnusson et al., 1990; Kavounoudias et al., 1998). For example, the reported effects of reducing plantar sensation by implementing an ice immersion technique (Nurse and Nigg, 2001; Eils et al., 2002; Elis et al., 2004) suggest that plantar sensation plays a critical role in gait modification. Similarly, various researchers have reported on the effects of impaired plantar sensation on gait plasticity due to ageing (Sorock and Labiner, 1992), diseases, such as diabetes mellitus (Cavanagh et al., 1993), or congenital insensitivity to pain with anhidrosis (Zhang et al., 2013; Yozu et al., 2016). Decreased tactile sensation, with ageing-related impaired sensory function in limbs, has been reported to lead to elderly falling accidents (Sorock and Labiner, 1992). Additionally, patients with diabetic neuropathy, which is commonly associated with damage to nerves in the feet, have been reported to have significantly impaired control of gait and posture (Cavanagh

et al., 1993). Thus, our results, which demonstrate that implementing a plantar sensory feedback mechanism in a systematic control scheme improved adaptability and walking stability, are consistent with the findings of previous human and animal studies on the influence of plantar sensation on gait and postural control.

The realisation of adaptive bipedal walking is known to be dependent on the generation of a limit cycle in the state space, which comprises a brain-nervous system (i.e., the control system), musculoskeletal system (i.e., the mechanical system), and environment (Taga et al., 1991; Taga, 1994, 1995). For robots, the structural stability provided by a limit cycle affords robustness against environmental perturbations. However, design principles that can be applied to concretely establish a limit cycle with a large basin of attraction have yet to be conceptualised. One significant reason for this is that not enough sensory information is fed back to the control system in a limit cycle. Thus, sensory-motor coordination, which refers to the condition that movement induces sensory stimulation, which in turn influences the movement, must be considered to generate a more stable limit cycle (Pfeifer and Bongard, 2006; Pfeifer et al., 2007). Considering this, we must focus on the deformability of the underlying soft body of a robot. A soft body allows a robot to stabilise its motion as it extracts various types of sensory information; this is possible because it is flexible enough to deform to maintain stability during movement, resulting in a close relationship between motion and perception. Human soles are considered to be relatively soft. As a human walks, their relatively soft feet come into direct contact with the environment; the deformability of the feet, i.e., the softness of the sole and mobility of the joints of the feet, allows them to conform to the ground surface, enabling the extraction of diverse sensory information. Thus, the soft deformability of the foot of our bipedal walking model is also believed to have contributed to the high adaptability and stability observed in our results.

It should be noted that the phase-modulation mechanism underlying the proposed model is significantly different from that of any previous model, e.g., the previously reported phase-reset scheme (Tsujita et al., 2003; Aoi and Tsuchiya, 2005, 2006; Aoi et al., 2010). The phase-reset scheme, which entails resetting the phase of the oscillator to zero once the foot makes contact with the ground, only utilises qualitative information about the status of contact between the foot and ground (i.e., on or off). In contrast, our design methodology uses quantitative information that describes the extent to which each foot “feels” the GRF, representing the sensory information resulting from the deformation of soft feet. This was possible because highly adaptive behaviours emerge in response to environmental changes, and we were able to exploit these behaviours in our proposed design. Nevertheless, this study has several limitations. First, we only modelled a two-dimensional walking robot in the sagittal plane. This is because we wanted to focus on evaluating and validating our control scheme. Secondly, we utilised actuators, i.e., PD-based servo motors, as the model for each joint. Humans have antagonistic muscles that generate joint torques that allow us to exploit mono-articular and biarticular

muscles for motion generation. This difference will be the focus of future work as we plan to design a more complex model. Lastly, the proposed model needs to be validated by performing real-world experiments; this is also a focus of future studies.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

DO, JN, and AI conceived the research idea and performed data collection. SH designed the model and controllers and conducted the simulations. SH and DO conducted the analysis. All authors participated equally in the preparation of this manuscript.

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FUNDING

We acknowledge the support of JSPS KAKENHI (grant number JP18H03167 and JP20H04260), and CREST, JST (grant number JP-MJCR14D5).

ACKNOWLEDGMENTS

The authors would like to thank Dr. Y. Sekiguchi and Dr. K. Honda (Tohoku University Hospital) for their assistance in human data collection on the **Supplementary Materials**. A part (**Figures 1A, 3–5**) of this manuscript has been presented at the Living Machines 2016 (Owaki et al., 2016).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fnbot.2021.629595/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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From Motor-Output to Connectivity: An In-Depth Study of *in-vitro* Rhythmic Patterns in the Cockroach *Periplaneta americana*

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OPEN ACCESS

Edited by:

Poramate Manoonpong,
University of Southern
Denmark, Denmark

Reviewed by:

Holk Cruse,
Bielefeld University, Germany
Wolfgang Stein,
Illinois State University, United States

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Specialty section:

This article was submitted to
Insect Neurobiology,
a section of the journal
Frontiers in Insect Science

Received: 21 January 2021

Accepted: 22 April 2021

Published: 20 May 2021

Citation:

David I and Ayali A (2021) From
Motor-Output to Connectivity: An
In-Depth Study of *in-vitro* Rhythmic
Patterns in the Cockroach *Periplaneta*
americana.
Front. Insect Sci. 1:655933.
doi: 10.3389/finsc.2021.655933

The cockroach is an established model in the study of locomotion control. While previous work has offered important insights into the interplay among brain commands, thoracic central pattern generators, and the sensory feedback that shapes their motor output, there remains a need for a detailed description of the central pattern generators' motor output and their underlying connectivity scheme. To this end, we monitored pilocarpine-induced activity of levator and depressor motoneurons in two types of novel *in-vitro* cockroach preparations: isolated thoracic ganglia and a whole-chain preparation comprising the thoracic ganglia and the subesophageal ganglion. Our data analyses focused on the motoneuron firing patterns and the coordination among motoneuron types in the network. The burstiness and rhythmicity of the motoneurons were monitored, and phase relations, coherence, coupling strength, and frequency-dependent variability were analyzed. These parameters were all measured and compared among network units both within each preparation and among the preparations. Here, we report differences among the isolated ganglia, including asymmetries in phase and coupling strength, which indicate that they are wired to serve different functions. We also describe the intrinsic default gait and a frequency-dependent coordination. The depressor motoneurons showed mostly similar characteristics throughout the network regardless of interganglia connectivity; whereas the characteristics of the levator motoneurons activity were mostly ganglion-dependent, and influenced by the presence of interganglia connectivity. Asymmetries were also found between the anterior and posterior homolog parts of the thoracic network, as well as between ascending and descending connections. Our analyses further discover a frequency-dependent inversion of the interganglia coordination from alternations between ipsilateral homolog oscillators to simultaneous activity. We present a detailed scheme of the network couplings, formulate coupling rules, and review a previously suggested model of connectivity in light of our new findings. Our data support the notion that the inter-hemiganglia coordination derives from the levator networks and their coupling with local depressor interneurons. Our findings also support a dominant role of the metathoracic ganglion and its ascending output in governing the anterior ganglia motor output during locomotion in the behaving animal.

Keywords: locomotion control, central pattern generator, cockroach, levator, depressor, pilocarpine, intersegmental coordination, coupling strength

INTRODUCTION

Insect hexapedal design is known to enable very stable and highly adaptable locomotion (1–4). These abilities intrigue both neuroethologists, who study the mechanisms underlying animal behavior, and researchers of bioinspired locomotion systems and their controllers (5–10). Functional coordination is achieved, in all legged locomotion, through a dynamic interplay between brain descending commands (11, 12), local central pattern generator networks [CPGs; see reviews (13–15)], and sensory feedback, which modify and adapt the endogenous motor-pattern to suit the behavioral context and environment (16–20). The convention states that slow-walking insects, or animals navigating through a complex environment, mostly depend on sensory feedback and weak central coupling to coordinate their limbs; while fast-walking insects rely more on strong central coupling and a feedforward control strategy (21). We note that feedback and feedforward control refer to the extent to which the endogenous oscillators' (e.g., CPGs) frequencies are influenced by those of the corresponding actuators, as manifests in the proprioceptors' afferents (21). In addition, central and local control refer to the extent to which an hemiganglionic oscillator's activity is influenced by that of its neighbors. Central control is mediated via central connectivity between hemiganglionic networks, while local control is governed by sensory feedback from the hemiganglionic proprioceptors, as well as sensory feedback mediated inputs from other sensors. Although all insects share the same basic architecture of their central nervous system (22), the behavior it generates varies greatly within and between species. Among the leading insect models for locomotion control research, the slow-walking stick insect and the remarkably fast American cockroach (*Periplaneta americana*) present two extreme examples of these control strategies (23), while a third common model, the locust, fits somewhere in-between (24). Insects usually demonstrate one of three prototypical inter-leg coordination patterns or gaits: metachronal wave; tetrapod; or double-tripod (hereafter tripod), in which five, four, or three legs, respectively, are simultaneously maintained on the ground at any given time (25–27). Intermediate footfall patterns that cannot be classified as one of the prototypical gaits have been reported [cockroach (25, 27); *Drosophila* (28–30); stick insect (31, 32)]. Insects alter their gait either in response to changing circumstances (33, 34), or to adapt leg-coordination in response to a change in as little as a single speed-related parameter, like a load sensor (35, 36); as also seen in the speed-dependent phase-shift toward ideal tripod phases in intact and semi-intact deafferented cockroaches (37, 38). Most insects increase their speed by increasing stride frequency up to a certain speed, and then increase stride length to reach their maximum speed (39). *P. americana* is unique in that it can increase both stride frequency by 30% and stride length by up to 300%, due to its extremely long hind legs and extraordinary ability to fast cycle them, which enables it to reach a top speed of 1.5 m/s, or 50 body length per second (1, 37). During fast locomotion the hind legs extend farther to increase stride length and cover greater distance, while hardly changing the duration of the swing (the leg's airborne phase), by increasing swing velocity, as also

found in flies (40, 41). The insect leg incorporates three main leg-joints: the thorax-coxa, the coxa-trochanter, and the femur-tibia. Studies of pilocarpine-stimulated preparations suggests that each joint is controlled by a dedicated CPG (42, 43), which also maintains the coordination with the neighboring joints' CPGs (44). Most research, from the early 1970s on [(45–49); review (23, 43)], focused on the coxa-trochanter joint and its levator-depressor control network, by monitoring the corresponding MNs motor-output. This control network also underlies body propulsion, which is almost exclusively generated by depression torque at the coxa-trochanter joint (50). Recent work on locusts and stick insects focused on the depressor side of the network, following the assumption that the levator mirrors its conjugated depressor activity (51–55). However, this narrative, although useful, is incomplete. Pearson and Iles (1970) observed that in a deafferented cockroach, levator MNs can fire independently of depressor MNs, but never vice versa. This phenomenon was also observed *in-vitro* in locusts (56). In addition, levator MNs, but not depressor MNs, were found to fire in correlation with intersegmental signals recorded from the thoracic connectives of the deafferented cockroach, which led to the suggestion that levator premotor networks are centrally controlled (47). Based on these and other observations, including our own findings [(38) and references within], we have previously suggested a parsimonious connectivity model of the CPGs network in which levator interneurons (INs) are centrally controlled (i.e., directly by the hemisegmental oscillator which shares a common drive with homolog oscillators and is connected to neighboring oscillators by mutual inhibition), while the output of depressor INs is influenced by their neighboring levators and not directly and exclusively by the hemisegmental oscillator (38). In the current study we reexamine our and others' previous findings to fill in major gaps in the architecture of the parsimonious connectivity model and the coupling scheme it is based upon (38). This is crucial for uncovering the details of the central control of insect locomotion and for designing models for CPG-based artificial controllers (57). Here we study in depth the relations between frequency and phase relations, as well as the coupling between the cockroach thoracic CPGs. Throughout, we directly monitored both the depressor and levator nerves in order to study the neural control that underlie the coxa-trochanter joint movements, and to obtain a broader description of the network's intra- and inter-hemisegmental connectivity. We first examined each thoracic ganglion in complete isolation from any sensory, descending, or central intersegmental inputs, in order to identify their intrasegmental connectivity. We then examined a novel whole-chain preparation, comprising the thoracic ganglia connected to the subesophageal ganglion (SEG), in order to investigate the intersegmental connectivity and its effects. The whole-chain preparation was also established in order to enable future research into insect locomotion control using a preparation that generates stable prolonged fictive locomotion rhythms, to which effectors and manipulations can be applied and studied. We therefore included the SEG which is known to generate a drive that sustains activation of the thoracic motor networks and participates in intersegmental (but not intrasegmental) coordination [(11, 52, 53) and ref's within]. Our

findings present significant and detailed differences between the thoracic ganglia motor-output, including a first description of bi-phasic frequency-dependent endogenous prothoracic motor-output, differences in the coordination and coupling strength between homolog pairs of MNs, and between the anterior and posterior sub-networks. Our findings of coupling strength are summarized in a comprehensive coupling scheme, and we revisit and update our connectivity model based on our new findings. Finally, this work offers extensive data for a future comprehensive comparative studies of the main insect models used for electrophysiology-based locomotion control research in recent years: the cockroach, the stick insect, and the desert locust.

MATERIALS AND METHODS

Experimental Animals

Experiments were conducted on 22 adult male *Periplaneta americana* cockroaches obtained from our colony at the School of Zoology, Tel-Aviv University. The insects were maintained in a 60-liter plastic cage at a room temperature of 30°C, under a light:dark cycle of 12 h:12 h. Their diet comprised dry cat food (La-Cat, BioPet, Israel) and water *ad libitum*.

Neurophysiological Procedure

Cockroaches were anesthetized with CO₂ before being fixed to a Sylgard-coated plate ventral side up (Dow Corning 184 Sylgard Silicone Elastomer, Michigan, USA), using minute pins. A ventral longitudinal cut was made, and the entire digestive tract was then gently removed. The head capsule was opened and the desired parts of the central nervous system—isolated thoracic ganglia or a ganglia chain comprising the SEG and the three thoracic ganglia—were dissected out from the cockroach together with their peripheral nerves and main trachea intact, and fixed in a clean Sylgard-coated Petri dish, filled with cockroach saline (58). Levator nerves (6Br4) and depressor nerves (51r) were retained intact while all other peripheral nerves were cut close to their origin (see illustration in **Figure 1A**). Air was supplied to the ganglia by teasing open the tracheae at the surface of the saline to prevent hypoxia, which is known to be detrimental to thoracic MNs (59). Simultaneous extracellular recordings were conducted using self-fabricated suction electrodes placed on levator and depressor nerves—four for each isolated ganglion or 4–7 electrodes for the whole-chain preparation. The preparations were stimulated by a final concentration of 1×10^{-5} M pilocarpine (pilocarpine-HCl 99%, Sigma Aldrich, St Louis, MO, USA), freshly prepared in cockroach saline, and bath applied 15 min before recording onset. Motoneuron (MN) activity was acquired using two four-channel differential amplifiers (Model 1700, A-M Systems, USA) and Axon Digidata 1440A digitizer, played in real-time on a PC using Axo-Scope software (Molecular Devices, Sunnyvale, CA, USA). Signals were processed with DataView (W.J. Heitler, University of St. Andrews, Scotland) and MATLAB R2017a (The MathWorks Inc., Massachusetts, USA) with CircStat toolbox (60). For linear statistics and graphs we used Prism 8 (GraphPad Software, San Diego, California USA). Circular graphs were generated using Oriana 4 (Kovach

computing services). The preparation and experimental setup are presented in **Figures 1A,B**.

Signal Processing and Data Analyses

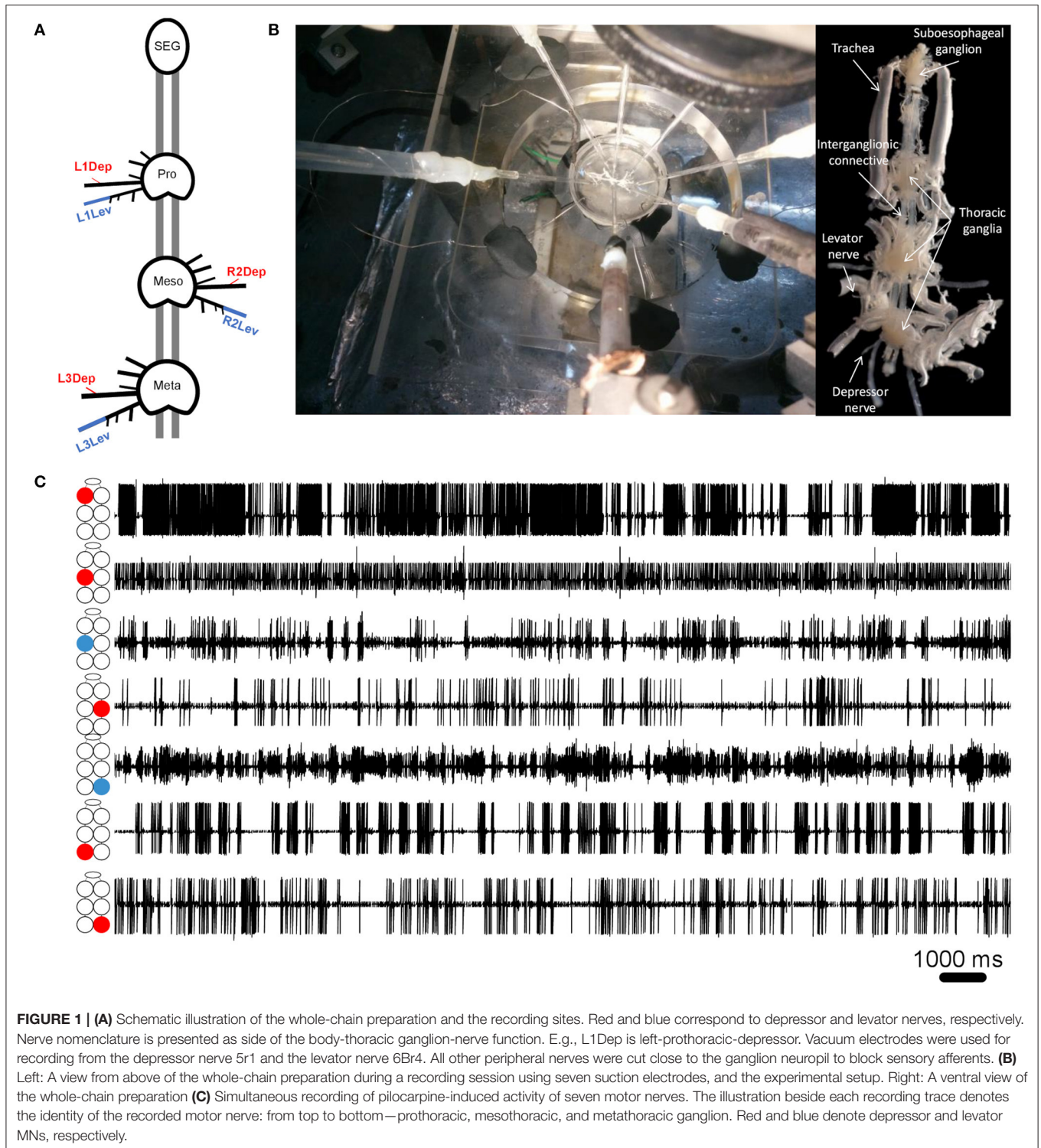
Ten minute recording bouts were analyzed (see **Figure 1C** for example of a short recording segment). Threshold spike detection generated event traces of fast and slow depressor MNs, and of levator MNs 5–12 (levator activity mostly comprised MNs 5 and 6). Data were analyzed for the MNs' firing patterns and for the coordination between MNs. Two parameters, *Rhythmicity* and *Burstiness*, describe the dynamic firing pattern of the investigated MNs: *Rhythmicity* is the consistency of the phase relations between time points separated by an interval. Here we calculate the lag coherence between two epochs of the analyzed signal as a measure of rhythmicity, following Fransen et al. (61). In short, the most prominent frequency in the Fourier transformed recording bout was identified, and the original signal was fragmented into adjacent, equal length, non-overlapping epochs of 5 cycles of this frequency (e.g., for 0.5 Hz each epoch's length was 10 s). The Fourier coefficient of each epoch was calculated by Fourier transforming the Hanning-tapered signal. Each coefficient is a vector in the complex plane. The vector's angle is the phase relative to the positive horizontal axis and its length is the amplitude. We then calculated for each pair of adjacent epochs the product of $F(x_n)_k F(x_{n+1})_k^H$, where $F(X)$ denotes the Fourier transform of the signal $X(n)$. The signals $X(n)$ (for $n = 1..N$) are ordered equal length epochs (5 cycles of the prominent frequency) that were cut from the original 10 min signal. k is the k th Fourier coefficient. H denotes the Hermitian transpose. The results were summed over all epoch pairs (equation 1 numerator). The final sum was then averaged with the number of epochs, to give the consistency of phase relations. Last, the outcome was normalized by the average amplitude in all epochs, to eliminate the dependency on amplitude in favor of the pure measure of rhythmicity, which is valued between 0 (arrhythmic) and 1 (perfect rhythmicity), as depicted by equation 1:

$$\text{Rhythmicity}(k) = \left| \frac{\sum_{n=1}^{N-1} F(x_n)_k F(x_{n+1})_k^H}{\sqrt{\left(\sum_{n=1}^{N-1} |F(x_n)_k|^2\right) \left(\sum_{n=1}^{N-1} |F(x_{n+1})_k|^2\right)}} \right|$$

Burstiness: bursts are short periods of intense activity followed by periods of inactivity/lesser activity. Burstiness is calculated from the distribution of interspike intervals, and is valued between -1 and 1 (62). $B = 1$ is a purely bursty signal, $B = 0$ is neutral (Poisson distribution of interspike intervals), and $B = -1$ is a completely regular (tonic) signal, as depicted by equation 2:

$$B = (\sigma_T - m_T) / (\sigma_T + m_T)$$

where B = burstiness, σ is the standard deviation of interspike intervals and m is the mean interspike interval. **Figure 2A** presents the burstiness of five MNs in a whole-chain preparation. The coordination between MNs was analyzed by a way of cross-spectrum analysis to assess the *coherence* and *phase-relations* between two event traces (63, 64). Event traces were first



bandpass filtered for 0.05–10 Hz, to exclude most of the non-bursting activity. This bandpass is 20-fold wider than usually seen and analyzed in similar *in vitro* insect preparations. This relatively fast activity could be due to greater excitability of the cockroach motor centers, which also manifests in the 10–50-fold

lower concentration of pilocarpine needed to induce long-lasting rhythmic activity in the cockroach preparation in comparison to locust (51, 65), stick insect (42), and moth (66). Additional parameters comprised the *Coherence* and *Phase-relations* of two signals. *Coherence* is defined by the IEEE Standard Dictionary

(67) as “the correlation between electromagnetic fields at points which are separated in space or in time, or both.” It is the measure of the causal relationship between two signals in the presence of other signals and will always satisfy $0 \leq \text{Coherence} \leq 1$. Coherence is used to measure mono-synaptic iso-frequency (i.e., “direct”) coupling between elements in a network (68); and is used here to assess the association between activity recorded from two MNs within an isolated ganglion, but not the whole-chain preparation. Confidence intervals of coherence were calculated following Rosenberg et al. (69). Here, the coherence is normalized to the highest value we calculated from our analyzed data. *Phase-relations* (phase) measures the relative timing of activity in one MN with respect to the activity of another MN. Here, phases were further processed for analysis only if their corresponding coherence was statistically significant (i.e., significant phases). The significant phases were averaged to give a single value of phase for each pair of MNs in each experiment. The products of different experiments were grouped to enable comparisons between different pairs of MNs. Hereafter phase refers only to significant phase. Two additional related parameters were calculated. The first, *Coupling strength* (CS), was calculated in order to also account for the variability of phase. CS is calculated by multiplying the length of vector of the phase by the mean coherence. Unlike the phase-independent coherence, CS also considers the phase-lock to produce a measurement of functional coupling. This distinction is important, since pairs of network units can present high or low coherence, regardless of the consistency of their phase. The second parameter is the *Synchronization index* (SI), which is a combined measure of the mean and variability of the phases. The linear SI (as opposed to the circular phase) represents the type of coordination (in-phase or antiphase) that a pair of MNs demonstrates, and the phase-lock. In brief, SI is the product of projecting the mean phase vector onto the 0–180 axis. The calculation is based on Knebel et al. [(51) and references within] but differs in that SI was calculated separately here for each experiment, to enable statistics and comparisons. The use of the linear SI instead of the circular phase also enabled the use of linear statistics instead of the relatively limited circular statistics. SI is defined between 1 (perfect in-phase) to –1 (perfect antiphase) with $\pm 5\%$ confidence intervals of ± 0.081 (see **Supplementary Figure 1** for more details). All data are presented as Mean $\pm$ Confidence-Intervals (CI) unless noted otherwise. Detailed data tables are presented in the **Supplementary Materials**.

Terminology and Abbreviations

In order to correctly identify the MN pairs referred to here, each MN is coded as followed: side of the body (right/left, R/L)-thoracic segment (1,2,3 for pro-, meso-, and meta-thorax, respectively)-function (levator/depressor, Lev/Dep). For example: R2Dep-L2Lev represents the pair comprising the right mesothoracic depressor and left mesothoracic levator (see illustration in **Figure 1A**). In addition, pairs comprising two MNs performing the same function are referred to as “homogenous.” Moreover, we use the terms “in-phase” and “antiphase,” which correspond to phase relations of 0 and 180°, to describe a range of phase relations according to their proximity to the ideal

values noted above: in-phase between 270 and 90° and antiphase between 90 and 270°.

RESULTS

Before the application of pilocarpine, we observed either no activity or a motor output characterized by low burstiness, which usually did not persist for more than a few minutes before the preparation became quiescent. The following results are all from pilocarpine-stimulated preparations (see reference to this point in the Discussion).

Isolated Ganglia Preparations

Each thoracic ganglion controls a pair of contralateral legs. The pairs differ in their size, shape, and function. These differences suggest that the underlying neural control also differ. To investigate this, we characterized the burstiness and rhythmicity of the motor output recorded from homolog depressor and levator MNs in the three thoracic ganglia. In addition, we performed a comparative analysis of the temporal relations between motoneuron activity within the isolated ganglia: frequency, coherence, phase, the type of coordination (in-phase or antiphase), and the coupling strength. We further tested for frequency-dependent differences in the calculated parameters.

Levators Burstiness, but Not Rhythmicity, Varies Between Ganglia. Depressors Present the Opposite

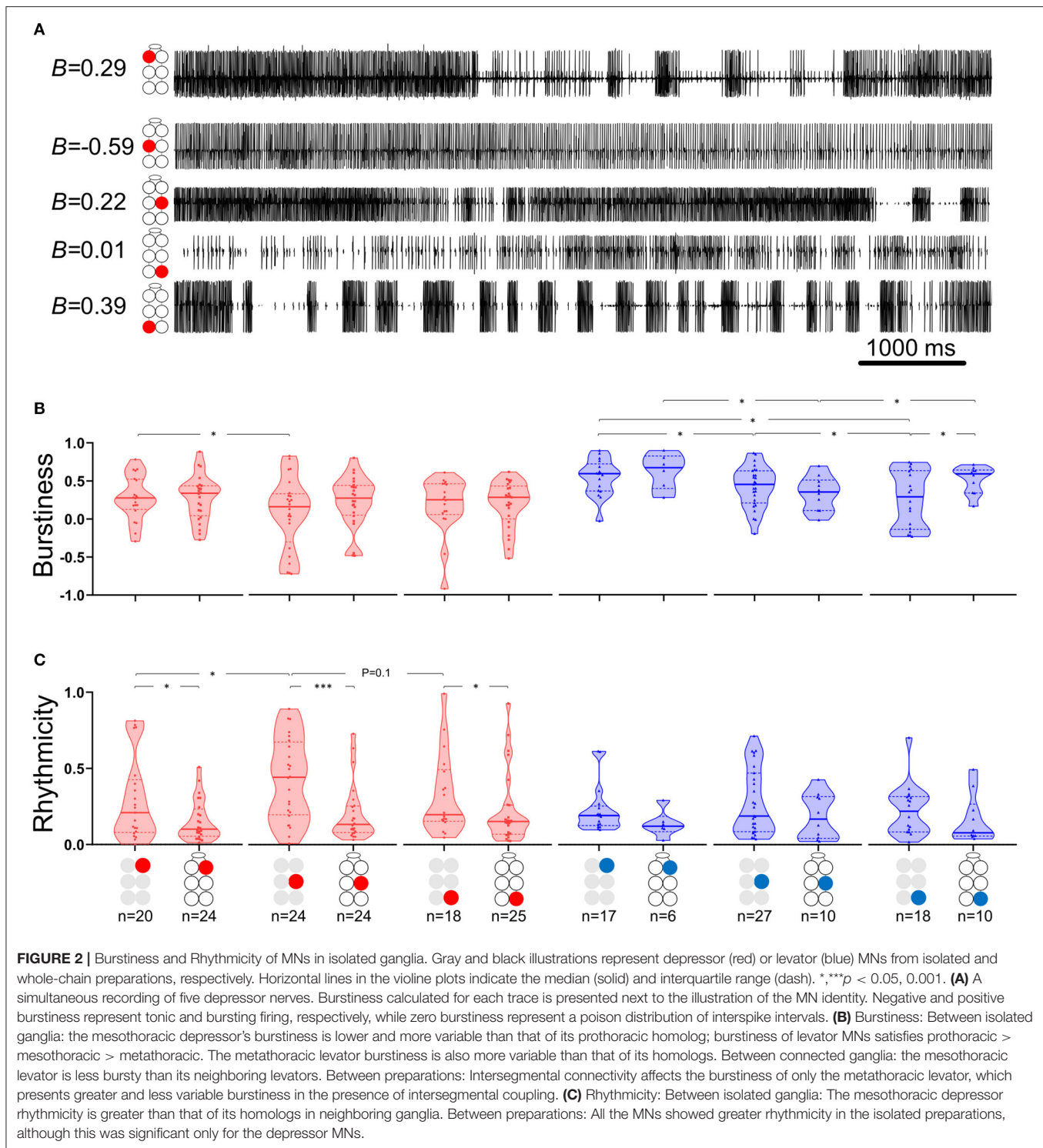
The data presented in **Figure 2** and in **Supplementary Tables 1, 2** describe the burstiness (**Figure 2B**) and rhythmicity (**Figure 2C**) of homolog MNs in the isolated pro-, meso-, and meta-thoracic ganglion. Burstiness of the R2Dep was lower than that of R1Dep (Welch's *t*-test, $p < 0.05$), and more variable than in both R1Dep and R3Dep (Brown-Forsythe, $p < 0.05$). Levator burstiness satisfied prothoracic > mesothoracic > metathoracic (Brown-Forsythe Anova, $p < 0.05$). Surprisingly, burstiness was not correlated with rhythmicity (Spearman's or Pearson's correlation, $p > 0.05$). R2Dep showed greater rhythmicity than both R1Dep and, although not statistically significant, R3Dep (Mann-Whitney, $p < 0.05$ and $p = 0.1$, respectively). Levator MNs rhythmicity was similar in all the ganglia ($p > 0.2$).

Temporal Relations Between Motoneurons in the Isolated Ganglia

Although similar studies of other insect *in-vitro* preparations have shown findings that were obtained from low-frequency motor activity of up to 0.5 Hz (42, 51, 65, 66), our cockroach *in vitro* preparation showed burst frequencies as high as 10 Hz (although 9–10 Hz activity was scarce and mostly uncoordinated). Therefore, we first analyzed a wide range of frequencies and then, following our findings, we limited the range of frequencies for further investigation.

Coherence Is Frequency-Dependent Only in the Contiguous Pairs

First, the coherence between paired MNs was calculated and filtered to include frequencies between 0.05:10 Hz and exclude non-bursting activity (step = 0.0167 Hz; coherence is presented



in **Supplementary Table 3**). The coherence was then binned in 10 frequency groups: 0.05–1, 1–2 Hz, ... 9–10 Hz. The first bin comprised two values less than the other bins (values lower than 0.05 Hz). Next, the relations between coherence and frequency were characterized for all possible pairs of MNs in each isolated thoracic ganglion: the contralateral pair of depressors,

the contralateral pair of levators, a pair of contralateral depressor and levator, and the contiguous pair (within a hemiganglion) of depressor and levator (hereafter, Dep-Dep, Lev-Lev, Dep-Lev, and contiguous, respectively). The findings are illustrated in **Figure 3A**. For an in-dept analysis we used two-way ANOVA with repeated measures of the row factor (i.e., frequency)

and a Tukey test for *post-hoc*. Our analysis revealed that the contiguous pair had greater mean coherence than that of the corresponding contralateral pairs at frequencies lower than 5 Hz in the metathorax ($p < 0.01$, **Figure 3Aiii**), and lower than or equal to 7 Hz in the mesothorax ($p < 0.01$, **Figure 3Aii**); and this was also the case for the prothoracic pair throughout the entire range of frequencies tested ($p < 0.001$, **Figure 3Ai**). In addition, a Friedman's test calculated based on the mean coherence of each bin, and followed by Dunn's post hoc test, revealed that R3Dep-L3Lev had a greater mean coherence than R3Dep-L3Dep and R3Lev-L3Lev; while in the mesothoracic ganglion the coherence was similar for all three contralateral pairs; and in the prothoracic ganglion R1Dep-L1Dep had greater mean coherence than R1Dep-L1Lev (Dunn's, $p < 0.05$). A second two-way ANOVA was calculated in order to examine the differences between pairs and between ganglia. R1Dep-R1Lev and R1Dep-L1Dep mean coherence was found to be greater than their homologs in the other ganglia (Tukey, $p < 0.01$). In addition, R3Dep-L3Lev was found to be greater than R2Dep-L2Lev. Moreover, the R1Dep-R1Lev and R1Lev-L1Lev showed greater mean coherence than their homologs in the other ganglia (Tukey, $p < 0.05$; data are presented in **Supplementary Figure 2** and **Supplementary Table 3**). Another difference between the ganglia is seen in the way the coherence of the contiguous pairs underwent change with frequency. R1Dep-R1Lev showed relatively high coherence throughout most of the investigated frequency band, with a wide parabolic distribution that peaks at about 5 Hz, while R2Dep-R2Lev peaks at about 0.5 Hz and sharply decreases above 2 Hz, and R3Dep-R3Lev decreases from the first indexed frequency (0.05 Hz) and onward. These findings may indicate that a strong intra-hemiganglion coherence is especially important for the appropriate function of the prothoracic control network, at all frequencies.

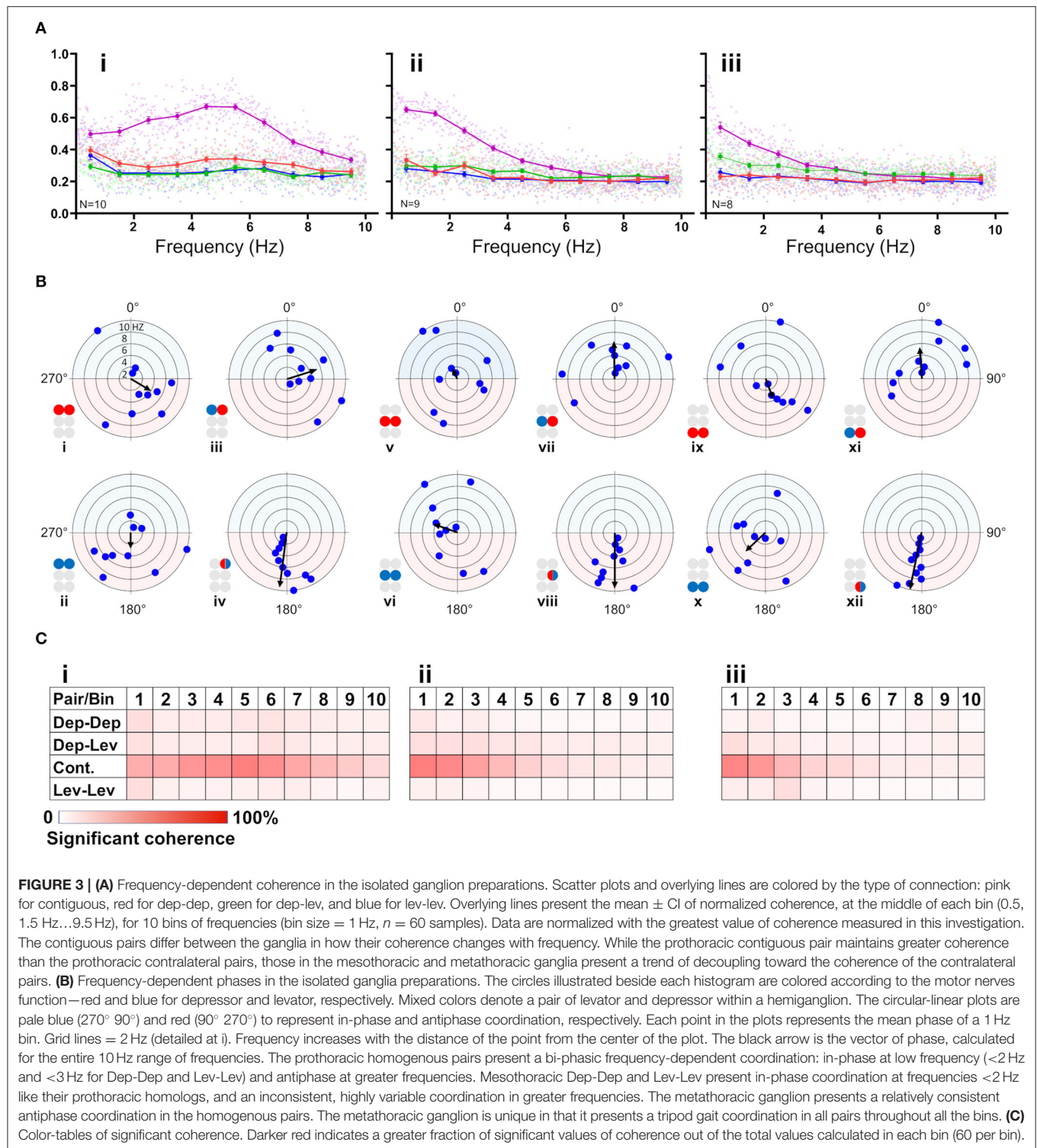
Phase-Relations Are Frequency-Dependent for Homogenous Prothoracic and Mesothoracic Pairs, and Frequency-Independent for Heterogenous and All Metathoracic Pairs

Frequency-dependent coherence suggested that phase might also vary with frequency. This had implications for our choice of the range of frequencies to be analyzed here, as well as for the possible interpretations of (partial findings from) previous studies. To investigate this, phase was calculated and binned in ten frequency groups: 0.05–1, 1–2 Hz, ..., 9–10 Hz. Mean phase was calculated for each preparation separately, for each of the 10 group of frequencies. **Figure 3B** and **Supplementary Table 4** present the mean calculated for all 20 preparations ($N = 20$). In general, the contiguous pairs displayed a consistent and frequency-independent antiphase coordination throughout all the bins, in all ganglia (**Figure 3Biv,viii,xii**). Moreover, the Dep-Lev pairs displayed a frequency-independent phase with lower variability than their corresponding Dep-Dep and Lev-Lev pairs (**Figure 3Biii,vii,xi**). R1Dep-L1Dep and R1Lev-L1Lev presented bi-phasic coordination: in-phase up to 2 and 3 Hz (respectively), and antiphase above it (**Figure 3Bi,ii**; Watson-Williams, $p <$

0.05). Likewise, R2Dep-L2Dep and R2Lev-L2Lev showed in-phase coordination up to 2 Hz, although weaker for R2Lev-L2Lev (**Figure 3Bv,vi**). The coordination of both pairs became inconsistent at higher frequencies. In contrast, R3Dep-L3Dep and R3Lev-L3Lev presented an overall frequency-independent antiphase coordination (**Figure 3Bix,x**). In addition, we found a frequency-dependent variability in the number of significant phases that were calculated for each of the frequency bins, mostly in favor of the lower frequencies (**Figure 3C**). This phenomenon is predominantly linear in the meso- and meta-thoracic ganglia (**Figure 3Cii,iii**), and parabolic in the prothoracic ganglia (**Figure 3Ci**), a pattern that corresponds to the frequency-dependent variability of coherence of the different contiguous pairs. The frequency-dependent decrease in coherence manifests as fewer bursts and more transient spikes in the medium-to-high range frequencies. At the highest investigated frequencies 9 and 10 Hz, the simultaneous bursting of different MNs was scarce, mostly with below-threshold coherence, and with an inconsistent phase. Since the major share of significant phases (i.e., eligible for analysis) was sampled between 0.05 and 3 Hz, and includes the changes we observed at 2 Hz in some of the pairs, and also to enable a better comparison with studies of other *in-vitro* insect models, as noted above, we chose to focus on the frequency band 0.05–3 Hz for the further analyses of the isolated ganglion preparations.

Contralateral Coordination Differs Between the Isolated Ganglia, and Is Functional Only in the Metathoracic Ganglion

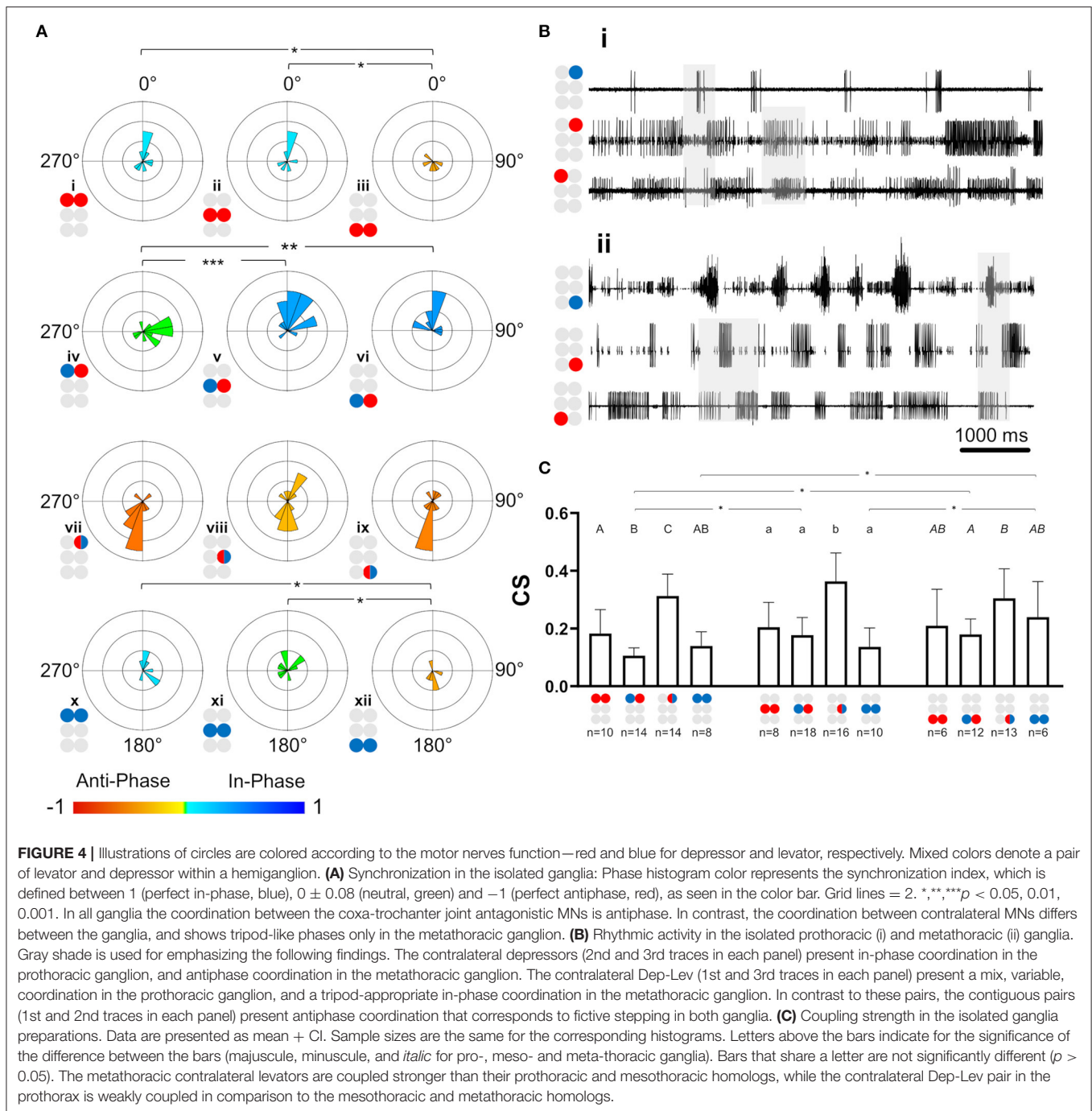
After the data had been filtered for the appropriate frequency band (0.05–3 Hz), the intra-ganglionic coordination was characterized. A synchronization index (SI) was calculated to give a combined, linear, and comparable measure of coordination and its strength, for the frequency range comprising most of our data. Data are illustrated in **Figure 4A** and detailed in **Supplementary Table 5**. Significance of differences was calculated using a Mann-Whitney test with a Bonferroni correction for two comparisons. Differences in SI were found between contralateral pairs. For Dep-Dep pairs, R3Dep-L3Dep antiphase coordination (**Figure 4Aiii**) significantly differed from the in-phase coordination found in R1Dep-L1Dep, R2Dep-L2Dep (**Figure 4Ai,ii,iii**. $SI = -0.483 \pm 0.34$, 0.125 ± 0.36 , and 0.097 ± 0.49 , respectively; $p < 0.025$). For Dep-Lev pairs, R1Dep-L1Lev showed neutral synchronization (i.e., between in-phase and antiphase: mean $\pm$ CI = 0 ± 0.08), in contrast to in-phase coordination in R2Dep-L2Lev and R3Dep-L3Lev ($SI = -0.062 \pm 0.1$, 0.355 ± 0.16 and 0.396 ± 0.21 , respectively; $p < 0.01$, **Figure 4A**). These differences are demonstrated in the recordings presented in **Figure 4B**. R1Dep and L1Dep were in-phase coordinated, and R1Dep and L1Lev coordination was inconsistent (**Figure 4Bii**), in contrast to the antiphase coordination of R3Dep and L3Dep, and the consistent in-phase coordination of R3Dep and L3Lev (**Figure 4Bii**). Last, the prothoracic and mesothoracic Lev-Lev synchronization was found to be in-phase and neutral, respectively, unlike the significant difference in the antiphase synchronization found in the metathoracic



ganglion ($SI = 0.122 \pm 0.3$, 0.046 ± 0.25 and -0.418 ± 0.38 , respectively; $p < 0.025$, **Figure 4Ax,xi,xii**). Overall, only the isolated metathoracic ganglion showed an intra-ganglion coordination that corresponded to that expected for the tripod gait (**Figure 4Aiii,vi,xii**).

Coupling of Dep-Lev and Lev-Lev Is Ganglion-Specific

Following establishment of the type of coordination, the strength of the central coupling (CS) was examined (data are detailed in **Supplementary Table 6**). As presented in **Figure 4C**, Dep-Dep pairs were similarly coupled in all ganglia. This was also the case



for the homolog contiguous pairs, which also had greater CS in comparison to the other pairs of MNs in the prothoracic and mesothoracic ganglia (*t*-test or Mann-Whitney with Bonferroni correction, $p < 0.017$). In contrast, the comparison between ganglia revealed two significant differences: Dep-Lev coupling was weaker in the prothoracic ganglion and Lev-Lev coupling was stronger in the metathoracic ganglion, in comparison to their homologs in the other ganglia (Mann-Whitney with Bonferroni correction $p < 0.025$). These findings provide further evidence that the intrinsic local networks themselves are not identical and

that their endogenous connectivity and/or the synaptic strength of the connections, are designed to enable different functionality.

The Whole-Chain Preparation

With the exception of coherence, the same set of parameters and analyses used for the investigation of the single isolated ganglion preparations was also used for characterization of the activity and coordination of the depressor-levator network in an intact chain of the thoracic and subesophageal ganglia. The overall connectivity network of this preparation potentially

comprises 36 different pairs of MNs, for which recording and analyzing a reliable sample is an overwhelming task. A total of seven intra-ganglion connections were investigated in the whole-chain preparation: R1Dep-L1Dep, R2Dep-L2Dep, R3Dep-L3Dep, R2Dep-L2Lev, R3Dep-L3Lev, R2Dep-R2Lev, and R3Dep-R3Lev. We then focused on 16 interganglia connections: six Dep-Dep, eight Dep-Lev, and two Lev-Lev, detailed in **Figure 5C**. The network was divided into two sub-networks: anterior for the prothoracic-mesothoracic connections and posterior for the mesothoracic-metathoracic connections (see **Figure 5B** for illustration). This was done in order to examine the differences and similarities between homolog connections in the two sub-networks. The calculated phases between MNs are referred to as tripod-gait-appropriate if they corresponded to those recorded (or could be recorded) in the intact walking insect. Here we focused mostly on mesothoracic-metathoracic pairs of MNs (8 pairs), rather than on prothoracic-mesothoracic or prothoracic-metathoracic ones (4 pairs each), because most of the previously published relevant research refers to mesothoracic and metathoracic MNs (38, 48, 70–72). Moreover, we chose to focus our investigation on connections between the depressor MNs (all 9 pairs), which again enabled comparison to the ample related previous research (46, 51, 54, 55, 73).

Levators Burstiness, but Not Rhythmicity, Differ Between Preparations and Between Ganglia, While Depressors Present the Opposite

The effects of intersegmental connectivity on MNs burstiness and rhythmicity were studied by comparing the isolated with the whole-chain preparations. As can be seen in **Figure 2B** and **Supplementary Table 1**, the intersegmental connectivity had a statistically significant effect on the burstiness of only one motor nerve—the metathoracic levator, which had twice the mean burstiness, and half the variability, in the presence of intersegmental connectivity (mean $\pm$ SD for isolated and whole-chain preparations: $0.51 \pm 0.18 > 0.25 \pm 0.36$, $n = 18$ and 10 accordingly; Welch's t -test, $p < 0.01$). This was followed by a comparison between homolog MNs in the whole-chain preparation, which revealed that the mesothoracic levator was less bursty than the other levators (Welch's t -test, $p < 0.05$). **Figure 2C** and **Supplementary Table 2** present a similar analysis of rhythmicity, demonstrating that it was consistently greater in the isolated ganglion, although the differences were statistically significant only for the depressor MNs (Mann-Whitney, $p < 0.05$). Moreover, the variability in rhythmicity of the prothoracic depressor MN was found to be lower than that of its meso- and meta-thoracic homologs; while for the levator the difference was significant only in comparison to its mesothoracic homolog (Brown-Forsythe, $p < 0.05$).

Temporal Relations Between MNs in the Whole-Chain Preparation

The relations between phase and frequency were studied in the whole-chain preparation for a frequency band of 0.05–10 Hz (data are given in **Supplementary Table 7**). First, the seven intra-ganglion connections were studied and compared between the isolated and whole-chain preparations. Overall, 6 out of 7

intra-ganglion connections showed similar phase relations in both preparation types throughout the entire frequency range (**Supplementary Figure 3**), suggesting that their coordination is not significantly influenced by intersegmental or SEG inputs. In contrast to the other pairs, R1Dep-L1Dep fired in-phase at low frequencies and in antiphase at frequencies > 2 Hz in the isolated preparation, as opposed to the consistent in-phase coordination it showed in the whole-chain preparation ($\Phi_{\text{isolated}} = 121.2 \pm 77.8$, $\Phi_{\text{whole-chain}} = 306.7 \pm 58.2$, $p < 0.001$, **Figure 5A**). In addition, although R2Dep-L2Dep had an overall similar mean phase in both preparations, the vector length of the mean phases was 3-fold greater in the whole-chain preparation ($R = 0.185$ and 0.563 for isolated and whole-chain preparations, respectively), suggesting a stabilizing input to the mesothoracic ganglion.

Frequency-Dependent Phase-Relations Differ Substantially Between the Anterior and Posterior Sub-networks

As noted above, the network was divided into two sub-networks: anterior and posterior (**Figure 5B**). Frequency-dependent phase data for four pairs recorded from the anterior sub-network are presented in **Figure 5C**. R1Dep-R2Lev and R1Dep-L2Dep maintained a tripod-gait-appropriate in-phase coordination throughout the examined frequency range (**Figure 5Cv,xiii**, respectively). The latter is in accordance with a finding from locusts that a front leg and its diagonal middle leg are always strictly coordinated in phase (74). In contrast, R1Dep-R2Dep and R1Dep-L2Lev, which showed an antiphase coordination during tripod locomotion, had in-phase coordination below 2 Hz, and a robust antiphase coordination only at greater frequencies (**Figure 5Ci,ix**, respectively). This pattern corresponds to that seen in the prothoracic and mesothoracic Dep-Dep and Lev-Lev pairs in the isolated ganglion preparations (**Figure 3Bi,ii,v,vi**). In addition, eight pairs were recorded from the posterior sub-network. In contrast to their anterior sub-network homologs, R3Dep-L3Dep and R3Lev-L3Lev showed a tripod-appropriate antiphase coordination from the lowest end of the frequency band, and roughly to its middle (5 and 4 Hz for R2Dep-R3Dep and R2Lev-R3Lev, **Figure 5Cii,iii**, accordingly). Similarly, the ipsilateral mixed pair R2Lev-R3Dep had in-phase coordination only at frequencies < 5 Hz (**Figure 5Cvii**). These findings are also demonstrated in the recording sample of mostly low-frequency activity (< 5 Hz) in the posterior sub-network which is presented in **Figure 5D**. A comparison between calculated phases from the two halves of the frequency range (lower and higher, all phases are given in **Supplementary Figure 4**) further support these findings. R2Dep-R3Dep and R3Lev-L3Lev practically inverted from predominantly antiphase to in-phase coordination with the increase in frequency, while in R2Lev-R3Dep the change was the opposite (R2Dep-R3Dep: $\Phi_{<5\text{Hz}} = 202.8^\circ \pm 45.4$, $\Phi_{5-10\text{Hz}} = 307.1^\circ \pm 48.9$, $p < 0.05$, **Figure 5Ei**; R2Lev-R3Lev: $\Phi_{<5\text{Hz}} = 211^\circ \pm 54.2$, $\Phi_{5-10\text{Hz}} = 62.1^\circ \pm 62.7$, $p = 0.01$, **Figure 5Eii**; R2Lev-R3Dep: $\Phi_{<5\text{Hz}} = 6.5^\circ \pm 51.7$, $\Phi_{5-10\text{Hz}} = 173.9^\circ \pm 31.8$, $p < 0.001$, **Figure 5Eiii**). This finding may suggest that the posterior sub-network is wired to generate fast locomotion (faster than that using the tripod gait) that shows at least a partial overlap in the swing phases of the ipsilateral neighboring legs. Oddly, unlike R2Lev-R3Dep, the reciprocal pair R2Dep-R3Lev showed

in-phase coordination throughout the entire frequency band ($\Phi = 52^\circ \pm 70.4$, **Figure 5Cvi**). This asymmetry, along with others, is addressed in the Discussion. Next, we studied the diagonal pairs and found that the homogenous pairs R2Dep-L3Dep and R2Lev-L3Lev were in-phase coordinated regardless of frequency (**Figure 5Cxiv,xv**, respectively). However, as in the ipsilateral pairs, the mixed diagonal pairs were asymmetrical: while R2Dep-L3Lev had an overall in-phase coordination throughout the frequency band ($\Phi = 315.2^\circ \pm 67$, **Figure 5Cx**), R2Lev-L3Dep had antiphase coordination ($\Phi = 227.3^\circ \pm 65.2$, $p < 0.001$, **Figure 5Cxi**). Finally, we examined the coordination between the prothoracic and metathoracic ganglia. Only R1Dep-L3Dep showed frequency-dependent phases ($\Phi_{<5\text{Hz}} = 334.3^\circ \pm 21.3$, $\Phi_{5-10\text{Hz}} = 182.8^\circ \pm 71.2$, $p < 0.01$, **Figure 5Cxi**). R1Dep-R3Dep had a consistent in-phase coordination (**Figure 5Civ**), while the two heterogeneous pairs had dysfunctional (i.e., not corresponding to known insect gait) phases (**Figure 5Cviii,xii**).

Tripod-Appropriate Coordination Is Found Only in the Posterior Sub-network

As in the case of the isolated ganglion preparations, and for similar reasons, the following analyses of the whole-chain preparation relate to data obtained within the frequency band 0.05–3 Hz. The SI was calculated for the 23 pairs of MNs (data provided in **Supplementary Table 8**). First, the seven intra-ganglion pairs were compared with their parallels in the isolated preparations and found to not significantly differ (Mann-Whitney, $p > 0.1$). This indicates that intersegmental connectivity has an insignificant or weak effect on the coordination type and consistency of intra-ganglion connections of Dep-Dep, meso- and meta-thoracic Dep-Lev, and the contiguous pairs, in the 0.05–3 Hz frequency range. Next, the 16 interganglia pairs were studied for their SI, as presented in **Figure 6A**. In a comparison between homolog connections in the anterior and posterior sub-networks we found significant differences only in pairs that are expected to fire in antiphase during tripod-gait locomotion (SI = 0.043 ± 0.24 and -0.25 ± 0.31 for R1Dep-R2Dep and R2Dep-R3Dep, **Figure 6Ai,ii**, respectively; SI = 0.353 ± 0.23 and -0.121 ± 0.29 for R1Dep-L2Lev and R2Lev-L3Dep, **Figure 6Aix,xi**, respectively. Mann-Whitney, $p < 0.05$). In-phase pairs were similarly synchronized in both sub-networks. Generally, as seen in the recording in **Figure 6B**, the anterior sub-network was active in-phase, while the posterior sub-network demonstrated tripod-like antiphase coordination, including antiphase coordination in the appropriate pairs. Moreover, the heterogeneous prothoracic-metathoracic pairs: R1Dep-R3Lev and R1Dep-L3Lev showed a dysfunctional neutral coordination (SI = 0.05 ± 0.16 and 0.03 ± 0.36 , **Figure 6Aviii,xii**, respectively), while R1Dep-R3Dep demonstrated weak in-phase coordination that approaches neutral coordination (**Figures 6Aiv,B**), and R1Dep-L3Dep was distinctly in-phase, unlike during tripod locomotion (**Figure 6Axvi**). This indicates that the prothoracic-metathoracic pathway is indirect, supporting the nearest-neighbor architecture which considers distant connections to be indirect (see Discussion for more details).

Coupling Strength Varies Between and Within the Sub-networks

Last, *coupling strength* (CS) between MNs in the whole-chain preparation was examined in order to study the effect of interganglia connectivity on intra-ganglion phase-lock, to enable a comparison with the isolated ganglion preparations, and also in order to reexamine and fill-in gaps in the coupling scheme previously suggested by David et al. (38). Results are presented in **Figure 6C**, **Supplementary Figure 5**, and in **Supplementary Table 9**. This inquiry started with the intra-ganglion pairs. Dep-Dep from different ganglia had similar CS (One-way ANOVA, $p > 0.1$, **Supplementary Figure 5**). In contrast, R3Dep-L3Lev and R3Dep-R3Lev were coupled significantly more strongly than R2Dep-L2Lev and R2Dep-R2Lev, respectively (t -test, $p < 0.05$, **Figure 6Ci**). A similar study of the interganglia connections followed. Another asymmetry of CS was found between reciprocal pairs (**Figure 6Cii**). CS of R2Dep-R3Lev was greater than that of R2Lev-R3Dep (CS = 0.28 ± 0.07 and 0.11 ± 0.06 , respectively, t -test, $p < 0.01$) and R2Dep-L3Lev had greater CS than R2Lev-L3Dep (CS 0.22 ± 0.11 and 0.11 ± 0.06 , respectively. $p < 0.05$). In addition, homolog connections in the anterior and posterior sub-networks were compared (**Figure 6Ciii**). Although all pairs from the posterior sub-network exhibited greater CS than their anterior homologs, the difference was significant only for the ipsilateral Dep-Lev pair (CS = 0.14 ± 0.4 and 0.28 ± 0.07 for R1Dep-R2Lev and R2Dep-R3Lev, respectively, t -test, $p < 0.01$). In a comparison between the posterior sub-network pairs, R2Dep-R3Lev was coupled more strongly than R2Dep-R3Dep (CS = 0.28 ± 0.07 and 0.19 ± 0.05 , respectively, t -test, $p < 0.05$). CS was also compared between the whole-chain and the isolated preparations (**Figure 6Civ**, data from the isolated preparations are also presented in **Figure 4C**). A significant difference was found only in R3Dep-L3Lev (0.18 ± 0.05 and 0.28 ± 0.15 for isolated and whole-chain, respectively, t -test, $p = 0.05$), and a less significant one in R3Dep-R3Lev (0.3 ± 0.1 and 0.43 ± 0.17 for isolated and whole-chain, respectively, t -test, $p = 0.069$). This finding indicates that interganglion inputs to the metathoracic ganglion strengthens the coupling between depressor and levator premotor networks, while having no effect on the contralateral depressors or on the mesothoracic pairs.

DISCUSSION

The controversy around the origin and control of the rhythmic motor patterns for locomotion go back as far as Sherrington and Brown that have suggested an instrumental role for feedback or feedforward control, respectively (75, 76). While it is generally accepted nowadays that central pattern generating circuits are responsible for locomotion-related rhythms in practically all studied organisms from humans to insects (19, 77, 78), there are still well-established studies demonstrating, particularly for insect walking, that the currently available experimental data can be very well-explained without the need for postulating central control (79). In the current study (as in most in the field), we assume the presence of CPG circuits in the thoracic CNS that comprise conditional oscillators, i.e., require

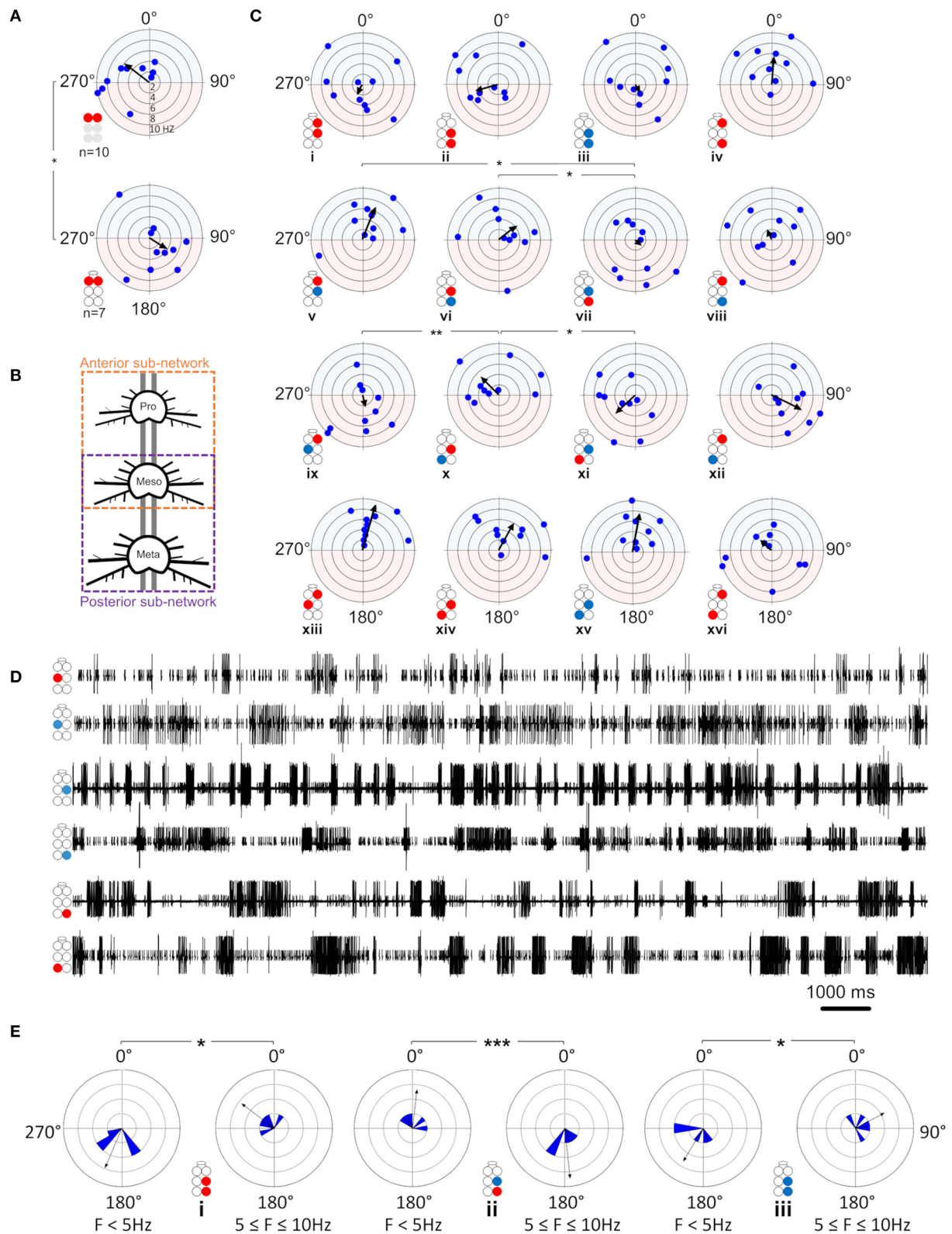


FIGURE 5 | Illustrations of circles are colored according to the motor nerves function—red and blue for depressor and levator, respectively. Illustrations with gray circles represent the isolated preparation and illustrations with black empty circles represent the whole-chain preparation. The circular-linear plots are pale blue (270°–90°) and red (90°–270°) to represent in-phase and antiphase coordination, respectively. Grid lines = 2 Hz (detailed at **A**, top plot). Arrow-vector of phases. *, ** $p < 0.05$; *** $p < 0.001$. (Continued)

FIGURE 5 | 0.05, 0.01 **(A)** Interganglion connectivity affects the coordination of the prothoracic depressors. The prothoracic pair of depressors presents a similar in-phase coordination at frequency <2 Hz in both isolated (top) and whole-chain (bottom) preparations, and different types of coordination at greater frequencies. The other six intraganglion pairs of MNs that were compared between the preparations were found to present non-significant differences in phases at the different frequencies. **(B)** Illustration of the division of the whole-chain preparation into two sub-networks- anterior and posterior. **(C)** Frequency dependent interganglia phases. Left column- anterior sub-network, middle columns- posterior sub-network, right column- between non-neighboring ganglia. Rows from top to bottom: ipsilateral homogenous, ipsilateral mixed, diagonal mixed, and diagonal homogenous. Significant differences between the sub-networks were found only in the mixed Dep-Lev ipsilateral and diagonal pairs, and not in the homogenous pairs. In the anterior sub-network, R1Dep-R2Dep (i) and R1Dep-L2Lev (ix) which alternate during tripod locomotion changed from in-phase to antiphase coordination at frequencies > 2 Hz, while R1Dep-L2Dep (xiii) and R1Dep-R2Lev (v), which fire in-phase during tripod locomotion, demonstrated a frequency-independent coordination. In the posterior sub-network, asymmetries were found between reciprocal mixed pairs in the ipsilateral [R2Dep-R3Lev (vi) and R2Lev-R3Dep (vii)], and the diagonal [R2Dep-L3Lev (x) and R2Lev-L3Dep (xi)] pathways. **(D)** Rhythmic activity in the posterior sub-network. Both contiguous pairs show antiphase coordination (1st and 2nd traces, and 4th and 5th traces). The ipsilateral pairs R2Lev-R3Lev (3rd and 4th traces), and L2Dep-L3Dep (1st and 6th traces) show weaker coupling strength and less rigid phase relations than the intraganglion pairs. **(E)** Frequency-dependent coordination inversion of ipsilateral pairs in the posterior sub-network. Grid line = 1. The phase histograms illustrate three pairs switching from tripod-like coordination at low frequencies into a faster gait at higher frequencies in which two ipsilateral legs can simultaneously perform the aerial phase.

the appropriate neuromodulatory environment for producing their rhythmic output (80). Neuromodulation is known to be essential for CPGs' appropriate functioning (15, 81, 82). Here, the required modulation is provided by pilocarpine, a muscarinic agonist known to non-specifically activate premotor networks of thoracic MNs in deafferented arthropod thoracic ganglia (70, 83). Pilocarpine has been repeatedly used to induce reliable long-lasting rhythmic activity in leg-motor neurons of *P. americana* (17, 38, 71), *Manduca sexta* (66), *C. morosus* (42, 54), *S. americana* (56, 65), and *S. gregaria* (51, 52). Although pilocarpine activates both flight- and walking-CPGs, at the low concentration used here the two networks do not affect one another's output (84). In this study we analyzed the intra- and inter-ganglion motor patterns and interactions between the coxa-trochanter CPGs that control the levator-depressor networks in the American cockroach, by monitoring the pilocarpine-induced motor-patterns of levator and depressor MNs in the three isolated thoracic ganglia and in an interconnected thoracic-subesophageal ganglia chain.

Unique Characteristics Found in Each of the Thoracic Ganglia Correspond to Their Roles in Locomotion

The cockroach's three pairs of legs differ from each other substantially in their overall size, length, foot trajectory, angle with respect to the body and to the ground, and musculature (85). The general simplified notion is that during 'normal walking' [i.e., straight-walking on a smooth horizontal surface (86)] the front legs steer the body, are used as probers and feelers, and decelerate the body during the stance phase. The middle legs are stabilizers, pivotal axis-leg during turning, first decelerate and then accelerate the body during the stance phase, and support some of the body load. Accordingly, the hind legs are the main motor that accelerates the body forward and also support its load (50, 55, 87–89). David et al. (38) found differences in the intraganglion coordination and coupling between the meso- and meta-thoracic ganglia, as well as differences in endogenous spike frequency of depressor MNs in a semi-intact cockroach preparation. Here we examined the Levator-Depressor network in each of the three thoracic ganglia in isolation. We reveal some common features as well as differences between the ganglia,

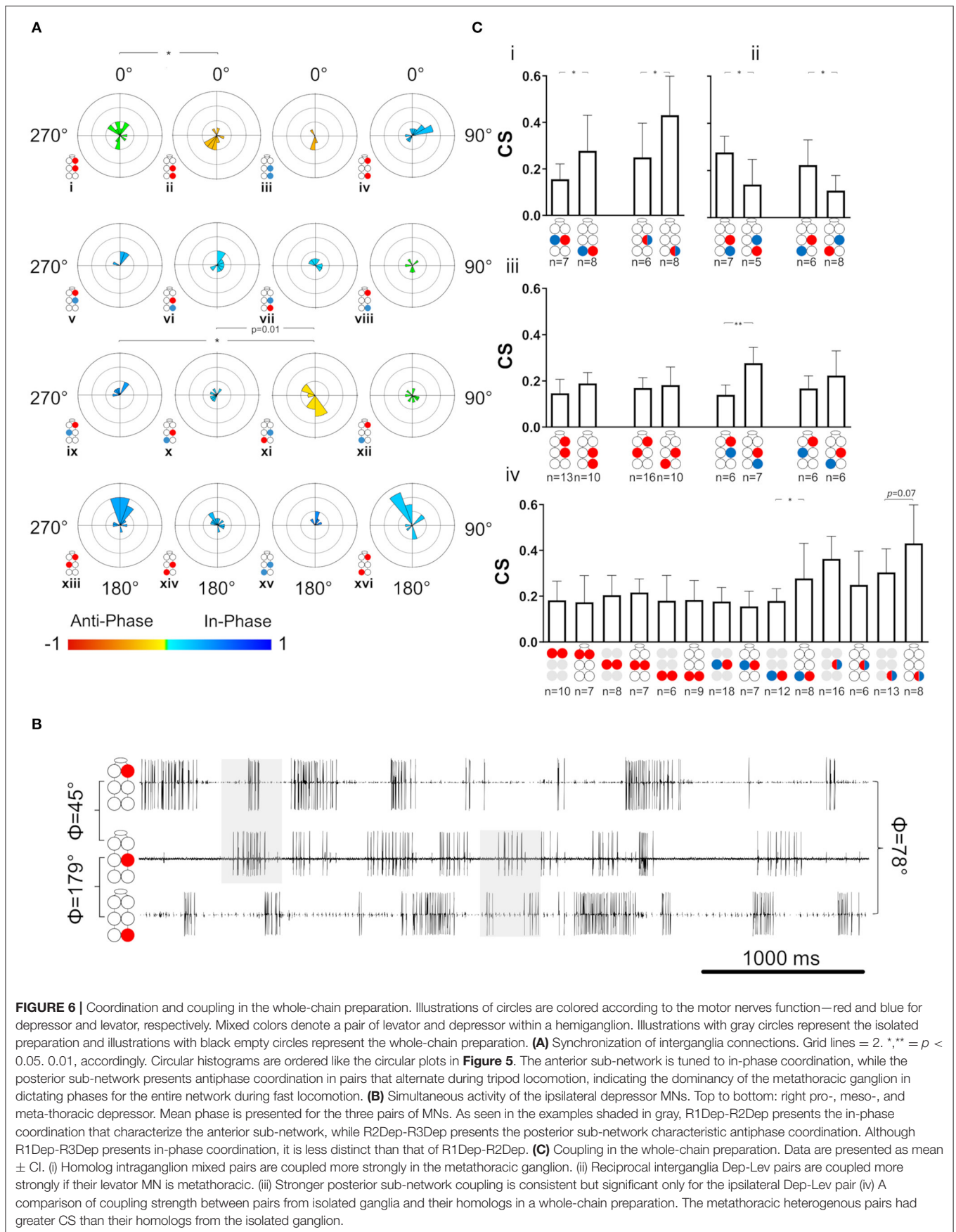
which are reflected in the nervous system connectivity and in turn affect the insect's behavior.

Central Control of Levator Premotor Networks

Previous studies have suggested that the levator premotor networks are predominantly controlled centrally, while those of the depressor are controlled locally (38, 45, 47, 49, 90). Our following findings support this hypothesis and suggests that interganglia coordination is best reflected in the activity of levator, rather than depressor, MNs: (i) Dep-Dep pairs showed common CS throughout the network, in both preparations, while contralateral pairs comprising a levator MN differed in their CS between ganglia. (ii) Descending inputs to the metathoracic ganglion increases the burstiness of R3Lev, as well as the CS of R3Dep-L3Lev and R3Dep-R3Lev, while not affecting R3Dep burstiness, or R3Dep-L3Dep CS. (iii) Considering that tripod gait is propagated back-to-front, and that the metathoracic ganglion dominates the overall motor pattern of a walking cockroach, our finding that in homolog and reciprocal pairs the presence of metathoracic levator accompany greater CS than when the levator is mesothoracic (Figure 6Ci,ii), also strengthens this notion. (iv) levator MNs showed similar rhythmicity between ganglia and between preparations, which indicates their oscillations are independent of local influences. In contrast, levators burstiness satisfies prothoracic > mesothoracic > metathoracic (Figure 2B), like the coherence of the contiguous pairs (i.e., Figure 3A). This suggests that burstiness is mostly influenced locally and decreases followings, or alongside, a decrease in the coherence of contiguous pairs. These findings also highlight the importance of studying levator activity.

Gait Transition Requires Modifications of Prothoracic and Mesothoracic Contralateral Phases

Frequency-dependent variability in coupling and inter-leg coordination have been mostly attributed to sensory-feedback and to head ganglia descending inputs (24, 79, 91–94). Our analyses, however, revealed solid evidence of endogenous frequency-dependent mechanisms in the completely isolated ganglia. Pro- and meso-thoracic homogenous pairs demonstrated frequency-dependent phase relations, indicating that gait transition is achieved also by modulating



intra-segmental coordination. In addition, we found frequency-dependent coherence in the contiguous pairs. These two findings may suggest that pairs that are coordinated in antiphase during tripod locomotion, are those that are susceptible to frequency-dependent modifications. This latter finding supports Reches et al. (24), and studies of stick insect [(79), and references within], who speculated that the default coordination between all the network units is in-phase, and that functional gaits result from modifications of the default phase between some of the network units.

Frequency-Dependent Coherence in the Contiguous Pairs Suggests for a Mechanism of Speed-Dependent Transition Into Central Control

Next, we examined the differences in frequency-dependent variability of coherence in the contiguous pairs. Our data in **Figure 3A** indicate three key frequencies: one around 2 Hz, another around 5 Hz, and a third around 7 Hz, that constitute points of change in the coherence. Behavioral studies in freely-walking cockroaches found that they walk in an undefined gait at low speed, while displaying a gradual transition to tripod-gait locomotion: slow unsteady gait at ~ 2 steps/s, robust tripod-gait at 5 steps/s, and fast and less variable gait, which is often referred to as “running” or “trot,” above 7 step/s (27, 37, 47, 49, 95–97). Similarly, David et al. (38) reported frequency-dependent inter-leg coordination in a semi-intact preparation, gradually changing toward an ideal tripod phase, reached at 5 Hz. Interestingly, although isolated and deafferented insect preparations are known to generate much slower motor patterns than those seen in intact animals, the reported endogenous thresholds of 2, 5, and 7 Hz correspond well to the threshold for transitions into the slow, robust, and then fast tripod locomotion that was measured in intact walking cockroaches. Our results support the hypothesis that the frequency-dependent decoupling of the meso- and meta-thoracic contiguous pairs underlies a transition from the feedback to the feedforward control that enables fast locomotion in insects. During slow walking, the coupling of these contiguous pairs is strong, and local feedback governs the hemiganglion motor output. As speed increases, the general gradual decoupling allows the frequency-independent weaker central contralateral coupling to exert greater influence on the local CPG; and, if ipsilateral coupling is added, the overall central coupling prevails to dominate the motor output of the local CPG at high speed. At ~ 5 Hz—the estimated stride frequency limit for sensory feedback cycle-by-cycle modulation (95, 97, 98)—the local and central coupling strengths are similar, resulting in a greater central coupling influence underling the inter-leg coordination during fast locomotion. Our hypothesis is also in agreement with a report that faster cockroaches recover from perturbation within a smaller fraction of their step cycle and more uniformly than slower ones, and that they display greater uniformity in intersegmental coupling among all legs, compared to the slower cockroaches (99). Furthermore, our finding of an antero-caudal gradient in the coherence of contiguous pairs (**Supplementary Figure 2**) agrees with the finding of a similar gradient in stick insect

(100). The strength of inter-leg coordination in the slow-walking stick insect depends on local sensory inputs to the local coxa-trochanter CPG. In the slow-walking stick insect, as oppose to our cockroach preparation, this gradient in coherence results in an antero-caudal gradient in coupling strength. Berendes et al.’s (94) finding of a speed-dependent increase in intersegmental cycle-to-cycle coupling in semi-intact walking flies is also in accord with our hypothesis. The endogenous frequency-dependent coherence of the contiguous meso- and meta-thoracic pairs also explains a fundamental characteristic of insect locomotion: the speed-dependent increase in protraction/retraction or levator/depressor duration ratios, mainly due to shortening of the stance phase duration (37, 38, 96). In a previous study we suggested a connectivity model of the levator-depressor network (38). Here we present this model with updates based on our new findings, and also provide the empirical data to support those parts of the model that were based on theoretical ideas and deductions (hereafter, “our model”; **Figure 8**). In our model we posit local hemiganglionic Lev-to-Dep inhibition and contralateral and ipsilateral Lev-to-Dep excitatory connections. Lev-to-Dep inhibition weakens toward the end of the levator burst to enable the on-time onset of the depressor burst for leg touch down. Decoupling of the contiguous pair weakens this inhibition, allowing Lev-to-Dep inter-hemiganglia excitations to induce an earlier and more intense depressor burst. This enables the same propulsion to be generated within the much shorter stance duration observed during fast running. Moreover, our results are supported by the positive correlation between burst frequency and spike frequency found in the deafferented cockroach (38).

The Prothoracic Network Enables Independent Activity of the Front Legs to Serve Their Unique Functioning

The cockroach front legs play a minor role in carrying the body load and in generating propulsion; however, they have a unique role in grooming, probing, steering, and negotiating obstacles. Insects turn by changing stride frequency or length without changing contralateral phases (32). Reports from various insects have shown turning also requires a change in the foot-trajectory, especially in the front legs (30, 33, 101–106). During curve walking the inner front leg performs a shorter swing, the outer counterpart extends its swing, and often also generates the perpendicular force necessary to deflect the body into the turn, while both legs retain their antiphase relation as in straight walking (102, 106), although not always (91, 103). These maneuvers require each front leg both to act independently of its counterpart leg, and to maintain an accurate coordination between its step phases and corresponding muscles. A strong coherence in the contiguous pairs enables these, first by ensuring accurate coordination of the antagonistic muscles within each leg; and second by prevailing over the central coupling that can hinder the intra-leg coordination through influence from the neighboring legs. Another mechanism that supports the front leg independence from neighboring legs is RIDep-L1Lev weak coupling, as also found in locust (56), and the resultant

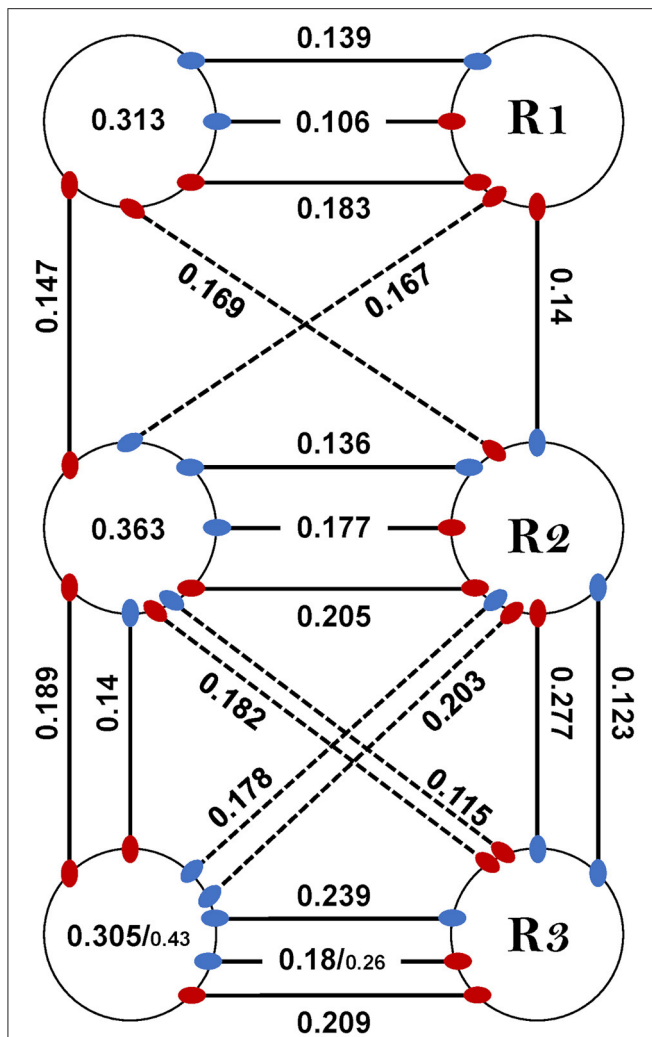


FIGURE 7 | Coupling scheme. Intraganglion and interganglia values of CS were obtained from the isolated and whole-chain preparations, respectively. Where a significant difference between the preparations was found we present two values as isolated/whole-chain. Following a nearest-neighbor architecture, the diagonal connections (dashed lines) are considered functional and not direct, and the prothoracic-metathoracic connections are absent (see text). Red or blue indicate for depressor or levator efferent, respectively (e.g., red-blue connection represents a depressor-levator connection). Values of contiguous pairs are presented within the corresponding circle. R1, R2, and R3 indicate for the right prothoracic, mesothoracic, and metathoracic ganglion, respectively. Pairs from the posterior sub-network present greater coupling than their homolog pairs in the anterior sub-network. Interganglia connectivity increases intraganglion coupling in the metathorax and decreases it in the mesothorax. Intraganglion Dep-Dep coupling is unaffected by interganglia connectivity.

endogenous neutral phase relations. Rigid contralateral Dep-Lev in-phase coordination is crucial for maintaining static stability during locomotion (2). This feature is compromised in the front legs in favor of flexible functioning. Contralateral excitation from stance- to swing-phase premotor networks have been previously suggested as centrally mediated in the cockroach (38), and sensory feedback mediated in the stick insect [rules 2

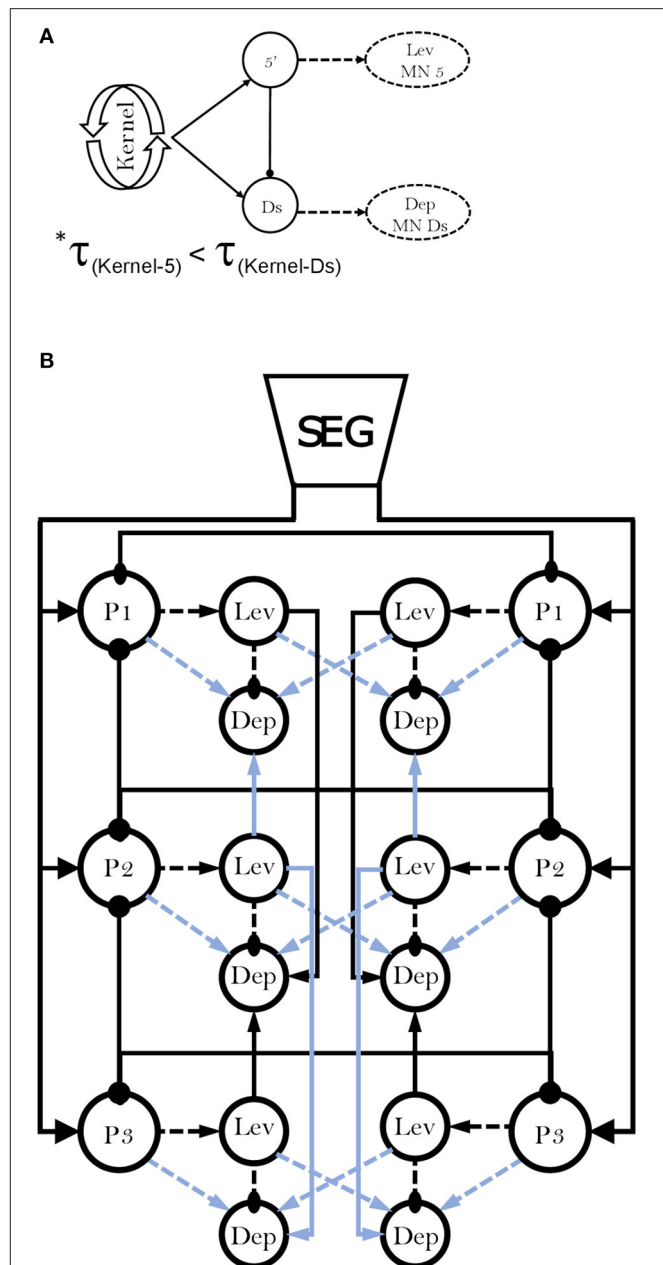


FIGURE 8 | Parsimonious connectivity model [modified from (38)]. Circles and arrows indicate for inhibitory and excitatory connections, respectively. **(A)** Reduced representation of the hemiganglionic CPG. 5' and Ds are levator and depressor interneuron pools that innervate the slow depressor MN (Ds) and levator MN 5'. *correction of a typo in Figure 7A in David et al. (38), in which the smaller-than sign (<) is mistakenly presented as larger-than (>). **(B)** Solid line- between CPGs, dashed line- within CPG. Black and blue represent strong and weak connections, respectively. P1, P2, and P3 indicates for pro-, meso-, and meta-thoracic hemiganglionic pacemaker. The model incorporates a descending excitatory drive from the SEG to the thoracic ganglia oscillators, alongside mutual inhibition between CPGs and direct excitation of the depressor interneuron pool by neighboring levators interneuron pools. In addition, mesothoracic inputs are stronger than mesothoracic outputs, and levator interneuron pools receives a single excitatory input, while the depressor interneuron pools are innervated simultaneously by three excitatory inputs and one inhibitory input.

and 3 (107)], suggesting that R1Dep-L1Lev coupling is context-dependent and decoupled at need. Interestingly, coupling and decoupling of the front legs from the walking system, without compromising the coordination of the other legs, have been reported for stick insect (31). The independence of the front legs may also serve a role in negotiating obstacles, or an unexpected terrain irregularity, by adaptations of the legs' kinematics (74, 89, 108–110). Here too, strong R1Dep-R1Lev coherence, throughout the frequency range, ensures the tight intra-leg coordination that enables the front legs' unique maneuvers. Complementary to the above, the relatively strong R1Dep-L1Dep coherence ensures the contralateral legs' functional antiphase coordination even when their stepping kinematics during curve walking is far from symmetrical. This finding is in contrast to the finding of a weak R1Dep-L1Dep connection in isolated ganglion of locust, and stick insect (51, 54), perhaps due to differences between species, or quantification methods used. Moreover, the above noted findings are also in contrast with a study in stick insects (55), which have suggested that weak central coupling of R1Dep-L1Dep underlies the front legs' independent functions. Our findings of a similar CS of Dep-Dep in all isolated ganglia, alongside greater R1Dep-L1Dep coherence, and weaker R1Dep-L1Lev CS, suggest that at least in the cockroach this flexibility depends on weak Dep-Lev coupling. Last, R1Dep-L1Dep and R1Lev-L1Lev had bi-phasic coordination, as also found, but not studied further, in locust *in-vitro* preparations (51, 56), and found here to be frequency-dependent. In-phase coordination between contralateral depressor MNs was also reported for locusts (51) and stick insects (54, 111, 112). However, these *in-vitro* studies focused on burst frequencies lower than 0.5 Hz, whereas we identified a threshold for changing coordination around 2 Hz.

High Variability of Mesothoracic Coordination Is Crucial for Its Appropriate Locomotive Functions

Cockroach mesothoracic legs move at a range directly below the body's center of mass (113), and were found to contribute significantly more to the generation of functional and stable coordination than the other legs (31, 114, 115). During tripod locomotion, a miscalculated stance movement of the middle leg is more likely to cause a catastrophic failure than in other legs (116). Consequently, the mesothoracic hemiganglionic premotor networks must be coordinated with the neighboring hemiganglia in order to enable fast responses to perturbations and quick adaptations to immediate and unpredictable changes in velocity, direction, slope, body posture, attack angle, etc., without compromising stability. This requires a high susceptibility to modifications of the motor output. In the walking animal, a mesothoracic hemiganglion receives both central and sensory inputs from the anterior, posterior, and contralateral hemiganglia, as well as from its own local proprioceptors. These inputs modify and fine tune the motor output between and within step cycles (92). However, in the isolated ganglion these inputs are absent, and the resultant endogenous motor-output is highly variable, as can be seen in the high variability of R2Dep burstiness, and also in the transition from in-phase to erratic coordination of R2Dep-L2Dep and R2Lev-L2Lev above 2 Hz, and the practically zero

synchronization index of R2Lev-L2Lev. Our data suggest that the mesothoracic intraganglion connectivity is designed for variability and susceptibility to modifications. A study on a centipede-like robot has demonstrated that straight-walking instability helps in turning maneuvers (117). This notion is also supported by the finding of weaker mesothoracic coupling in the semi-intact cockroach, and in the stick insect (38, 54), as well as the finding of bi-phasic R2Lev-L2Lev coordination in locust (56). Moreover, R2Dep-L2Dep default dysfunctional in-phase coordination, found in stick insect and locust, was suggested to be modified by sensory information to generate behaviorally relevant coordination (24, 54). Overall, these findings indicate that insects share similar principles of mesothoracic intraganglion connectivity, and that their locomotion behavior may be different due to the application of different effectors (e.g., neuromodulators, sensory inputs, etc.) on a similar default neuronal infrastructure.

The Metathoracic Network Presents Consistent Tripod-Like Coordination

The hind legs are the main motor that propel the body forward (1), and support much of the body load (88). The metathoracic ganglion that controls the hind legs receives ascending inputs from the abdominal ganglia and the cerci, including direct inputs from the giant interneurons that mediate the cockroach escape response (118). The isolated metathoracic network presents the consistent tripod-like coordination that is expected from the main motor during forward locomotion. R3Dep-L3Dep and R3Lev-L3Lev persistent antiphase coordination suggests the existence of a unique metathoracic central and frequency-independent contralateral mutual inhibition mechanism, which also explains the greater CS in comparison to the other ganglia, and prevents co-swinging of the hind legs. Additional evidence of such a mechanism is provided by the relatively high coherence of R3Dep-L3Lev throughout most of the frequency range, which alongside the consistent in-phase coordination is crucial for static stability of the hind legs and, therefore, the whole-body (2). The findings of a consistent antiphase coordination of R3Dep-L3Dep and R3Lev-L3Lev in locust isolated ganglion, and of a stronger coupling of the metathoracic Dep-Lev in comparison to the other ganglia (51, 56, 65), alongside the contralateral application of Cruse's rules II and III (107, 119) and the finding of a tendency to antiphase coordination of R3Dep-L3Dep in stick insects (54), suggest that this feature is conserved at least in hemimetabola insects. The extreme lower coherence of R3Dep-R3Lev suggests that local influences and accurate intra-hemiganglion coordination is less important in the hind legs. This notion is supported by our findings of low and more variable levator burstiness than in the other ganglia, which indicate that in the hind legs the accuracy of stepping is compromised in order to enable the high frequency leg cycling necessary for cockroach fast locomotion (1).

The Whole-Chain Preparation

Previous experimental research of deafferented locusts and stick insects focused solely on depressor MNs and found that all six of them are synchronized in-phase (51, 54), as also suggested

in a recent modeling study (24). These and other experimental studies of deafferented stick insects, and crustaceans have found only in-phase coordination between ipsilateral homolog MNs (42, 120–122). Our current cockroach preparation motor-patterns were found to profoundly differ from the above-noted findings.

The Effects of Intersegmental Connectivity on the Intrasegmental Motor Patterns

By comparing between the same pairs of MNs in the isolated and the whole-chain preparations, we examined the effect of the centrally generated inter-ganglia inputs on the intra-ganglionic motor outputs. Our finding of lower rhythmicity of depressor MNs in the whole-chain preparation, indicates that they are more susceptible than levator MNs to intersegmental interferences. This agrees well with the model we present in **Figure 8**, in which both levator and depressor premotor INs receive input from an oscillator that in turn is influenced by the neighboring oscillators. The depressors, however, also receive direct inputs from levator premotor networks in the neighboring ganglia, which increases their motor pattern variability in comparison to that in the isolated preparations and to the levator networks. For example, although mesothoracic Dep-Dep had a similar mean phase in both our preparations, the phase was 3-fold less variable in the whole-chain preparation. R1Dep-L1Dep displayed different coordination in the two preparations: frequency-dependent bi-phasic coordination in the isolated preparation; and a consistent in-phase coordination in the presence of intersegmental inputs. Descending inputs from the SEG have been found to induce in-phase synchronization between contralateral depressors in a locust *in-vitro* preparation, with a stronger effect on the prothoracic pair (52). The prothoracic MNs' low variable rhythmicity can suggest that this mechanism is common to locusts and cockroaches, although the R3Dep-L3Dep antiphase coordination could indicate that in the cockroach the metathoracic motor output is less influenced by the SEG descending inputs than in the locust. An even greater effect of intersegmental connectivity was that of stabilizing the motor pattern of the metathoracic MNs by increasing the CS of heterogeneous pairs and the levator MNs burstiness. In contrast, R3Dep-L3Dep was unaffected by descending inputs. These findings indicate that levator premotor networks are the targets of intersegmental influence on the cockroach metathoracic ganglion. In stick insects, mesothoracic inputs were found to be necessary for regular stepping of the metathoracic legs (31), as well as in strengthening intrasegmental coupling in intact and isolated deafferented preparations (55, 100). Moreover, mesothoracic-metathoracic connectivity was found to increase R2Dep-L2Dep coupling in stick insects (55), and decrease R2Dep-L2Dep phase variability in our cockroach preparation (**Supplementary Figure 3**). More generally, with the exception of R1Dep-L1Dep, intersegmental connectivity did not affect synchronization of the pairs investigated here, indicating that gait modifications are mostly executed by altering the coordination between, and not within, the ganglionic networks.

The Anterior Sub-network Transitions Into Tripod-Appropriate Coordination While the Posterior Sub-Network Presents Tripod-Appropriate Coordination Throughout the Frequency Range

During 'normal walking' cockroaches have presented similar phases of prothoracic-mesothoracic and mesothoracic-metathoracic legs, e.g., R1–R2 and R2–R3 present a similar mean phase (25, 37, 123). In contrast, our preparation exhibited significant asymmetries between the phases of homolog interganglia pairs. To investigate this, we divided the network into anterior and posterior sub-networks (prothoracic-mesothoracic and mesothoracic-metathoracic, respectively, **Figure 5B**). The anterior sub-network's coordination transitioned into tripod gait phases at 2 Hz (**Figure 5Ci,ix**), along the beginning of a sharp change in coherence of R1Dep-R1Lev and R2Dep-R2Lev. Considering R1Dep-L1Dep and R1Lev-L1Lev phase inversion above 2–3 Hz (**Figure 3Bi,ii**, respectively), these findings indicate that the prothoracic ganglion dominates this sub-network at low frequencies. In the posterior sub-network, this transition occurred at 5 Hz, with one exception - R2Dep-R3Lev maintained a consistent in-phase coordination, unlike its reciprocal pair R2Lev-R3Dep (**Figure 5Cvi,vii**). The frequency-dependent transition of R2Lev-R3Dep into antiphase coordination could indicate that Lev-to-Dep ipsilateral excitation (38) is overridden at high frequencies, which results in antiphase activity. The finding of weaker descending than ascending mesothoracic-to-metathoracic coupling in *P. americana* (38, 99) supports this notion. In the heterogeneous diagonal pairs, stronger coupling accompanied the dysfunctional in-phase coordination of R2Dep-L3Lev, while weaker coupling in R1Dep-L2Lev accompanied the bi-phasic coordination, and the weakest coupling, of R2Lev-L3Dep, accompanied a consistent tripod-appropriate antiphase coordination. Overall, we conclude that Dep-Lev pairs which are coordinated in-phase during tripod locomotion depend on a stronger CS to generate tripod coordination while pairs that are antiphase coordinated during tripod locomotion depend on a weak CS to generate appropriate coordination.

Ipsilateral Coordination Overturn at 5 Hz Suggests for an Endogenous Coordination Which Comprises Simultaneous Aerial Phases of the Ipsilateral Middle and Hind Legs

Three out of four ipsilateral pairs in the posterior sub-network inverted their coordination from tripod-appropriate asymmetry into a different motor-pattern around 5 Hz, which corresponds to the frequency threshold for the transition from local feedback-dominated control into central feedforward-dominated control. This new distinctive state corresponds to overlapping aerial phases of ipsilateral legs in an intact running cockroach, as also found between R2Lev and R3Lev in 40% of the burst-cycles in semi-intact cockroaches (38). Simultaneous swing phases of contralateral legs were reported for insects using the uncommon gallop, quadrupedal, or bipedal gaits (124, 125), and a faster-than-tripod gait has been characterized in the cockroach *N. cinereal* (123). However, we are unaware of evidence in the literature

for ipsilateral mesothoracic-metathoracic synchronized swing movements in intact walking insects. Following Weihmann et al.'s (123) definition that tripod gait satisfies $282^\circ \leq \Phi \leq 72^\circ$ between the front and hind ipsilateral legs, our findings indicate that *P. americana* still satisfies tripod coordination also at frequencies > 5 Hz. The differences in biomechanics between *P. americana* and other insects (1, 37, 39), with the underlying neural mechanism depicted here, may enable *P. americana* to maintain tripod coordination and its benefits throughout its speed range, by altering the ipsilateral coordination to include aerial phases without altering the contralateral, diagonal and even pro-to-meta thoracic phase relations. Slow and fast tripod gaits have been previously distinguished in cockroaches (27, 96), and a change from relying on the static stability of the tripod footfall pattern to a dynamic stability during very fast running was reported previously (2) and further support this notion.

The Mesothoracic Ganglion Serves as a Subordinate Mediator Between the Dominant Pro- and Meta-Thoracic Ganglia

Unlike the three other prothoracic-metathoracic pairs, R1Dep-R3Dep showed a consistent tripod-appropriate phase. The current lack of evidence for direct connectivity between the prothoracic and metathoracic motor networks suggests that this stable functional phase may be coordinated through the mesothoracic ganglion. One way of achieving such coordination is through a consistent in-phase coordination of diagonal Lev-Lev and Dep-Dep pairs, as found here (Figure 5C_{xiii,xiv,xv}). Furthermore, R1Dep-L3Dep, R1Dep-L3Lev, and R1Dep-R3Lev showed a dysfunctional motor-pattern that is likely to have resulted from the simultaneous activity of two different networks with shared elements, rather than from the coupling between distant parts of a single network. Hence, we suggest that the anterior and posterior sub-networks are separate networks that are connected and functionally coupled via a shared element- the mesothoracic network- to form the thoracic locomotion control network. The demonstrated ability of functionally specialized legs to couple to, or decouple from, the other legs, supports this notion (31, 74, 126). Moreover, although each ganglion can dominate the overall behavior in different contexts (51), our data suggests that the prothoracic ganglion dominates the overall motor pattern at frequency < 2 Hz, the metathoracic ganglion dominates during faster locomotion, and the mesothoracic ganglion mostly serve as a subordinate mediator connecting the sub-networks and following the motor pattern of the current dominant ganglion. This notion is supported by the relatively weak coupling found in R2Dep-R2Lev, and R2Dep-L2Lev (Figure 6C_i), which renders the mesothoracic network components more susceptible to influences from neighboring ganglia, since weak coupling is more easily overridden. R2Dep-R2Lev weaker coupling in the whole-chain preparation in comparison to the isolated preparation (Figure 6C_{iv}) provides additional support to this notion, as well as the mixed prothoracic and metathoracic characteristics presented by the isolated mesothoracic ganglion. Last, in the posterior sub-network, interganglion Dep-Lev had a weaker coupling if the levator was mesothoracic than if it was metathoracic (Figure 6C_{ii}). David et

al. (38) reported that meso-metathoracic descending coupling is weaker than the parallel ascending coupling. These facts suggests that Dep-Lev interganglia coupling between ganglia depends on the levator premotor networks. Weaker mesothoracic levator's coupling, and its resultant more variable phases, further indicate for the mesothoracic function as a subordinate mediator.

Rules for Couplings Between Cockroach Levator-Depressor Motor Centers

Finally, we used our data to posit a new coupling scheme (Figure 7), which updates and fills in gaps in the coupling scheme published by David et al. (38), and the coupling rules it offered. For intraganglion connections data were obtained from our isolated preparations and for intersegmental connections data were obtained from our whole-chain preparation. This approach is supported by our finding of significant influence of interganglion connectivity on intraganglion couplings only for R3Dep-R3Lev and R3Dep-L3Lev (Figure 6C_{iv}), for which we denote both isolated and whole-chain couplings. Our scheme is restricted due to a lack of sufficient data on the intraganglion Lev-Lev pairs in the whole-chain preparation. The identified coupling rules also manifest in our connectivity model (Figure 8) which was thoroughly discussed in David et al. (38), and will be discussed here only in light of the new findings which modifies it. Therefore, Rule 1 "levator INs excite neighboring depressor INs" and Rule 6 "meta-meso ascending coupling is stronger than meso-meta descending coupling" are not discussed here. Our recent findings (Figure 7) disagree with Rule 2 "Ipsilateral connections are coupled stronger than contralateral ones." Dep-Dep pairs which were not investigated by David et al. (38), were found here to contradict this rule, as did Lev-Lev and Dep-Lev pairs. We attribute the difference between our current and previous findings to ascending sensory inputs from the abdominal ganglia, which were the only inputs that were not deafferented in David et al. (38). This also indicates that abdominal sensory signals suffice to increase the ipsilateral coupling strength, at least in the posterior sub-network. In contrast, Rule 3 "Lev-Dep is stronger than the parallel Lev-Lev" is supported by our new findings (Figure 7), except for R1Dep-L1Lev. We further compared these couplings to those of the parallel Dep-Dep pairs and found no consistent difference, and that Dep-Dep pairs were generally similar in their coupling strength. Our findings also support Rule 4 "Metathoracic coupling is stronger than mesothoracic coupling" for Lev-Lev and Dep-Lev pairs, as in the semi-intact cockroach, but not for Dep-Dep pairs. We therefore redefine Rule 4 as: "Pairs comprising a metathoracic levator are coupled more strongly than homolog pairs comprising mesothoracic levators." To this we add our findings from the whole-chain preparation and note that pairs in the posterior sub-network are generally coupled more strongly than their homolog pairs in the anterior sub-network. Rule 5 "Diagonal coupling is functional and not direct." This assumption is derived from the nearest-neighbor architecture inferred from Spirito and Mushrush (96), and supported by Couzin-Fuchs et al. (99) and Aminzare et al. (127), and by findings from crustaceans swimming control network (128, 129). Diagonal intersegmental pathways were identified

in the cockroach and locust (52, 130–132), but were described as mediating sensory information or brain commands. Our findings of highly variable and dysfunctional phases between prothoracic and metathoracic MNs, in addition to the extremely weak CS of R1Dep-L3Dep, as also predicted by a simulation study in stick insects (79), all support this architecture at least for these long-distance connections. We note, however, that a different modeling effort of the stick insect locomotion control network postulated a direct coupling between the prothoracic and metathoracic ganglia (133).

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

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AUTHOR CONTRIBUTIONS

ID and AA designed the study and wrote the manuscript. ID conducted the experiments and analyzed the data. Both authors contributed to the article and approved the submitted version.

ACKNOWLEDGMENTS

We thank Daniel Knebel for the invaluable discussion and the support with MATLAB and Asael Ram for technical assistance.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fnsc.2021.655933/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Adaptive and Energy-Efficient Optimal Control in CPGs Through Tegotae-Based Feedback

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To obtain biologically inspired robotic control, the architecture of central pattern generators (CPGs) has been extensively adopted to generate periodic patterns for locomotor control. This is attributed to the interesting properties of nonlinear oscillators. Although sensory feedback in CPGs is not necessary for the generation of patterns, it plays a central role in guaranteeing adaptivity to environmental conditions. Nonetheless, its inclusion significantly modifies the dynamics of the CPG architecture, which often leads to bifurcations. For instance, the force feedback can be exploited to derive information regarding the state of the system. In particular, the *Tegotae* approach can be adopted by coupling proprioceptive information with the state of the oscillation itself in the CPG model. This paper discusses this policy with respect to other types of feedback; it provides higher adaptivity and an optimal energy efficiency for reflex-like actuation. We believe this is the first attempt to analyse the optimal energy efficiency along with the adaptivity of the *Tegotae* approach.

Keywords: central pattern generator, sensory feedback, tegotae approach, efficiency, optimal control, learning, embodiment

OPEN ACCESS

Edited by:

Claudius Gros,
Goethe University Frankfurt, Germany

Reviewed by:

Eduardo J. Izquierdo,
Indiana University Bloomington,
United States
Guoyuan Li,
NTNU Ålesund, Norway

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Specialty section:

This article was submitted to
Computational Intelligence in Robotics,
a section of the journal
Frontiers in Robotics and AI

Received: 24 November 2020

Accepted: 03 May 2021

Published: 26 May 2021

Citation:

Zamboni R, Owaki D and Hayashibe M
(2021) Adaptive and Energy-Efficient
Optimal Control in CPGs Through
Tegotae-Based Feedback.
Front. Robot. AI 8:632804.
doi: 10.3389/frobt.2021.632804

1 INTRODUCTION

The ability to efficiently move in complex environments is a key property for animals and their survival. This implies that many aspects of their morphology and central nervous system are shaped by constraints related to their locomotor skills. Animal locomotion is not generated merely from neural systems; instead, it is generated from the close interaction between neural systems, musculoskeletal systems, and the real-world environment (Pfeifer and Bongard, 2006; Pfeifer et al., 2007). Thus, it is essential to elucidate the locomotion generation mechanism by analysing the interaction dynamics among these three systems and by analysing the neural systems themselves. Understanding these mechanisms is expected to result in contributions to biology and robotics by facilitating the design of durable and resilient robots that are energy-efficient.

Central pattern generators (CPGs) are neural circuits that are found in invertebrate (Pearson and Iles, 1973; Bässler and Wegner, 1983; Bässler, 1986) and vertebrate animals (Shik et al., 1966; Grillner, 1975; Grillner, 1985). CPGs can produce rhythmic patterns of neural activity without receiving any rhythmic inputs. The term *central* indicates that the sensory feedback from the *peripheral* nervous system is not needed for generating the rhythms (Marder and Bucher, 2001; Ijspeert, 2008). Biological CPGs underlie many fundamental rhythmic activities such as chewing, breathing, and digesting. In addition, they also serve as the fundamental building blocks for locomotor neural circuits. From the perspective of control, they have several interesting characteristics such as a distributed control, the ability to deal with redundancies, the presence

of fast control loops, and the ability to modulate the locomotion by using simple control signals. Owing to these properties, CPGs are considered to be transferred mathematical models. In addition, CPGs serve as the building blocks of robotic locomotion controllers and are being increasingly used in the robotics community (Ijspeert, 2008). To enable biologically inspired robotic control, the architecture of CPGs has been extensively adopted to generate periodic patterns for locomotion control owing to the properties of nonlinear oscillators (Kimura et al., 1999; Fukuoka et al., 2003; Tsujita et al., 2003; Aoi and Tsuchiya, 2005; Buchli et al., 2006; Kimura et al., 2007; Righetti and Ijspeert, 2008; Wang et al., 2011).

Although sensory feedback in CPGs is not necessary for generating rhythmic patterns, it plays a central role in guaranteeing adaptivity to the environmental conditions (Ijspeert, 2008).

Sensory feedback in CPGs for animal locomotion was first studied in the pioneering work on bipedal walking conducted by Taga et al. (1991), Taga (1994), Taga (1995). In these studies, sensory information from the environment was fed back into the nervous system model to generate a walking pattern from the interaction among the nervous system model, musculoskeletal model, and environment (“Global Entrainment”). Kimura et al. (1999); Fukuoka et al. (2003) proposed a model by integrating CPG and reflex mechanisms to realise uneven terrain quadruped walking. Aoi and Tsuchiya (2005), Aoi and Tsuchiya (2006) focused on “phase resetting” (Schomburg et al., 1998), a feedback mechanism found in animals, to include gait stabilisation in CPG-based control models. Aoi’s group also applied the phase resetting feedback in CPGs to human-like musculoskeletal models of bipedal walking (Aoi et al., 2010), quadrupedal gait transitions (Aoi et al., 2011; Aoi et al., 2013), and a hexapod walking model (Ambe et al., 2018). Steingrube et al. (2010); Manoonpong et al. (2010) proposed a modular neural control with bio-inspired CPG-based network and sensory feedback, demonstrating environmental adaptability, such as walking on uneven terrain and avoiding unknown obstacles, and then extended the models by introducing forward models (Manoonpong et al., 2013; Dasgupta et al., 2015), visual feedback (Goldschmidt et al., 2014; Grinke et al., 2015), muscle models (Xiong et al., 2014; Xiong et al., 2015), and so on. Buchli et al. (2006); Nachstedt et al. (2017) proposed an adaptive frequency oscillator that could learn motion frequency adaptively and verified the generation of gait according to body characteristics. Furthermore, an interlimb coordination model that employed load information as sensory information and generated adaptive and diverse quadruped walking patterns was proposed (Maufray et al., 2010; Fukuoka et al., 2015; Owaki and Ishiguro, 2017a). Sensory feedback inclusion significantly modifies the dynamics of the CPG’s architecture, which often leads to bifurcations and other dynamic phenomena (Aoi et al., 2011; Wang et al., 2011; Aoi et al., 2013).

To establish a systematic design principle of the sensory feedback in the CPGs to achieve biologically inspired robotic locomotion, a novel concept called “Tegotae” is proposed. Tegotae is a Japanese concept that describes the extent to which a perceived reaction matches the intended motor

command. The potential of the Tegotae approach in reproducing animals’ locomotion and understanding the underlying mechanism has been previously demonstrated based on synthetic approaches. The Tegotae approach was first used by Owaki et al. (2017) to develop a minimal model for interlimb coordination on hexapod robot locomotion with CPG-based control. Kano et al. (2018) demonstrated gait transition between the concertina and scaffold-based locomotion in a snake model simulation with reflex-based control. Kano et al. (2019) proposed the detailed design of the Tegotae function, particularly for motor commands, using the genetic algorithm (GA) to simulate a simple 1-D earthworm model with CPG-based control. Owaki et al. (2021) demonstrated adaptive walking control on a biped model with CPG and reflex-based controllers.

The main contribution of this study is the construction of a specific proprioceptive feedback law through the so-called Tegotae approach (Owaki et al., 2017). Together with a specific control policy, i.e. reflex-like actuation, it exploits it fruitfully based on the concept of embodied intelligence (Pfeifer and Bongard, 2006; Pfeifer et al., 2007). Then, the feedback is applied to certain mechanical systems, i.e. hopping systems; is first considered for the simplest case of one leg, and is then extended to two legs. In such circumstances, the sensory feedback plays an important role in shaping the rhythmic patterns and ensuring coordination between the CPGs and body movements. This study demonstrates the adaptation processes as well as the acquirement of the different gait. In addition, it compares the analytical solution for the single-leg case with an optimal controller solution that is based on direct methods such as the multiple shooting methods (Bock and Plitt, 1984; Diehl et al., 2005; Fagiano, 2019). This confirms the intuitions for the energy efficiency of the control policy. Finally, we extensively analyse the approach in relation with the considerations for learning and energy efficiency (Hayashibe and Shimoda, 2014).

The following section presents the materials and methods used in this study. First, we briefly describe the Tegotae approach. Second, we present the mathematical model for the Tegotae-based control. Third, we discuss the Tegotae approach based on the learning framework by comparing it with *tacit learning* as described in Hayashibe and Shimoda (2014). Then, we present the simulation results to validate the Tegotae controller and then evaluate the energy efficiency. Finally, in **Section 5**, we discuss the results and future work.

2 METHODS

2.1 Tegotae Control

2.1.1 Theory

The inclusion of feedback in the architecture of the CPG is a natural extension of these structures. However, any modification to the canonical form leads to a modification in the main dynamics, which may affect the effectiveness. This is achieved by considering a particular family of feedback functions in terms of the local effect of this inclusion on the dynamics of a neural oscillator. The approach to define these feedback functions is

called the Tegotae approach, as described in Owaki et al. (2017). Tegotae is a novel concept that describes the extent to which a perceived reaction matches an expectation, or intention, of a controller. Tegotae stems not only from the reaction that is received from the environment, but also from the consistency between the perceived reaction and the intention or expectation of the controller, i.e. what the controller intends to do. In the case of matching, it is said that either “good” or “bad” Tegotae is obtained. In this manner, a cognitive meaning is added to the control framework, in which it denotes some actions as “positive” and others as “negative”. The objective is to maximise the Tegotae function. In this section, the Tegotae formalism is introduced. For the initial step of the investigation, Tegotae is quantified in the simplest mathematical form, i.e. a function that is based on the separation of the variables as follows.

$$T(u, e) = C(u)S(e) \quad (1)$$

Hereafter, the function T is referred to as the Tegotae function (T-function), which is a function that quantitatively measures the Tegotae. In Eq. (1), u represents a control variable and e represents the sensory information obtained from multiple sensors that are embedded in the body. The T-function is expressed as the product between $C(u)$ and $S(e)$. The former expresses the intention of the controller, while the latter denotes the reaction obtained from the environment. T is designed such that it becomes more positive when an enhanced Tegotae is detected. Therefore, for a given T-function, the local sensory feedback f is designed in such a way that the control system modulates u to increase the amount of Tegotae received. Thus, with regard to the continuous-time systems, f is expressed simply as a mono-dimensional gradient system of the T-function T with respect to the control variable u , as follows.

$$f = \frac{\partial T(u, e)}{\partial u} \quad (2)$$

With this formulation, it is possible to systematically design the decentralised controllers by only designing the T-functions that are required. When considering the CPGs’ framework, the i -th controller can be first defined as a generic Kuramoto oscillator (Kuramoto (1984)) of phase ϕ_i without the coupling terms but with a specific external field f_i that consists of the local sensory feedback.

$$\dot{\phi}_i = \omega_i + f_i(\phi_i, e) \quad (3)$$

As a result, this equation leads to the following expression.

$$f_i(\phi_i, e) = \frac{\partial T_i(\phi_i, e)}{\partial \phi_i} \quad (4)$$

In Owaki et al. (2017), the T-function was expected to reproduce the hexapedal inter-limb coordination that was observed in insect locomotion by using the Kuramoto oscillators. For this reason, it was generally defined in the first case as follows.

$$T_i(\phi_i, N_i) = (-\sin \phi_i)N_i^V, \quad (5)$$

where the sensory information e consists of the vertical ground reaction forces N_i^V that are acting on each leg. In the basic control of the hexapod robot in Owaki et al. (2017), the leg was controlled to be in the swing phase for $\phi_i = 0$ to π and the stance phase for $\phi_i = \pi$ to 2π based on the function $C(\phi_i) = -\sin \phi_i$. In this formulation, T_i quantifies the Tegotae on the basis of the information that is only locally available at the corresponding leg. When the local controller intends to be in the stance phase ($-\sin \phi_i > 0$) and receives a ground reaction force ($N_i^V > 0$), T_i evaluates the situation as “good” Tegotae, and vice versa. As stated above, the reaction in Eq. 1 is generic, and other types of reactions may be taken into account. In our study, the force passing through the body was taken into account, i.e. an elastic force. This definition is inspired by the Golgi tendon organ (Moore (1984)), which is a proprioceptive sensory receptor organ that senses changes in the muscle tension. The T-function is then defined for a generic i -th phase oscillator and the feedback signal is expressed as follows.

$$T_i(\phi_i, F) \triangleq (-\sigma \sin \phi_i)F \quad (6)$$

$$f_i(\phi_i, F) = \frac{\partial}{\partial \phi_i} T(\phi_i, F) = -\sigma \cos \phi_i F \quad (7)$$

where σ denotes a proportionality factor and F represents the force passing through the body. By the nature of Eq. (6), it follows that this sensory feedback will be absent when there is no contact with the ground.

2.1.2 Tegotae Control Policy: Preliminary Design and Extensions for Reflex-like Actuation

In majority of the CPGs’ controllers, the actuator is driven by a proportional-integral-derivative (PID) control scheme, which compares the actual state of the physical system with the reference signal that was originated by the CPGs’ network (Ijspeert, 2008). One of our main contributions is to attempt to maintain the model-free control approach while taking into account some of the most recent considerations for the above embodied intelligence (Pfeifer and Bongard, 2006; Pfeifer et al., 2007) and control by using neural-like dynamic systems and reflex-like motor control. Buchli et al. (2006) demonstrates the manner in which the neuro-mechanical coupling provided by the feedback forces the secondary dynamics in the phase oscillator; our goal is to analyse and possibly exploit this effect. This study aims to use a critical point for the feedback dynamics, which is a minimum, or a specific section of it, to control the system. This section briefly describes the evolution of the Tegotae control policy towards its current form. In the former control policy law established by Owaki et al. (2017), a constant actuation force with the value A was used, and actuation was observed when the phase of the oscillator ϕ was within a certain interval containing the selected critical point of the dynamics ϕ_0 .

$$\phi_i \in (\phi_0 - \Delta/2, \phi_0 + \Delta/2) \Rightarrow F_a(\phi_i, \cdot) = A \quad (8)$$

This implies that the force $F_a = A$ is applied when the phase ϕ_i ranges from $\phi_0 - \Delta/2$ to $\phi_0 + \Delta/2$. It is apparent that a critical

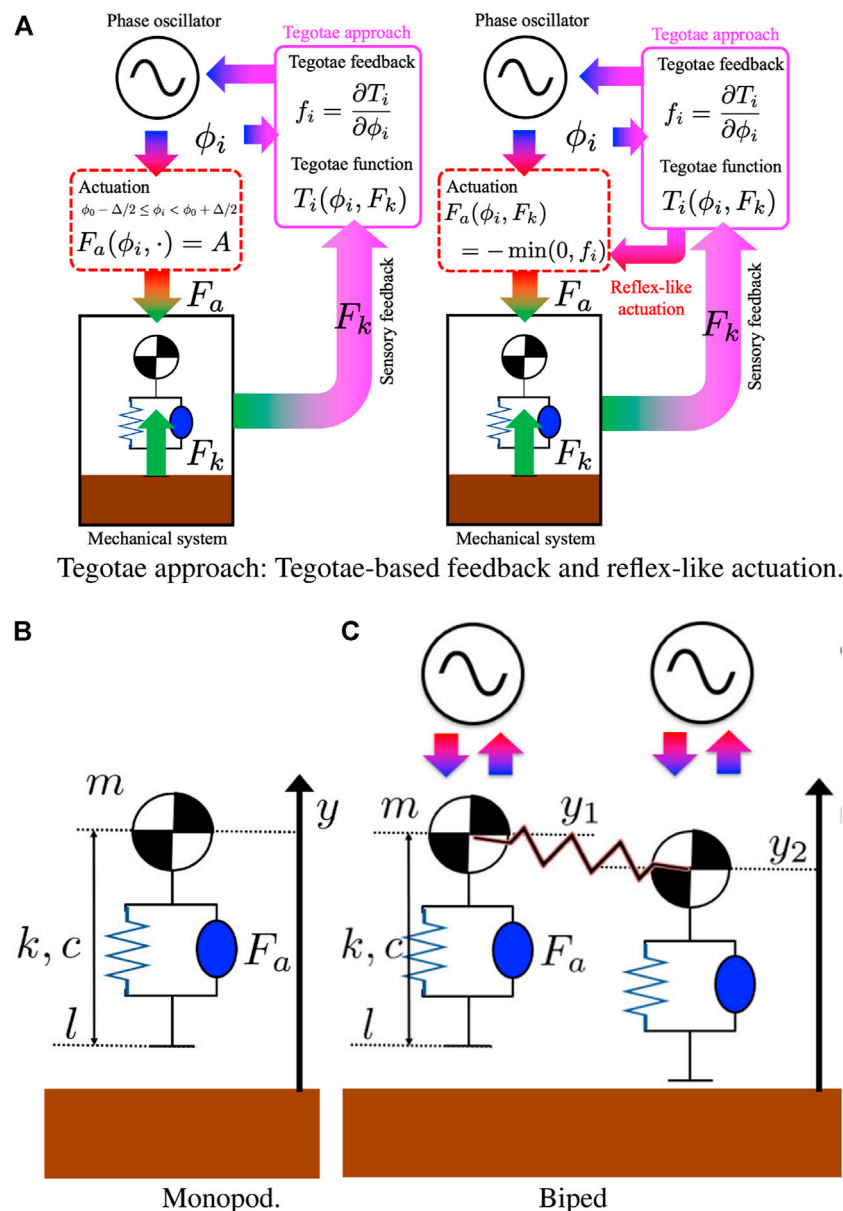


FIGURE 1 | Tegotae approach: **(A)** The reflex-like actuation is designed to be opposite in sign to that of the Tegotae feedback and disappear once the feedback is positive, indicating an increasing Tegotae in Eq. 11. **(B,C)** Neuro-mechanical structure of the mono-dimensional hoppers. **(B)** Monopod: a mass is connected to a massless spring and a damper system. A linear actuator is parallel to the spring and damper and it determines the vertical thrust. The Kuramoto model for the phase oscillators was used as a model for the CPGs' oscillator. **(C)** Biped: Two vertical hoppers are connected with a mechanical spring. Each hopper is controlled by using a decoupled Kuramoto oscillator with Tegotae feedback.

factor of this preliminary policy is the on-line adaptation of the values of ϕ_0 and Δ according to the evolution of the dynamics from the transient to the steady state (assuming it is reached), which is non-trivial. In the first instance, these values are considered to be a posteriori once the specific dynamic of the oscillator has been studied and maintained constantly throughout the entire simulation. The results obtained with this simple control policy are analysed in the monopod case study, which demonstrates how even this simple policy can guarantee good performance. Clearly, this policy can be made smoother by

substituting the square wave with other types of functions such as bell-shaped trends.

$$F_a(\phi_i, \cdot) = \frac{A}{\sqrt{2\pi}\Delta} e^{-\frac{1}{2} \left(\frac{\phi_i - \phi_0}{\Delta} \right)^2} \quad (9)$$

Although this leads to an easier actuation and solves the numerical issues that are introduced by the switching controller, this control policy does not simplify the method of selection of the specific values of ϕ_0 and Δ . In contrast, the entire

negative section that is centered around the minimum of the Tegotae feedback can correspond to a critical phase of the entire dynamics. The following expression can be considered.

$$f_i(\phi_i, F) = \frac{\partial}{\partial \phi_i} T(\phi_i, F) \leq 0 \quad (10)$$

This specifically indicates that the Tegotae is decreasing. By definition, the aim is to maximise it. It is clear how this area is the designated area to inject a certain force. In particular, this force is required to lead to the maximisation of the Tegotae, which is dependent on the case study. In this study, a positive force leading to a jump satisfies the requirements. Thus, following Eq. (6), the final mathematical form for the reflex-like actuation that is newly proposed in this study is defined as follows.

$$F_a(\phi_i, F) = -\min(0, f_i) = -\min(0, -\sigma \cos \phi_i F). \quad (11)$$

The reflex-like actuation is designed to be opposite in sign to the Tegotae feedback and disappear once the feedback is positive, indicating an increasing Tegotae (Figure 1A). Thus, the negative sign can be attributed to fact that the force actuated in the feedback should be in a direction opposite to that of the force used as the feedback itself. This clearly reintroduces the numerical issues of the switching controller. However, it directly links the actuation and Tegotae feedback in a more biologically inspired reflex-like manner. It also assures an online adaptation to the variation of the dynamics since the Tegotae feedback corresponds to this variation itself, as shown in Figure 1A.

2.2 Mechanical Model

2.2.1 Monopod Model

First, a one-dimensional (1-D) hopping system was considered, which is characterised by a mass connected to a mass-less spring and a damper system (Figure 1B). A linear actuator is parallel to the spring and damper and determines the vertical thrust. The Kuramoto model (Kuramoto, 1984) for the phase oscillators was used as a model for the CPGs' oscillator, simplifying the analysis of the effects of the feedback. The integration of the ordinary differential equations (ODEs) was performed using MATLAB, which automatically stopped the integration when switching was detected. The initial step of the integration was set to $1e^{-3}$, which is equal to the maximum step of the integration. The evolution of a single phase of the oscillator ϕ and the vertical height of the mass y is described by an ODE as follows.

$$\dot{\phi} = \omega + f(\phi, F), \quad (12)$$

$$\ddot{y} = \frac{1}{m} \{F_c(\dot{y}) + F_k(y) - mg + F_a(\phi, F)\}, \quad (13)$$

$$F_c(\dot{y}) = -c\dot{y}, \quad (14)$$

$$F_k(y) = k(l_0 - y), \quad (15)$$

where $f(\phi, F)$ is the sensory feedback in the CPG oscillator, while $F_k(y)$, $F_c(\dot{y})$, and $F_a(\phi, \cdot)$ represent the spring, damper, and actuator force, respectively. These three components are absent during the flight phase, assuming that there no forces that act from the environment.

As previously described, according to Owaki et al. (2017), the Tegotae sensory feedback $f(\phi, F)$ is defined directly by the Tegotae function $T(\phi, F)$, where we selected $F = F_k(y)$.

$$T(\phi, F_k) \triangleq (-\sigma \sin \phi) F_k \quad (16)$$

$$f(\phi, F_k) = -\frac{\partial}{\partial \phi} T(\phi, F_k) = -\sigma \cos \phi F_k \quad (17)$$

with σ being a proportionality factor. From Eq. (11), F_a is described as follows:

$$F_a(\phi, F) = -\min(0, f) = -\min(0, -\sigma \cos \phi F_k) \quad (18)$$

Here, as a first step in the evaluation, we used the force passing through the spring F_k . An advantage of the Tegotae-based approach is that it can use different forces as sensory feedback. Further extensions may be a combination of many different forces. The novelty of this study lies in the reflex-like actuation equation and the validation of energetic optimality.

2.2.2 Biped Model

The effects of the Tegotae approach on a more complex mechanical and oscillatory system were also studied to prove its effectiveness and ability to sustain different patterns, which were also described by Owaki et al. (2017). The mechanical system was extended to a 1-D bipedal hopping robot as illustrated in Figure 1C. The system corresponds to a slight modification of the previous case.

$$\dot{\phi}_1 = \omega_1 - \sigma F_{k1} \cos \phi_1 + \epsilon_{12} \sin(\phi_1 - \phi_2) \quad (19)$$

$$\dot{\phi}_2 = \omega_2 - \sigma F_{k2} \cos \phi_2 + \epsilon_{21} \sin(\phi_2 - \phi_1) \quad (20)$$

$$\ddot{y}_1 = \frac{1}{m_1} \{F_{c1}(\dot{y}_1) + F_{k1}(y_1) - m_1 g + F_{a1}(\phi_1, F_{k1}) + F_{k12}\} \quad (21)$$

$$\ddot{y}_2 = \frac{1}{m_2} \{F_{c2}(\dot{y}_2) + F_{k2}(y_2) - m_2 g + F_{a2}(\phi_2, F_{k2}) + F_{k21}\} \quad (22)$$

In Eqs (19, 20), the Tegotae feedback is already taken into account, while the last term on the right-hand-side represents the weak-coupling between the phase oscillators (Kuramoto, 2003). In Eqs (21, 22) the components are the same as those that are defined in Eq. (12), which is from a simple additional elastic force that is introduced by the connecting spring $F_{kij} = k_c(y_j - y_i)$. In contrast, the control policy was left unchanged with respect to the monopod case Eq. (18).

3 TEGOTAE IN THE LEARNING FRAMEWORK

The Tegotae approach has certain interesting similarities with other learning frameworks, which motivates some of the intuitions for its energy efficiency. The adaptivity in the learning processes is typically defined for the parameters/weights of the controller/learning agent. In the Tegotae framework, although a further adaptation of the feedback coefficients σ may be included, the main adaptation is induced by modifying the dynamics of the oscillators. This factor is taken

into account in the comparison, since the eventual adaptation of the parameters is straightforward.

First, it is interesting to note how the Tegotae approach shares some similarities with the *tacit learning*, which is a learning framework that was introduced in Berenz et al. (2014); Berenz et al. (2015). In tacit learning, the control law consists of an extension for the PD controller with a tacit learner block with the time frame (Lt). By using the scalar case for simplicity, the following expression can be obtained.

$$\begin{aligned} u &= kx_c^T + q \\ q &= \int f(e)dt \quad (\text{Lt}) \end{aligned} \quad (23)$$

where u , x_c , k , and e are respectively the control, the state variable that is expressed in the control space, the proportional and derivative gain, and any type of quantity that needs to be minimised. The learning process is obtained in the (Lt) block by accumulating the integral over the time of the quantity that needs to be minimised. On this basis, we neglect the proportional and derivative terms in this study.

$$\begin{aligned} u &= q \\ q &= \int f(e)dt \quad (\text{Lt}) \end{aligned} \quad (24)$$

The function $f(e)$ is recommended to have the form $f(e) = p(\xi)a(e)^T$. In the one-dimensional case, $a(e)$ can be a simple linear transformation $a(e) = ae$ and $p(\xi)$ is a periodic function of ξ . Both of these additional terms are selected to guarantee the following.

$$\begin{aligned} \frac{p(\xi)x_e}{\|p(\xi)\|\|x_e\|} &= 1 \quad \text{if } \alpha = 0 \\ \frac{p(\xi)x_e}{\|p(\xi)\|\|x_e\|} &= -1 \quad \text{if } \alpha = \pi \end{aligned} \quad (25)$$

In Eq. (25), x_e represents the state variable that is expressed in the task space, in which the error e is minimized. In contrast, α is generically defined as the angle between $\dot{e}$ and $D(e)$; the latter is the direction toward which e is minimized. In the one-dimensional case, $\alpha = 0 \wedge \pi$. This formulation guarantees that $\min(f(e)) = \min(e)$. Now, let us consider the Tegotae framework. The objective is to construct feedback and not a feedforward controller. To do this, let us consider the factor that needs to be minimized that corresponds to $e = -F_k$, the virtual variable ξ to the physical variable ϕ , and the error function $a(e) = \sigma e$. By neglecting the constant terms due to the integration, the feedback over the oscillator results in the following expressions.

$$\begin{aligned} u &= q \\ e &= -F_k \\ p(\phi) &= -\sin(\phi) \\ q &= \int f(e)d\phi = \int \sigma \sin(\phi)F_k d\phi \\ &= -\sigma \cos(\phi(t))F_k \quad (\text{L}\phi) \end{aligned} \quad (26)$$

In the Tegotae framework, $x_e = \Delta l$ represents the elongation speed of the spring length. This variable points towards the

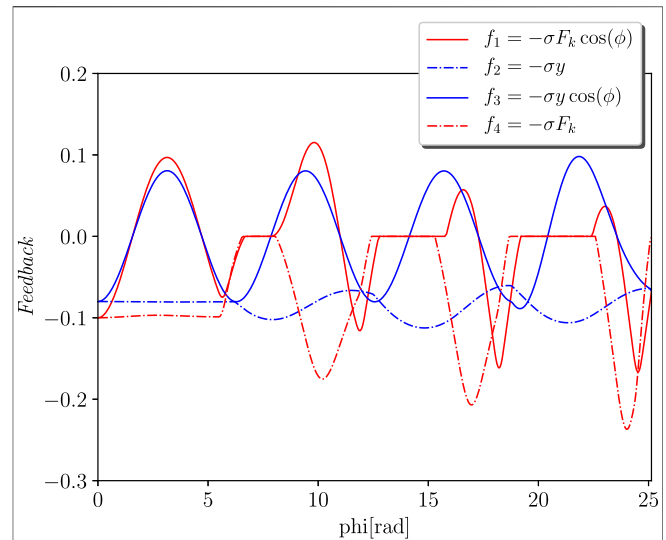


FIGURE 2 | Feedback dynamics over the phase ϕ . The different lines represent four different instances for the sensory feedback dynamics. f_1 : Tegotae feedback, f_2 : height feedback, f_3 : feedback in Buchli et al. (2006), f_4 : force feedback.

direction of the minimisation of the value of $e = -F_k$. Thus, the following expression is obtained.

$$\begin{aligned} \frac{-\sin(\phi)x_e}{\|\sin(\phi)\|\|x_e\|} &= 1 \quad \text{if } \alpha = 0 \\ \frac{-\sin(\phi)x_e}{\|\sin(\phi)\|\|x_e\|} &= -1 \quad \text{if } \alpha = \pi \end{aligned} \quad (27)$$

This shows how the Tegotae approach is *de facto* obtaining a tacit learning feedback (Lt) as previously described. Nevertheless, this is achieved by accumulating the quantity that needs to be minimised for the integral of the state space variable that is directly from $(\text{L}\phi)$. The integration over the state space frame ϕ is coherent with the CPGs' framework. The role of the oscillators is to provide a different time frame to the dynamics, which is reproduced by the linear transformation $\phi = \omega t$. Thus, in the CPGs' framework, the integration/derivation over the state variable of the oscillator ϕ is conceptually equivalent to the integration over the time. Interestingly, it has been demonstrated in Hayashibe and Shimoda (2014) that this controller can guarantee energy efficiency during the task realisation in case the quantity that needs to be minimised is the actuation torque.

4 RESULTS

4.1 Case1: Monoped

4.1.1 Adaptation Transient and Energy Efficiency

The goal of the simulations is to analyse the effects of the different feedback in terms of the stability, transient periods, and power injection that is required from the actuator. Four different

TABLE 1 | Comparison of performance index, transient period Δt , energy efficiency E_e , and power injection J , for the feedback types on 1D hopping.

Feedback	f_1	f_2	f_3	f_4
A [N]	4	12	12	4
ϕ_0, Δ [rad]	$1.75\pi 0.1\pi$	$1.96\pi 0.1\pi$	$1.96\pi 0.1\pi$	$1.75\pi 0.1\pi$
Δt [s]	3	4	5	$\nexists$
E_e [m/Ws]	1.50	1.16	1.15	1.25
J [W]	5.49	17.69	20.15	10.56

instances were taken into account for the sensory feedback dynamics, as illustrated in **Figure 2**. Although f_2 corresponds to the height of the jump, f_4 is the force that passes through the spring. Then, f_1 and f_3 respectively represent the Tegotae feedback and the feedback that is proposed in Buchli et al. (2006). Interestingly, both of these share a neuro-mechanical coupling. It is evident that all of them introduce a strong polarisation with the critical points, which is defined as ϕ_0 . The mechanical parameters and the natural length of the spring are $m = 0.1$ kg, $k = 5$ N/m, $c = 0.2$ Ns/m, and $l_0 = 1$ m, respectively. The parameters of the oscillator are $\omega = 8$ rad/s and $\sigma = 2$, whose dimensionality is determined on the basis of the feedback law. The initial conditions are respectively $y_1 = 0.7$ m, the velocity is null, and the angle of the oscillator is randomly selected to guarantee a certain robustness with respect to the initial conditions. The actuation parameters and the results of the simulations were obtained from the oscillations in the steady state and are reported in **Table 1**. The transient period Δt is defined at the point at which the limit cycle is reached. The case f_4 is unable to provide a stable orbit. Finally, it is evident that the introduction of the Tegotae feedback is optimal in terms of the synchronisation transient period. In addition, the energy efficiency E_e is defined by the limit cycle of the period T^* with the actuation force F_{act} as follows.

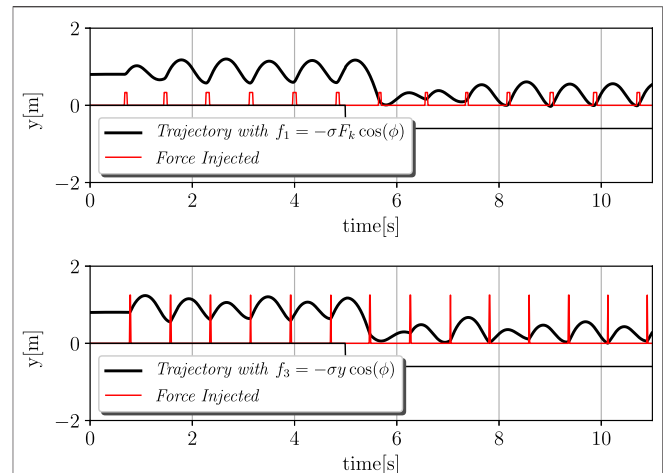
$$E_e = \frac{h_{max,T^*} - h_{min,T^*}}{E}, \quad (28)$$

$$E = \int_{T^*} F_{act}(t) \dot{h}(t) dt, \quad (29)$$

Interestingly, to obtain a similar hopping in terms of the height, the cases f_2 and f_3 are required for a higher amplitude of the actuation force.

4.1.2 Robustness and Adaptivity

Second, the case of the Tegotae approach f_1 and the f_3 case that is presented in Buchli et al. (2006) were taken into account. In addition, the adaptivity was evaluated based on the dynamical change in the environment. In particular, at $t = 5$ s, the ground level was lowered from 0 to -0.6 m. The results are depicted in **Figure 3**. It is evident that our approach can cope with these variations by performing a proper re-polarisation of the oscillator, even without the adaptation of σ , ϕ_0 , or Δ . It is possible to notice how the Tegotae approach can quickly react to these variations, by modifying the force injection as shown in **Eq. (11)**.

**FIGURE 3** | Dynamic environment and adaptation process. The ground level was lowered from 0 to -0.6 m at $t = 5$ s. The upper and lower graphs depict the cases of f_1 : Tegotae feedback and f_3 : feedback in Buchli et al. (2006). The black and red lines represent the trajectories and force injected, respectively. The Tegotae approach can quickly react to these variations, by modifying the force injection as shown in **Eq. 11**. The initial state of the monopod robot was the equilibrium point of the spring-mass-damper system. Thus, the height is unchanged while no force is applied.

4.2 Case2: Biped

4.2.1 Gait

The objective in the biped case is to first obtain two different gaits, namely in-phase and anti-phase bipedal hopping. As already stated in Owaki et al. (2017); Owaki and Ishiguro (2017b), for the architecture of the CPGs, the frequency of the oscillation ω is a useful control variable that can be exploited to introduce a gait transition in the pattern generation. This frequency can be observed as one of the few high-level control variables that are required by CPG architectures, as already presented in Ijspeert (2008). Interestingly, our Tegotae control policy can maintain these properties, even without introducing any oscillator couplings, i.e. $\epsilon_{12} = \epsilon_{21} = 0$.

Two distinct gaits, in-phase hopping and anti-phase hopping, are reported in **Figures 4 (Top and Bottom)**. The case of **Figure 4 (Top)** is obtained with a frequency $\omega_{in} = 6$ rad/s, while the second case of **Figure 4 (Bottom)** is obtained with $\omega_{anti} = 7.5$ rad/s. At first, we determined these parameters by trial and error. Then, we performed a study on the attractors of the dynamics via Lyapunov Exponents; however, this analysis is out of the scope of this article. The values of the mechanical parameters are generally equal to those in the monopod case, with the addition of a spring constant $k_c = 1$. The feedback strength was $\sigma = 2.4$ to guarantee a higher vertical excursion. We considered a few σ values, and found that the motion was stable for certain values, while it was unstable for others, suggesting that the value of σ has an effect on the stability. However, the effect of σ is not considered in this paper because it is out of the scope of this study. The initial conditions are $y_1 = 0.8$ m, $y_2 = 0.7$ m, the velocities are null, and the angles of the oscillators are selected randomly to guarantee a certain robustness with respect to the initial conditions. These figures represent the mechanical section of the system (heights and forces) and the

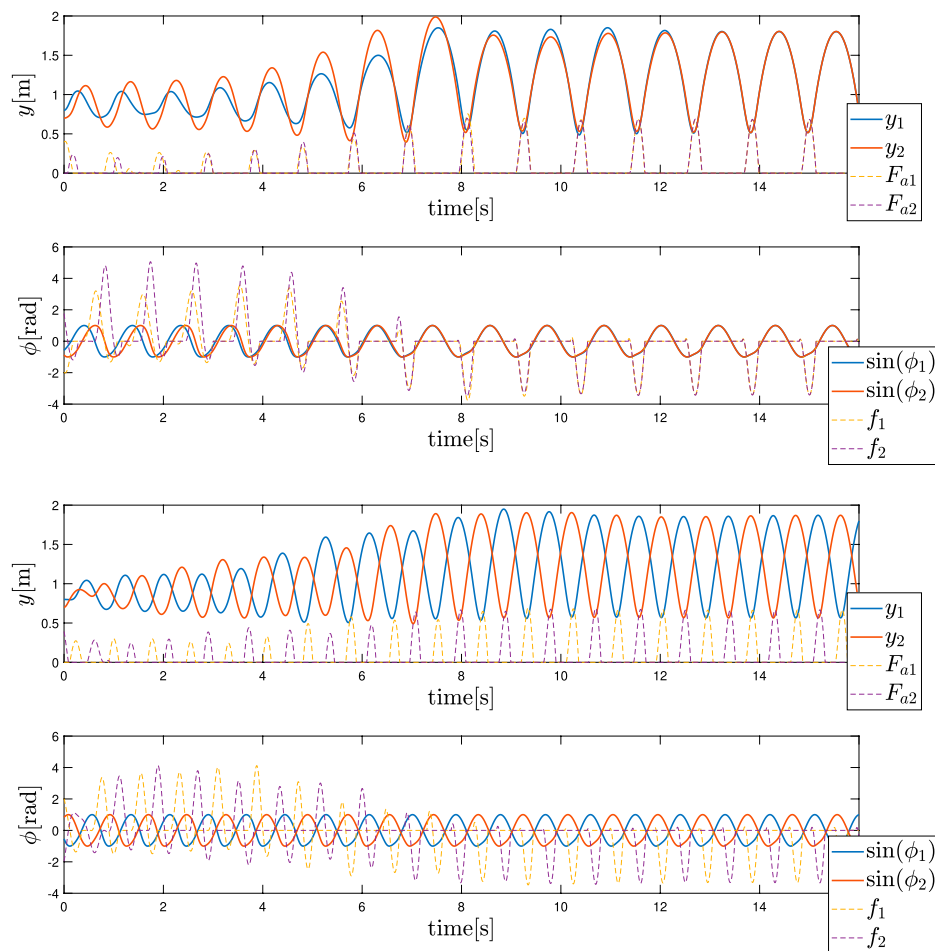


FIGURE 4 | Hopping gait patterns (Top) in-phase hopping: $\omega_{in} = 6$ rad/s (Bottom) anti-phase hopping: $\omega_{anti} = 7.5$ rad/s. The upper and lower graphs show the mechanical section (heights and forces) and control section (phases and feedbacks), respectively. The blue and red colors represent the left (1) and right legs (2), respectively.

control section (phases and feedbacks), with the actuation force and Tegotae feedback, respectively.

Finally, it was evident that by changing the control variable from ω_{in} to ω_{anti} , it is possible to reproduce a gait transition, as depicted in **Figure 5**. As demonstrated, the value is changed at $t = 8$ s and the trend of the actuation forces and feedback are hidden for clarity reasons due to the presence of several transient sections. The motivations for these specific gaits are shown for the different values of ω that are still an open point thus far. This also considers the fact that due to the random initialisation of the phase angles, the other gates are seldomly shown. These cases can be avoided by constructing a more robust architecture that can integrate several types of sensory feedback.

4.2.2 Robustness and Adaptivity

Finally, in equivalence to the monopod case, the way in which the control policy expressed in **Eq. 11** can sustain a change in the environmental conditions was also examined for the biped case. As depicted in **Figure 6A**, the ground was first lowered to -0.6 m for both the legs as demonstrated in the monopod case.

Meanwhile, the angular frequency was maintained equal to ω_{in} . Second, as depicted in **Figure 6B**, the ground was lowered again to -0.6 m for both the legs. Meanwhile, the angular frequency was equal to ω_{anti} . The results confirm a good robustness of the control policy to the environmental conditions, which in this case is the ground level.

4.3 Optimal Control for the Monopod Case

The optimisation was run for several values of the mass to validate the results for the different feedback dynamics. Meanwhile, all the other parameters were the same as described in the monopod case study. In contrast, the Tegotae controller was applied in **Eq. (11)** to exploit the adaptivity of the Tegotae feedback.

The values of the weights for the cost functions are reported in **Table 2** with respect to each simulation to determine the effectiveness of the weights. It follows that the actual effect of the weights is restricted to the power injection by the controller. Meanwhile, the optimal controller does not have access to the energy stored in the spring and the damping system or to the

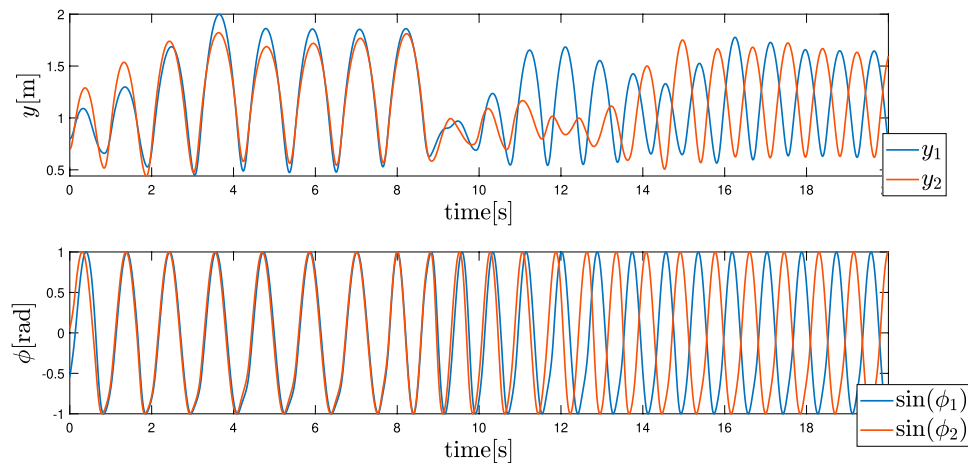


FIGURE 5 | Hopping gait transition. The frequency ω is changed from ω_{in} to ω_{anti} at $t = 8$ s. The upper and lower graphs depict the height of each leg and phase $\sin\phi_i$ of each leg, respectively.

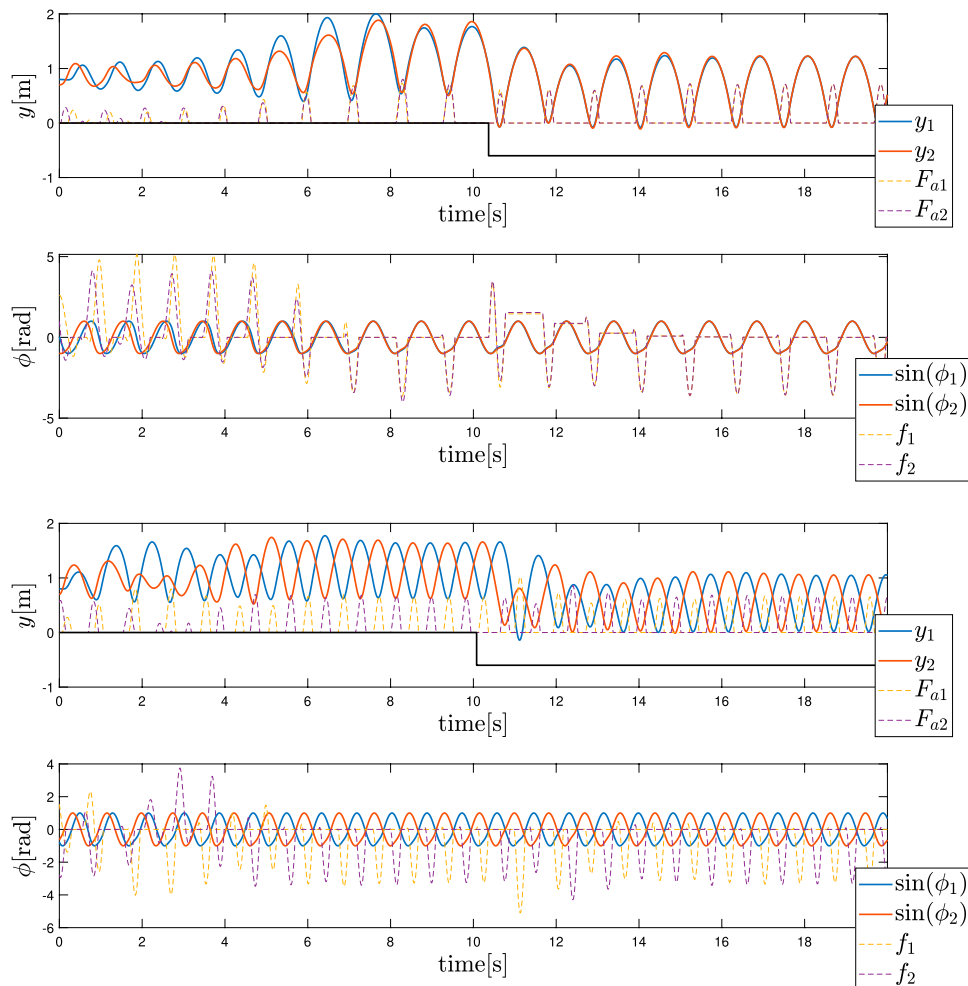


FIGURE 6 | Adaptation to a lower step (Top) In-phase hopping (Bottom) Anti-phase hopping. The ground level was lowered from 0 to -0.6 m at $t = 10$ s.

TABLE 2 | Weight values for the cost functions and RMSE y , $\dot{y}$, and, q for MS.

Simulation	m	Q_1	R_1	L_1	RMSE y	RMSE $\dot{y}$	RMSE q
MS 1	0.1	1e1	-1e1	-1e1	0.03	0.34	0.58
MS 2	0.1	0	-1e1	-1e1	0.03	0.34	0.58
MS 3	0.1	1e1	0	-1e1	0.03	0.34	0.58
MS 4	0.1	1e1	-1e1	0	0.03	0.34	0.58
MS 5	0.3	1e1	0	0	0.03	0.34	0.58
MS 6	0.6	1e1	0	0	0.03	0.34	0.58

vertical excursion, as shown in **Supplementary Figures S1–S3** in the Supplementary Material (SM). In contrast, the ability of dynamically adapting to the mass changes of the Tegotae controller is verified by the optimal controller as well, as shown in **Figures 7** (Top) to (Bottom). It is evident that the effect of the first term Q_2 is sufficient to reproduce, for three different values of masses, to reproduce the effects of the Tegotae control. This term corresponds to the energy consumption of the controller. Therefore, the Tegotae control and an optimal control that attempts to maximise the energy efficiency provide similar results for different masses, thereby validating our hypothesis. Further increments of the mass may require a change in the value of σ or the use of a non-linear spring to avoid negative values of vertical movements.

Not only was the Tegotae control action extremely similar to the MS optimal control (see the **Supplementary Material**) in all the cases, but also the position and velocity profiles demonstrated certain similarities. In all the MS cases, the root mean squared errors (RMSE) were found to be similar, as reported in **Table 2**, as expected from previous considerations. Finally, for all the cases considered in the MS examples, the energy efficiency of the optimal controller as expressed in **Eq. (29)** converged to a value similar to that of the Tegotae controller, whose value was determined considering 1 m as the maximum height reached, for comparison purposes. The convergence is reported in **Figure 8** for MS1 and leads to a final RMSE of 0.22. This seems to limit to the efficiency given the physical constraints of the system. Moreover, increasing the weight Q slightly increases the efficiency.

These results represent the MS case alone. The SS (see the **Supplementary Material**) has several practical drawbacks, which motivates this choice. First, it requires extremely high weights for the sensitivity function of the final conditions and the smoothness of the control policy. The conditions are automatically satisfied by the continuity constraints in the MS. Second, the convergence is more difficult to obtain. The FHOC for the SS method is formulated by using the norm notation and the additional weights to guarantee a sensitivity to the final conditions and control policy.

$$\min_q \int_0^T \|q_i \dot{y}\|_{Q_2}^2 + \|F_k \dot{y}\|_{R_2}^2 + \|(l - y)\|_{L_2}^2 + \|q_i\|_{S_2}^2 + \|q_i - q_{i-1}\|_{\gamma_1}^2 dt + y_{end} - y(T)_{F_2}^2 + \|\dot{y}_{end} - \dot{y}(T)\|_{F_2}^2 \quad (30)$$

Subject to

$$\begin{bmatrix} y_0 - y_{in} \\ \dot{y}_0 - v_{in} \end{bmatrix} = 0, \text{ (Initial Value Constraints)}$$

$$m\ddot{y}(t, q) - (F_c + F_k - mg + q) = 0,$$

$$t \in [0, T], \text{ (ODE Constraint)}$$

$$\begin{bmatrix} y - 0 - \epsilon \\ -y + l + \epsilon \\ \dot{y} - v_{min} \\ -\dot{y} + v_{max} \\ q_i - 0 - \epsilon \\ -q_i + F_{max} \end{bmatrix} \geq 0, \quad i = 0, \dots, N, \text{ (Inequality Constraints)}$$

In our case, $\gamma_1 = 1e4$ and $F_2 = 1e10$. As previously mentioned, these values are extremely high in comparison with the remaining weights in the cost function as presented in **Table 2**. Meanwhile, for the MS case, the weights remain the same as MS five in **Table 3**. Interestingly, it has not been a trivial fact to obtain similar results between the two optimal controllers. It is possible to obtain similar control trends with respect to the MS case, as shown in **Figure 9**. (Top) and (Bottom) However, there are also cases that are similar to the Tegotae controller, as shown in **Supplementary Figures S5, S6** in the SM; this is achieved by varying the values of the weights. For the SS case, the cost function is sensitive to the terms that are proper to the monopod cost function in **Eq. 29** and the spring force.

The MS routine is solved by using the interior-point method that is provided by the MATLAB built-in function FMINCON. In contrast, the SS routine is solved by using the BFGS method and the SQP that is designed on the material, provided by Fagiano (2019). With regard to the integration of the dynamics, the time interval was split into 40 nodes with 2 points per sub-interval for the MS case. Meanwhile, a sampling time of 0.01 s was used for the SS case. In both cases, the integration of the dynamics was conducted using an explicit Runge-Kutta method with an order of four since the restricted dynamics were non-stiff. The step size was 0.01 s in both the methods.

5 DISCUSSION

The main contribution of this study is to propose a control policy with a reflex-like actuation (**Eq. (11)**) for the Tegotae-based feedback law in the CPG in such a way that the controller fruitfully exploits the *embodiment* (Pfeifer and Bongard, 2006; Pfeifer et al., 2007). For the validation of the proposed method, we first demonstrated the energy efficiency of the monopod model as well as its robustness and adaptability using the controller. Then, we demonstrated the gait transition for the bipedal model with its robustness and adaptability. Based on the optimal control theory, we designed an optimal controller and then compared it with the Tegotae-based control input. The results indicate the Tegotae-based feedback with reflex-like actuation results for optimal and energy-efficient motion. This suggests the first evidence concerning the optimal energy efficiency for the Tegotae approach.

This study is the first attempt to analyse the optimal energy efficiency along with the adaptivity of the Tegotae approach. Previous studies (Owaki et al., 2017) have mainly focused on the temporal (timing/phase) modulation in the oscillators by the

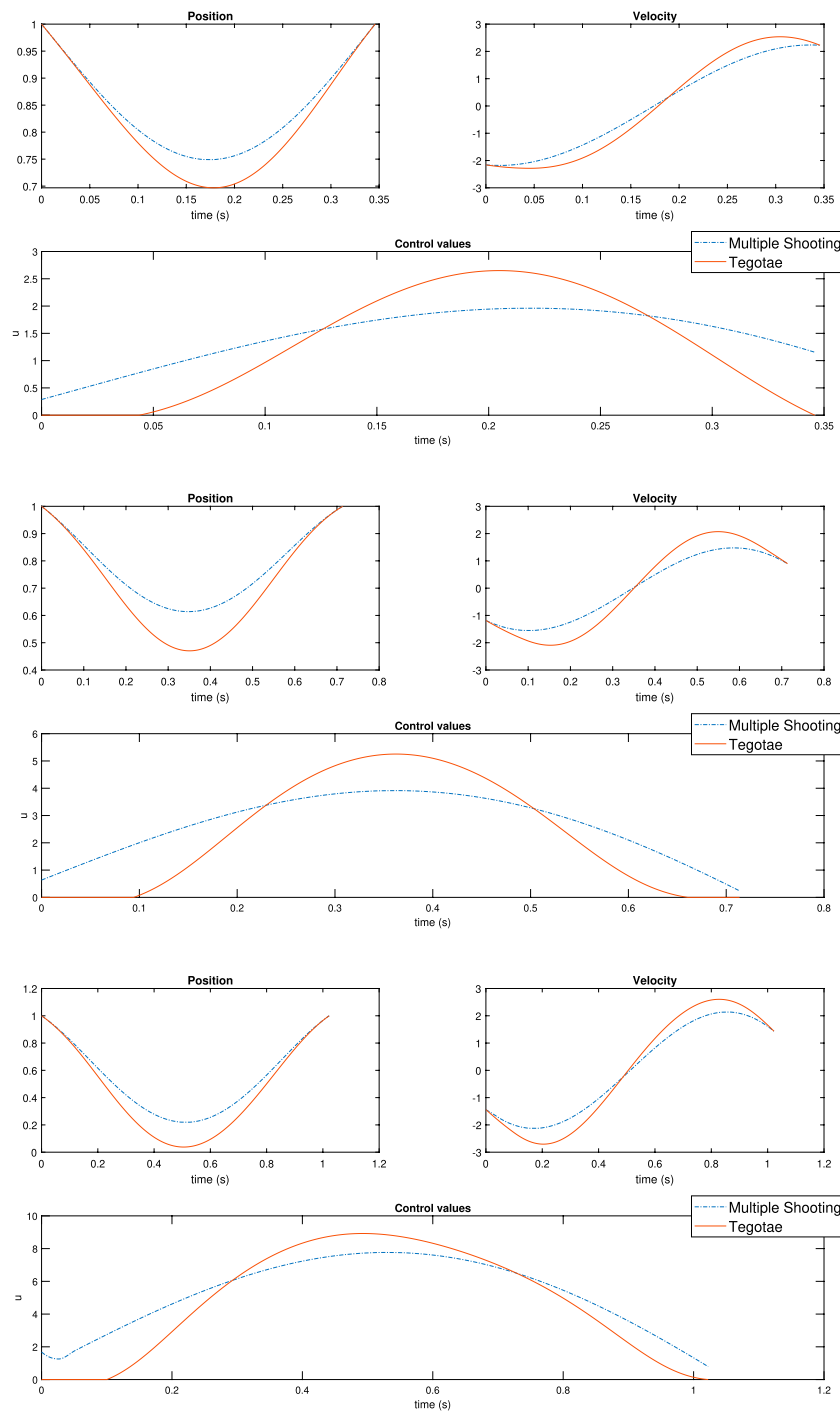


FIGURE 7 | Results of multiple shooting methods. The blue and solid red dotted lines represent the designed optimal controller (MS method) and Tegotae controller, respectively Top case MS1 in **Table 2**: $m = 0.1$ (Middle) case MS5 in **Table 2**: $m = 0.3$ Bottom case MS6 in **Table 2**: $m = 0.6$. Not only was the Tegotae control action extremely similar to the MS optimal control in all the cases, but also the position and velocity profiles demonstrated certain similarities.

Tegotae feedback on GPG-based models. The proposed reflex-like actuation can modulate the “amplitude” of the actuation via F_a function (Eq. (11)), depending on sensory feedback F_k . As presented in **Table 1**, in comparison with the previous methods, the introduction of the Tegotae feedback f_1 was optimal in terms

of the transient period for synchronisation and energy efficiency. The reflex-like pathway (**Figure 1A**) resulted in a rapid response (fast control loop) on motion generation, leading to the first convergent time in **Table 1**. Furthermore, the proposed reflex-like actuation (Eq. (11)) induced by the Tegotae feedback in the

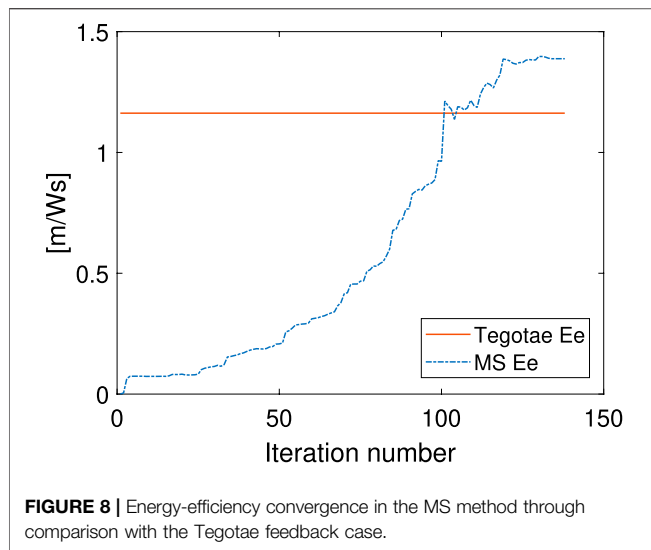


FIGURE 8 | Energy-efficiency convergence in the MS method through comparison with the Tegotae feedback case.

CPG could generate an input (Figures 7, 9) identical to that of the optimally designed controller, resulting in energy-efficient motion, as presented in Table 1. As discussed in Section. 3, the Tegotae approach has similarities (Eq. (26)) with the *tacit learning* frameworks in Hayashibe and Shimoda (2014). Energy efficiency is also achieved by the accumulation of a quantity that needs to be minimised when directly integrating the state variable. These facts suggest that our control policy, i.e. reflex-like actuation with the Tegotae-based proprioceptive feedback in the CPG, accomplishes optimal energy-efficient motion through the dynamical learning process along with the interaction between the controller, body, and environments (Pfeifer and Bongard, 2006; Pfeifer et al., 2007).

The reflex-based leg coordination models (Ekeberg and Pearson, 2005; Manoonpong et al., 2007; Lewinger and Quinn, 2011; Schilling et al., 2013; Dürr et al., 2019) and reflex-like feedback integration into CPG (Ajallooeian et al., 2013; Dzeladini et al., 2014; Li et al., 2014) have been studied in the past two decades. Pioneering research on “event-driven” reflex models in cats (Ekeberg and Pearson, 2005) and insects (Lewinger and Quinn, 2011; Schilling et al., 2013; Dürr et al., 2019) has been conducted, successfully reproducing various aspects of animal inter- and intra-leg coordination during locomotion. Manoonpong et al. (2007) demonstrated that a reflex-based neural controller could achieve stable and fast bipedal walking. Following the pioneering work integrating a CPG with reflex models (Kimura et al., 1999), similar approaches have been proposed. Ajallooeian et al. (2013); Li et al. (2014) also proposed to integrate a CPG with “event-driven” reflex models for adaptability against perturbations and environmental changes; One of characteristic approaches in this line, Dzeladini et al. (2014) introduced CPG as feed-forward components in reflex-based neuromuscular models for human walking, confirming the idea of using CPGs as feedback predictors (Kuo (2002)) from the viewpoint of gait modulation. In our work, the CPG oscillator is not a feedback predictor, but can be considered as a representation of the

TABLE 3 | Weights values for the cost functions for the MS-SS.

Simulation	m	Q_2	R_2	L_2	S_2
MS-SS 1	0.3	1e1	-1e1	-1e1	1e3
MS-SS 2	0.6	1e1	-1e1	-1e1	1e3
MS-SS 3	0.4	1e1	-1e2	-1e2	1e3
MS-SS 4	0.6	1e1	-1e2	-1e2	1e3

movement (phase ϕ_i), that is, an internal model. In the Tegotae approach, the Tegotae function $T_i(\phi_i, F_k)$ is defined as the product of the function of intended motor command $C(\phi_i)$ and sensory information $S(F_k)$; hence, our reflex-like actuation always modulates the motion based on the Tegotae feedback f_i , which increases the value of the Tegotae function $T_i(\phi_i, F_k)$, leading to its adaptability and optimal energy efficiency, as mentioned in previous paragraph.

Past studies that have used the Tegotae approach (Owaki et al., 2012; Owaki and Ishiguro, 2017b; Owaki et al., 2017) have demonstrated adaptability and behavioural diversity for reproducing animal-like legged locomotion. For quadruped locomotion, the simple and local sensory feedback law in the CPG reproduced the adaptability against the change in mass distribution, which resulted in horse-like or primate-like walking patterns, and a spontaneous gait transition, from walking to trotting and galloping, in response to the locomotion speed. These studies for quadruped robots provide a basis for establishing a design scheme based on the Tegotae approach. For hexapod locomotion, Owaki et al. (2017) designed a minimal model for the inter-limb coordination in a systematic manner based on the Tegotae concept, successfully reproducing the various aspects of the insect locomotion patterns, which includes adaptability to changes in the body properties, e.g. leg amputation. In line with these studies, this investigation also successfully reproduces the adaptability (Figures 3, 6), and behavioural diversity (Figures 4, 5) as well as the energy efficiency. As discussed in previous studies, in the Tegotae approach, the main aim of designing the Tegotae function is to consider the physical consistency of the action and reaction for the desired motion, and to design the Tegotae function such that its value increases in such cases. Once such a Tegotae function is designed, it is possible to modify the control variables in a situation-dependent manner by increasing the value of the Tegotae function as a feedback term $\partial T(x, S)/\partial x$. Therefore, the Tegotae approach enables the design of an autonomous decentralised controller in a systematic manner, by designing the Tegotae function in line with the desired motions.

This study proposes a reflex-like actuation for the Tegotae-based feedback law in the CPG. This is a significant contribution for the actuation and sensory feedback on the adaptation process to the environment and the optimisation process for energy efficiency. However, one of the limitations of this study is that we did not test the applicability of the Tegotae approach to the real-world environment with a physical robot. In addition, it is extremely difficult to perfectly model the dynamics in the real-world environment. One of the key aspects based on the Tegotae approach is the verification in the real world as shown in Owaki

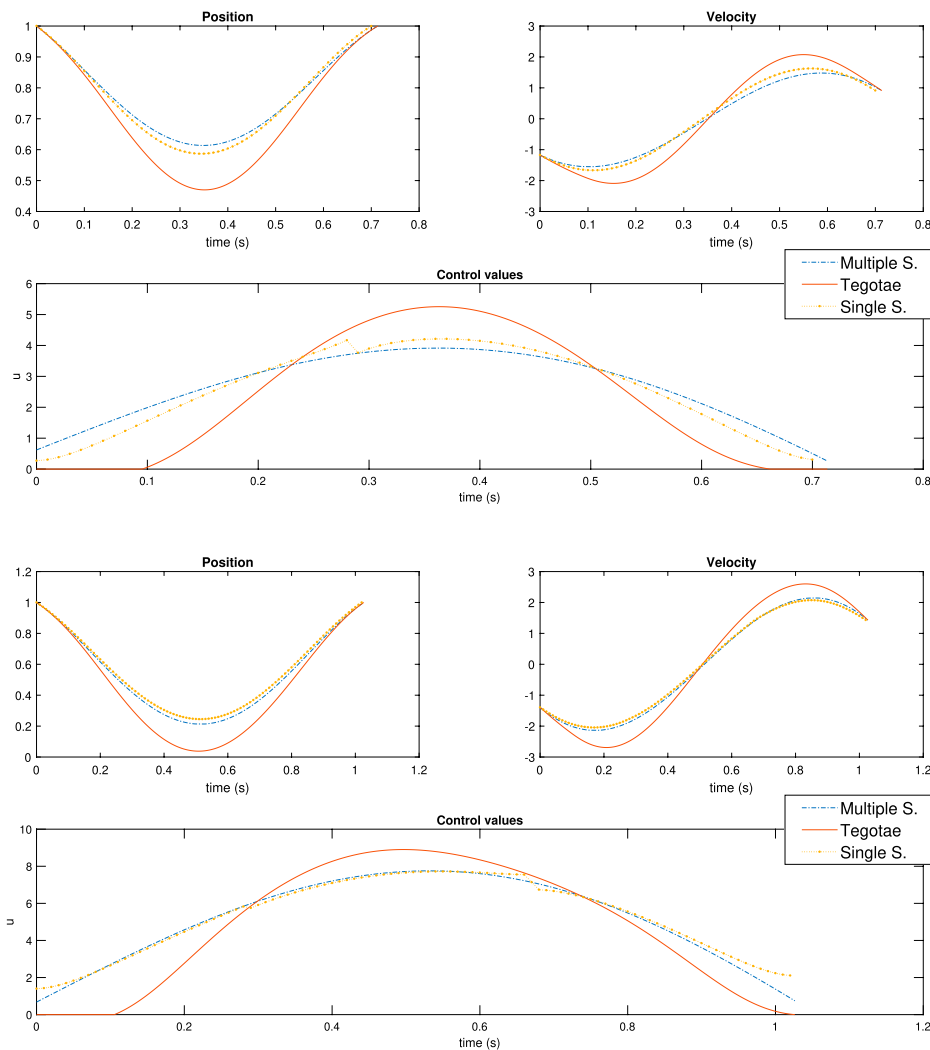


FIGURE 9 | Results of multiple shooting-single shooting (Top) case MS-SS1 in :Table 3 $m = 0.3$ (Bottom) case MS-SS2 in :Table 3 $m = 0.6$.

et al. (2012); Owaki and Ishiguro (2017b); Owaki et al. (2017). Instead, we analysed the Tegotae control by using the optimal control theory and provided evidence concerning the optimal control input. Regarding the energy efficiency of tacit learning in the real-world environment, it has been verified by achieving a task with a redundant arm in Hayashibe and Shimoda (2018). One potential future direction is to apply our control policy to a robot with more degrees of freedom that performs more complicated tasks. Our control policy is compatible with the force/torque-based control of a physical robot, which is a promising direction of study for future research.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

DO and MH conceived the research and managed the data collection. RZ designed the model and controllers and conducted the simulations. RZ and DO conducted the analyses. All of the authors wrote the manuscript together.

FUNDING

We gratefully acknowledge the support from the JSPS KAKENHI (grant number JP17KK0109, 18H01399, and 20H04260).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frobt.2021.632804/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Body and Tail Coordination in the Bluespot Salamander (*Ambystoma laterale*) During Limb Regeneration

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OPEN ACCESS

Edited by:

Poramate Manoonpong,
University of Southern Denmark,
Denmark

Reviewed by:

Masato Ishikawa,
Osaka University, Japan
Amir Ayali,
Tel Aviv University, Israel

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Specialty section:

This article was submitted to
Computational Intelligence in Robotics,
a section of the journal
Frontiers in Robotics and AI

Received: 15 November 2020

Accepted: 14 May 2021

Published: 28 May 2021

Citation:

Donatelli CM, Lutek K, Gupta K and
Standen EM (2021) Body and Tail
Coordination in the Bluespot
Salamander (*Ambystoma laterale*)
During Limb Regeneration.
Front. Robot. AI 8:629713.
doi: 10.3389/frobt.2021.629713

Animals are incredibly good at adapting to changes in their environment, a trait envied by most roboticists. Many animals use different gaits to seamlessly transition between land and water and move through non-uniform terrains. In addition to adjusting to changes in their environment, animals can adjust their locomotion to deal with missing or regenerating limbs. Salamanders are an amphibious group of animals that can regenerate limbs, tails, and even parts of the spinal cord in some species. After the loss of a limb, the salamander successfully adjusts to constantly changing morphology as it regenerates the missing part. This quality is of particular interest to roboticists looking to design devices that can adapt to missing or malfunctioning components. While walking, an intact salamander uses its limbs, body, and tail to propel itself along the ground. Its body and tail are coordinated in a distinctive wave-like pattern. Understanding how their bending kinematics change as they regrow lost limbs would provide important information to roboticists designing amphibious machines meant to navigate through unpredictable and diverse terrain. We amputated both hindlimbs of blue-spotted salamanders (*Ambystoma laterale*) and measured their body and tail kinematics as the limbs regenerated. We quantified the change in the body wave over time and compared them to an amphibious fish species, *Polypterus senegalus*. We found that salamanders in the early stages of regeneration shift their kinematics, mostly around their pectoral girdle, where there is a local increase in undulation frequency. Amputated salamanders also show a reduced range of preferred walking speeds and an increase in the number of bending waves along the body. This work could assist roboticists working on terrestrial locomotion and water to land transitions.

Keywords: coordination, gait transition, limb loss, locomotion, embodiment, bio-inspired robotics, robotics-inspired biology

INTRODUCTION

In nature, animals must adapt to a wide variety of perturbations to effectively move through their environments. Successful navigation of perturbations is necessary for finding food, escaping predation, reproduction, and nearly every other biological function requiring movement, meaning that animals have evolved to be behaviorally plastic (Beddard, 1902; Gillis and Blob, 2001; Dingemanse and Wolf, 2013; Touchon et al., 2013; Vega and Ashley-Ross, 2020). Even with advances in computational modeling, control algorithms, and robotics, technology is unable to match the behavioral flexibility of an animal in nature (Kim et al., 2013). This often results in models displaying unrealistic kinematics and robots getting stuck or damaged. Developing a greater

understanding of how animals overcome obstacles in nature could provide useful data for roboticists to design more robust machines.

Fewer perturbations are more severe than losing a limb, yet salamanders are able to survive through the loss and subsequent regeneration of limbs in nature (Arenas Gómez et al., 2017; Dwaraka and Voss, 2021; Joven et al., 2019). After limb loss, the animal must adapt its locomotion to this acute perturbation and then continue to modify their behavior over weeks and months as the limb grows back. In some cases, the lost appendage never fully recovers (Dwaraka and Voss, 2021), which must then result in a permanent change in behavior. Though the limb regeneration process has been studied extensively in the context of cellular signaling, development, and phylogenetics (Arenas Gómez et al., 2017; Dwaraka and Voss, 2021; Joven et al., 2019), the change in kinematics has not been well described. We therefore chose to study how the kinematics of the Blue-spotted Salamander (*Ambystoma laterale*) changes during the limb regeneration process.

Salamander kinematics have been well studied in a wide range of scenarios from forward and backwards walking to aquatic to terrestrial transitions (Ashley-Ross, 1994; Azizi and Horton, 2004; Cabelguen et al., 2010; Sheffield and Blob, 2011; Karakasiliotis et al., 2013). During walking, there are three motions used for forward propulsion: 1) girdle rotation (10–18%), 2) limb rotation (26–28%), and 3) limb retraction (56–62%) where the percentages describe the amount each motion contributes to forward movement (Karakasiliotis et al., 2013). Girdle rotation is of particular interest as it is a result of local lateral bending of the vertebral column. Modeling with robots has confirmed that axial bending (i.e., girdle rotation) indeed plays an important role in walking and found that higher coordination between the limbs and vertebral column results in an increase in stride length (Karakasiliotis and Ijspeert, 2009; Crespi et al., 2013).

In water, salamanders change their gait entirely, moving from a sprawled tetrapod gait with limbs moving in an alternating stepping pattern to an undulatory swimming gait with limbs tucked against the body (Frolich and Biewener, 1992). This swimming mode is more like that of a fish than other tetrapods, such as dogs, which tend to use their limbs as paddles without whole body undulation (Rivera et al., 2011). This pre-programmed tendency to switch to body undulation when limb frictional or loading forces disappear, suggests that, when limbs are removed a similar increase in body undulation may occur. In addition, one might expect that removing the hind limbs of a salamander might elicit a terrestrial “walking” gait similar to that of amphibious fish that use pectoral fins for support but lack substantial pelvic fins such as the Senegal Bichir (*Polypterus senegalus*). We include data from *Polypterus* walking and swimming in this study for comparison.

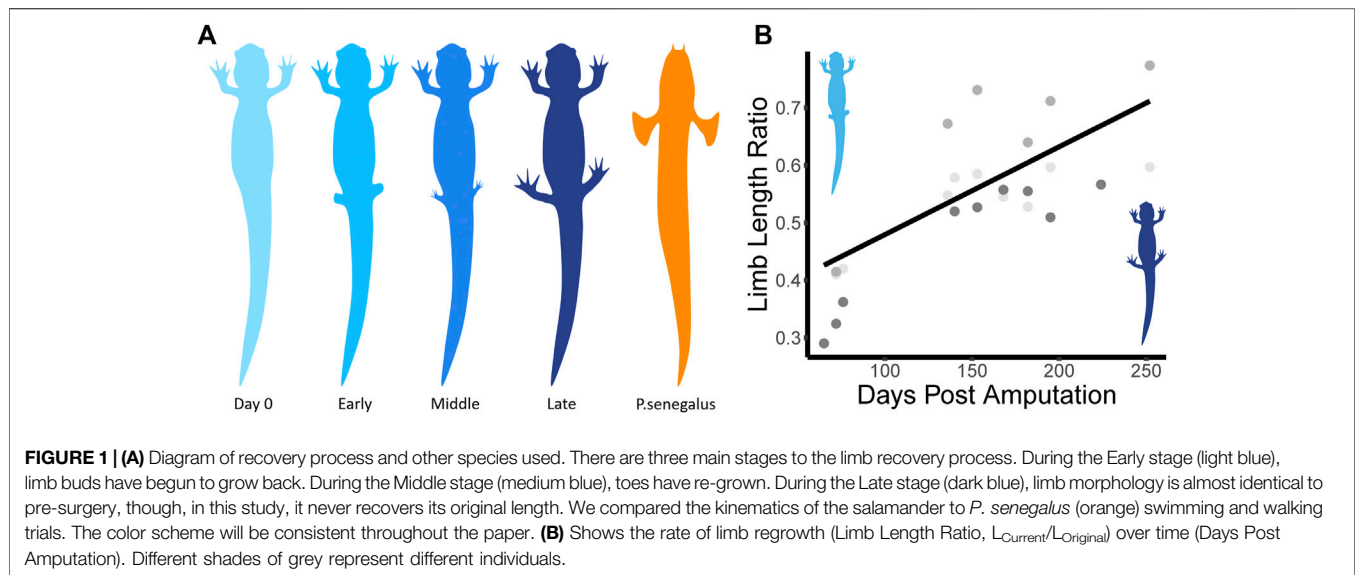
Central pattern generators (CPGs) are neural circuits that can produce a patterned output without top down control (Duysens and Van de Crommert, 1998). CPGs control rhythmic movements such as walking, running, and swimming in both

vertebrates and invertebrates and, along with local sensory feedback, make these movements robust to perturbations such as uneven terrain (Pflüger and Burrows, 1978; Kanou et al., 2007; Tytell et al., 2010; Garcia-Saura, 2015; Bidaye et al., 2018; Yasui et al., 2019). Local CPGs can be associated with axial and appendicular motion and decerebration and spinal transection studies have shown that CPGs with sensory feedback can remain active, resulting in effective locomotor function in the absence of signals from the brain (Zareen et al., 2016).

Since salamanders are one of the earliest diverging terrestrial tetrapods (Gould, 1992), it is thought that these axial CPGs are similar to those found in fish and other swimming vertebrates and that limb control evolved on top of the existing spinal CPGs (Chevallier et al., 2008). Computational and physical models of salamander gait transitions suggest that sensory feedback from the limbs causes the change in gait from a standing wave used in walking to an undulatory wave used in swimming (Ijspeert et al., 2007; Chevallier et al., 2008). This could mean that, without limbs, the salamander would return to a more fish-like undulatory gait. There is evidence for this in the kinematics of *S. lacertina*, a salamander species that does not have hindlimbs at all. During aquatic walking, its front limbs step in an alternating stepping pattern similar to the way the front limbs move during a tetrapod gait. However, its body moves in a traveling wave like swimming, as opposed to a standing wave like walking (Azizi and Horton, 2004). Amputation of limbs could have differing effects on an animal’s ability to locomote depending on the level of neuro-connection between body and limbs.

The field of robotics and control could learn a lot from how animals control motion and adapt to extreme perturbations such as the loss of one or more limbs (Trimmer and Lin, 2014; Chattunyakit et al., 2019; Kano et al., 2019). This is especially important for robots deployed in the field for long term missions such as deep sea or space exploration (Koos et al., 2013). There are existing algorithms for investigating new gaits after damage to a limb, but these are computationally expensive, require precise knowledge of the damaged part, and may result in further damage to the robot (Koos et al., 2013). Other options include pre-programming of gaits for specific limb-loss (Mostafa et al., 2010; Kano et al., 2019) but this may fail if the robot is damaged in an unexpected way. If we develop a deeper understanding of how animals use a combination of top-down control (CPGs), sensory feedback, and morphology to overcome extreme perturbations, this could be incorporated into future robotic design.

In this work we aim to understand more about how vertebrates change their locomotor patterns and possible control schemes to deal with perturbations by: 1) describing the change in body kinematics as the salamander regrows its hindlimbs, 2) discussing the control mechanisms that could drive these kinematic changes and 3) comparing the changing kinematics to the Senegal Bichir (*Polypterus senegalus*), an amphibious fish species in order to place this change in an evolutionary context.



MATERIALS AND METHODS

Animals

We collected adult, Blue-spotted Salamanders (*Ambystoma laterale*) during their spring migration in the summers of 2018 and 2019. Though we cannot control for the exact age of wild caught animals, we can be sure that all animals are adults (Canadian Herpetological Society, 2021). All salamanders were collected locally during spring thaw as they crossed roadways to reach breeding ponds (Ottawa, Canada; collection permit 1092653). They were housed at the University of Ottawa aquatic animal facility under Animal Care Protocol number BL-1926.

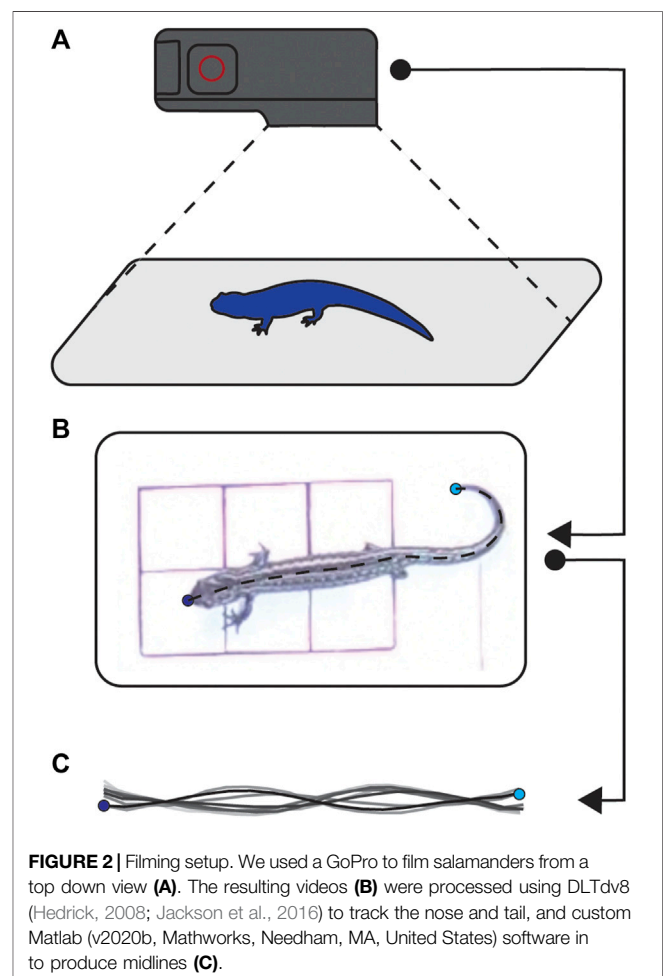
Surgery

Three individuals were chosen to undergo hindlimb removal surgery. We anesthetized them with a 0.1% ethyl 3-aminobenzoate methanesulfonate salt (MS222) for roughly 15 min or until they did not respond to stimuli. Once anesthetized, both hindlimbs were removed using a fresh scalpel blade (size 22) and pressure was applied to the wound to stop bleeding if required. Just after surgery, a lidocaine solution was infiltrated at the incision site and an intercoelomic injection of Buprenorphine (50 mg/kg) was administered for pain control. After surgery (**Figure 1**, Day 0), animals were allowed to recover for 1 month before trials. After 1 month, the wounds from surgery were healed and we could see that the regeneration process had begun (**Figure 1**, Early).

Walking Trials

We recorded bouts of walking for each salamander at 1- and 2-week intervals until their limbs were almost fully regenerated. When recording animal locomotion, we first transferred them in their home tanks from the housing facility to the filming room. Once in the filming room, we recorded salamanders walking, from above using a GoPro Hero 4 (GoPro Inc., San Mateo, CA,

United States) at 120 frames per second resulting in a top-down view of walking bouts (**Figures 2A,B**). We filmed either until the salamander was no longer interested in walking or until we had



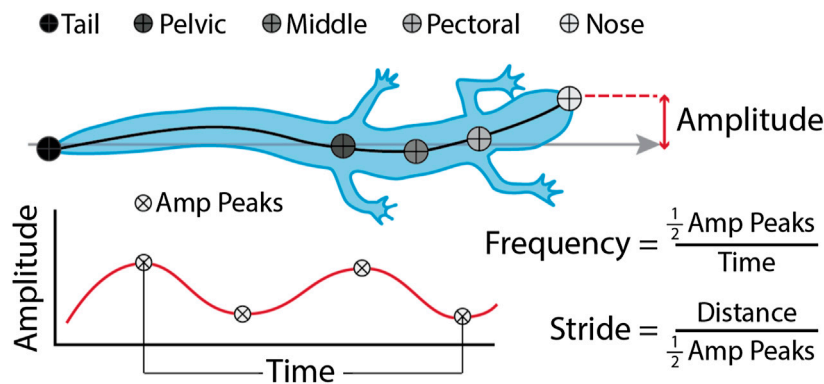


FIGURE 3 | Kinematic variables. Amplitude (BL) and frequency (Hz) were measured at 21 evenly spaced points along the body (1 being the nose, 21 being the tail). Amp Peaks are the number of peaks in the amplitude wave, Time (s) is the length of time between the first and last peak, and Distance (BL) is the distance the nose of the salamander travels between the first and last peak. Statistics were done on the whole dataset, but some figures show only anatomical points of interest: nose, pectoral girdle, middle (halfway between the pectoral and pelvic girdles), pelvic girdle, and tip of tail. Stride length (BL) measurements were based on movement of the tail.

five good runs. We considered a good run to have six full steps, and we excluded any trials with fewer steps post-filming.

Kinematic Analysis

We measured midline kinematics of the salamanders walking using DLTdv8 (Hedrick, 2008) and our own custom software written in Matlab (v2020b, Mathworks, Needham, MA, United States). We first semi-automatically tracked the nose and tail using DLTdv8. Once those points were digitized, we used our own software to automatically trace the midlines. Our software requests user input to threshold the videos, then it converts them to binary, and uses the location of the nose and tail digitized in DLTdv8 to locate the animal and trace the midline. The midline tracing primarily uses the *bwskel* function from the Image Processing toolbox, which extracts the centerline and branches of binary objects. Once skeletonized, we use the nose and tail points to find the endpoints of the branches, choose the shortest path between the two, and smooth the resulting midline. Once we extracted the midlines, we used another Matlab script to measure body bending amplitudes (BL), and frequencies (Hz) of 21 evenly spaced points along the body (Figure 3). We also measured speed (BL/s), body waves (waves/s), and stride length (BL). Body waves is presented in waves/s to normalize for swimming speed. Stride length is defined as the distance the animal traveled during one tail beat cycle which allowed us to compare across conditions and between species. *Polypterus* walking and swimming data from a previous experiment were processed through the same code and used to compare with the salamander walking.

In addition to these kinematic variables, we also measured the change in limb length over time. Values are reported as “limb length ratio” and represent the current length of the limb (L_{current}) as percentage of the original limb length (L_{original}).

Statistics

Kinematics data were imported into R (version 3.6.1) for statistics. We used the nlme and car packages to create linear mixed effect models. We chose to use linear mixed effects models since these models offer more flexibility when dealing with

unequal sample sizes than, for example, a standard ANOVA. This flexibility allows us to use all data from each individual, rather than being forced to compute averages in order to have the same number of data points per sample. We created four mixed effect models. Our dependent variables were frequency, bending amplitude, speed, and stride length. All models included limb length ratio as a fixed effect. Our frequency, amplitude, and stride length models also included speed as a fixed effect. For all these models we included a random slope, modeled as days post amputation nested inside individual. These variables were chosen as random effects since each individual was recorded at similar time intervals and could be prone to random fluctuations in behavior on a day-to-day basis simply due to the variable nature of animal behavior. Individual must also be included as a random effect because of the repeated measures structure within our dataset. We also performed pairwise *t*-tests to determine differences between regeneration phases.

RESULTS

Salamander Walking

Our first set of models looked at changes in kinematics as the limbs grew back. Here, limb length was included as a continuous variable (Table 1). Limb length ratio ($L_{\text{Current}}/L_{\text{Original}}$), walking speed (BL/s), and body position (%BL) had significant effects on body wave frequency (Hz) ($p < 0.001$ for all comparisons). Limb length ratio was a significant predictor of amplitude (BL) ($p < 0.001$) but position and speed were not ($p = 0.703$, $p = 0.082$, respectively). Limb length ratio was also a significant predictor of both walking speed ($p < 0.001$) and stride length (BL) ($p < 0.001$). Speed was also significantly affected by stride length ($p < 0.001$).

Our paired *t*-tests looked at differences between regeneration stages (Figure 1A; Table 2). These tests showed that there is a significant difference in mean bending frequency along the body between the Early regeneration stage and all other stages ($p < 0.01$ for all three comparisons). There is also a difference in mean stride length between the pre-amputation trials and the Early and

TABLE 1 | LMER results.

y~	Predictors				
	Limb length ratio	Days post amputation	Position	Speed	Stride length
Frequency	$p < 0.001$	$p = 0.065$	$p < 0.001$	$p < 0.001$	n/a
Amplitude	$p < 0.001$	$p = 0.002$	$p = 0.703$	$p = 0.082$	n/a
Speed	$p < 0.001$	$p < 0.001$	n/a	n/a	$p < 0.001$
Stride length	$p < 0.001$	$p = 0.023$	n/a	n/a	n/a

Bold entries indicate values that are significant (ie $p < 0.05$)

TABLE 2 | Paired *t*-test results. *p*-value adjusted using a Bonferroni correction. SDs were pooled.

	Frequency			Stride length		
	Early	Middle	Late	Early	Middle	Late
Middle	$p < 0.001$	—	—	$p = 1.00$	—	—
Late	$p = 0.011$	$p = 1.000$	—	$p = 0.184$	$p = 0.247$	—
PreAmp	$p = 0.001$	$p = 0.515$	$p = 0.317$	$p < 0.001$	$p < 0.001$	$p = 0.004$

Bold entries indicate values that are significant (ie $p < 0.05$)

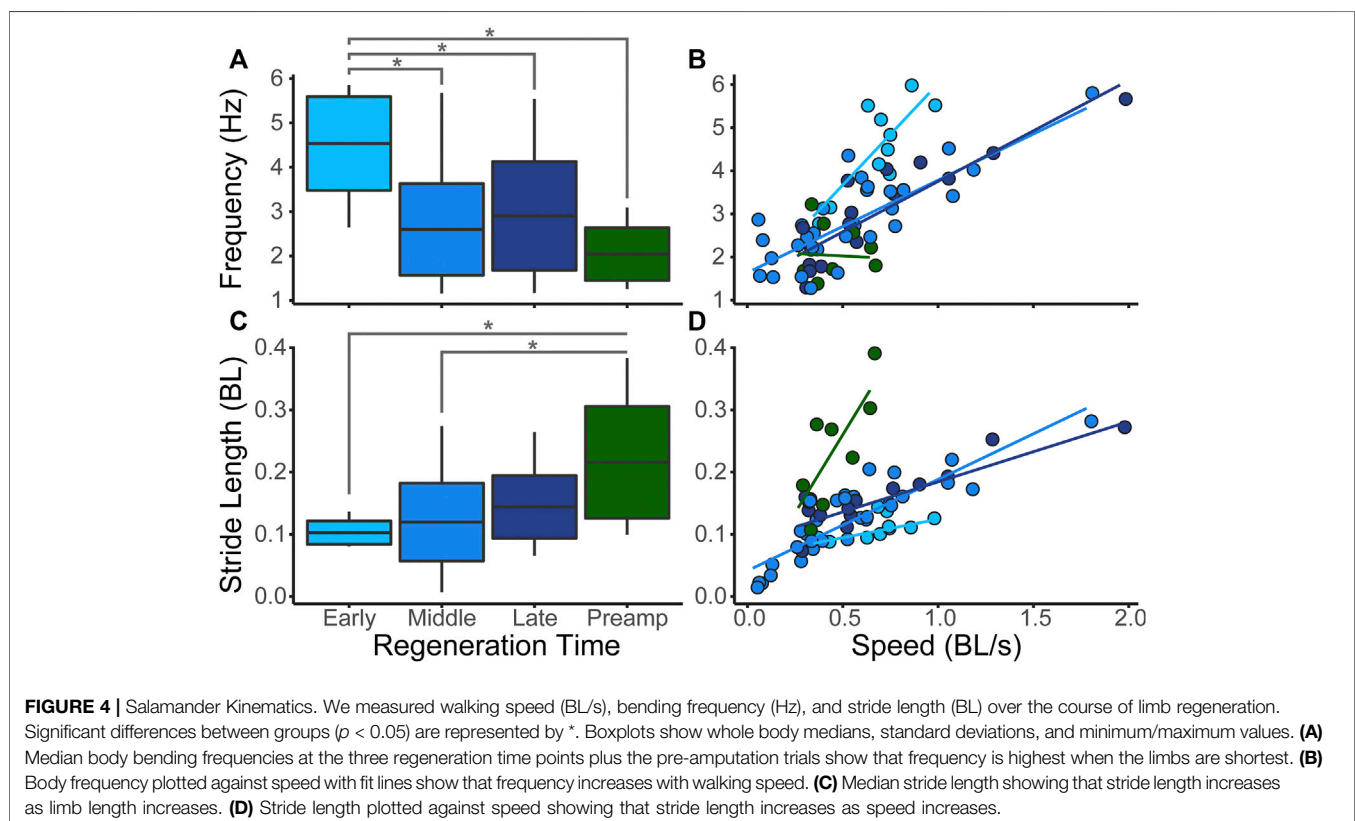
Middle stages ($p < 0.001$ for both) but no difference between the pre-amputation trials and the Late regeneration stage trials.

In the early stages of regeneration, salamanders walk using a higher undulation frequency than salamanders in later stages (Figure 4A). Stride length increases steadily throughout the regeneration process (Figure 4C). As expected, as walking

speed increases body undulation frequency and stride length also increase (Figures 4B,D).

Comparison with another species

During the early stages of salamander limb regeneration, there is a change in the way their bodies move. For salamanders in the early



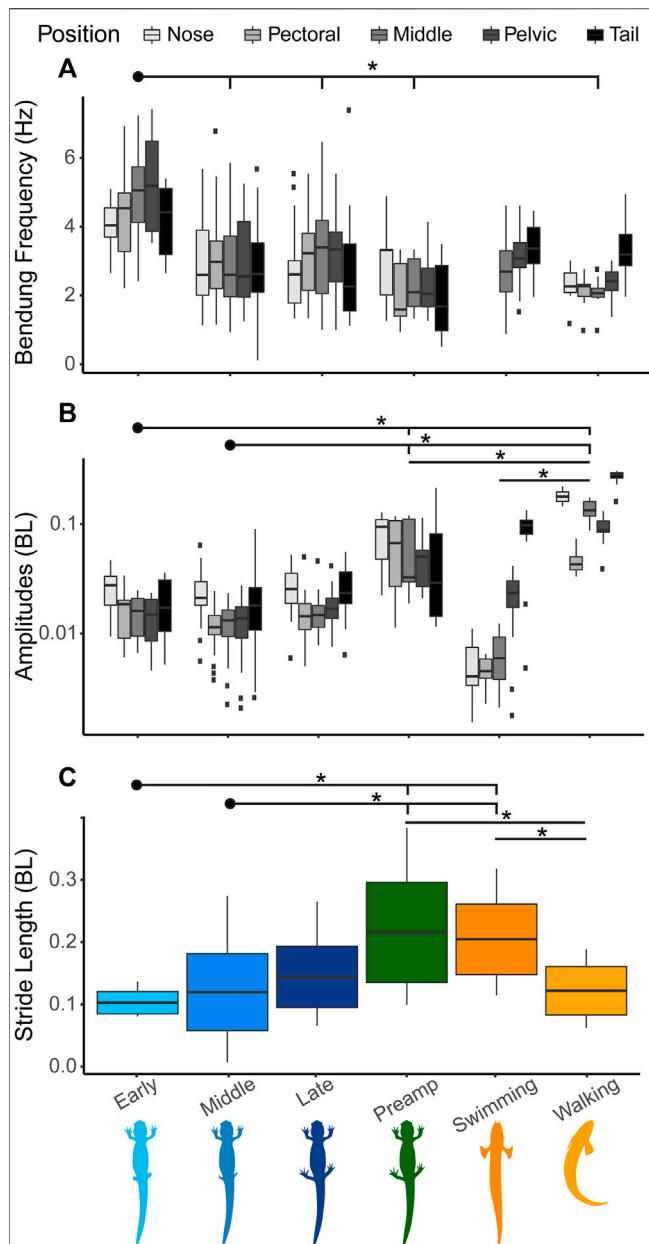


FIGURE 5 | Salamander kinematics during recovery compared with fish kinematics. Kinematic patterns change as the salamander regenerates its legs. Significant differences between means ($p < 0.05$) noted by *. **(A)** Bending frequency (Hz) at five specific body points indicated by different shades of grey. From lighter to darker the shades indicate nose, pectoral girdle, middle, pelvic girdle, and tail. In our frequency plot (A.), we did not include the nose and pectoral girdle points for *Polypterus* swimming, as the low amplitude and flapping pectoral fins lead to noise in the frequency calculations. **(B)** Bending amplitude (BL) at five body points shown on a log scale. General trends show that portion(s) of the body used for propulsion have the lowest frequencies and highest amplitudes. **(C)** Stride length (BL) of salamanders at different time points compared with *P. senegalus* swimming and walking. The salamander data here is the same data presented in **Figure 4C**.

stages of recovery, the frequency of the pelvic girdle is increased compared to other parts of the body (**Figure 5A**). As they recover, the frequencies of the pelvic and pectoral girdles begin to match

more closely. For amplitudes, the pattern of salamander walking is consistent throughout recovery, with the highest amplitudes at the head and tail, though the nodes about which the amplitudes oscillate, change (**Figures 5B, 6**).

Overall, stride length increases as limbs regenerate with a significant difference between the Early and Middle stages of regeneration and the Pre-Amputation trials. Although we predicted that salamanders walking without hind limbs would resemble walking *Polypterus*, we find the opposite. With their limbs removed, the body kinematics of salamander walking is more like *Polypterus* or salamander swimming in that the number of waves along the body is increased. As the limbs regenerate, the kinematics shift and more closely resembles intact salamander walking prior to limb amputation.

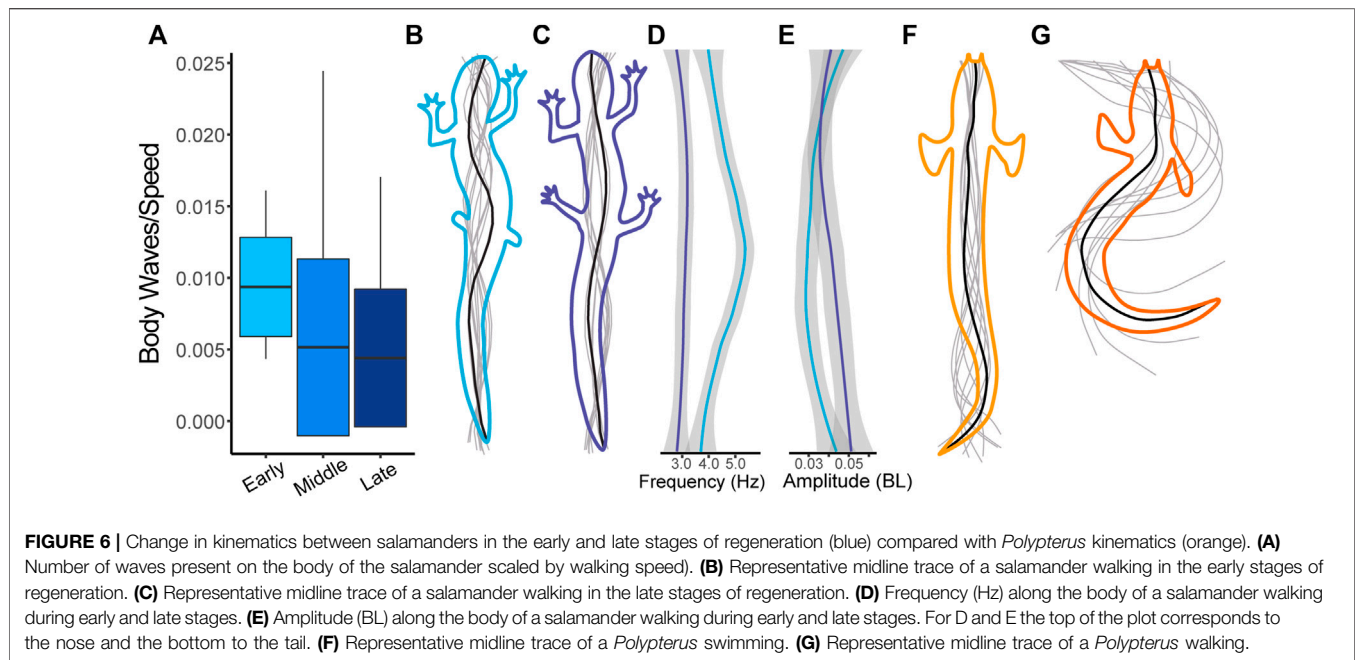
DISCUSSION

Salamander Kinematics Change During Regeneration

The most notable change in kinematics after hindlimb amputation in salamanders, is a shift in apparent undulation frequency of the pelvic girdle, the region where the hindlimbs articulate with the vertebra column. During the early stages of regeneration, the pelvic girdle sways back and forth at a frequency of 5 Hz while the rest of the body is swaying closer to 4 Hz (**Figure 5A**). Two potential explanations exist for this increase in frequency. First, without the sensory feedback associated with limb to ground contact, it is possible that *pelvic girdle CPG modulation changes*. Second, the increase in pelvic frequency may be due to a simple *mechanical constraint principle*.

If pelvic girdle CPG modulation is responsible for our observed change in kinematics, a change in local sensory feedback could be acting in two ways. If local force feedback from limb to ground contact inhibits axial (vertebral) CPGs in intact animals, the top-down (from the brain) signal that drives body oscillation would be uninhibited at the pelvis in amputated individuals, resulting in an increase in the speed of rotation of the hip. In contrast, if an absent or reduced sensory signal during regeneration is perceived as a misstep, the top-down signal could be “actively” increased, impacting local CPGs in the limbs and resulting in an increase in the speed of rotation of the pelvic girdle and local bending of the spine. Indeed, we observed that salamanders will occasionally take two steps with their reduced hindlimbs during a single front limb step, suggesting a perception of misstep may be the case. One could implant EMGs in the musculature along the body to investigate the change in CPG rhythm. If pelvic girdle CPG modulation changes are responsible for the increase in frequency, we would expect a change in intensity of the muscle signal at the pelvic girdle and/or an interruption in the standing wave of body muscle activation traveling from head to tail when the hindlimbs fail to contact the ground. If there is no change in axial muscle activation, the change in frequency must be due to mechanics.

One could also do an electrophysiology prep rather than use EMGs to measure the activation patterns of motor neurons directly. This type of work has been done in cockroaches and stick-insects using both *in-vitro*, fictive walking preps as well as semi-intact preps (Borgmann et al., 2009; Fuchs et al., 2011). The



downsides of experiments like this are 1) for an *in-vitro* experiment, one would have to eliminate the mechanical perturbation of a limb hitting the ground. As a result, it would be hard to eliminate mechanical constraints from one's conclusions. 2) The semi-intact prep procedure in vertebrates is incredibly invasive. There are ethical concerns regarding this type of procedure with vertebrates and the number of individuals one would need to use may be too high.

If the mechanical constraint principle is causing changing kinematics, we would expect the rhythm of the axial CPG to remain constant post amputation, which we could infer from axial EMGs. However, the mechanical constraint of the limb contacting the ground would be absent, allowing for more bending waves to be present along the body and an increase in rotation frequency at the girdle. Because there is no increase in the frequency of body sections not associated with lost limbs, mechanical constraint alone seems an unlikely explanation for the changes we see. It does not rule out the possibility that independent limb and axial CPGs at the girdles share in excitatory coupling, independent of sensory feedback, which, when free of mechanical constraint, increases the axial CPG oscillation signal locally at the limb (Delvolvé et al., 1997). This type of coupling has been shown in cockroaches, where an excitatory stimulation to one leg motor neuron results in coordinated activity in the ganglia of neighboring limbs (Fuchs et al., 2011). Other work on stick insects showed that front leg movement alone could activate descending pathways and coordinate the movement of the other limbs (Borgmann et al., 2009).

Interaction of limb and axial CPGs has been used to explain coordination between fore and hind limbs (Delvolvé et al., 1997). In this case, limb CPGs oscillate between increasing and decreasing the excitability of axial CPGs, resulting in the formation of coordinated limb motion and a standing body

wave during walking. During the middle and late stages of regeneration, when limbs are regaining contact with the ground, the frequencies of both the pectoral and pelvic girdles sync at 3.5 Hz (Figure 5). Because girdles become phase locked regardless of the size of the regenerating limb, this data suggests a threshold control mechanism where sensory feedback from the limb is playing a role in helping to coordinate limb and body oscillation frequencies independent from the strength of the mechanical constraint on the system.

Although sensory feedback may have an essential role in coordinating the walking cycle, mechanical constraint contributes to overall animal performance. During early stages of regeneration, the range of walking speeds is much lower than in the later stages (Figure 4D). Salamanders with no or very short hindlimbs have reduced stride lengths and a limited ability to raise their posterior trunk off the substrate. A higher speed may be necessary to overcome frictional forces and move at all, while shorter stride length limits distance per step cycle; both of these mechanically reduce the range of speeds that can be attained with reduced hind limbs (Figures 4B,D). In addition, the mechanical consequence of over rotation of the pelvic girdle, shifts the center of mass causing the head of the salamander to reflexively swing in the opposite direction correcting the overall path of the center of mass (Figure 7A). The result is that animals in the early stages of regeneration have a less optimal forward motion as the mass of the animal shifts more from side to side compared with later stage animals.

Salamander Kinematics Resemble a Swimming Fish When Limbs Are Removed

Salamander swimming, like most undulatory fish swimming, is characterized by a traveling wave passing from head to tail, while walking is a standing wave with nodes at the pelvic and

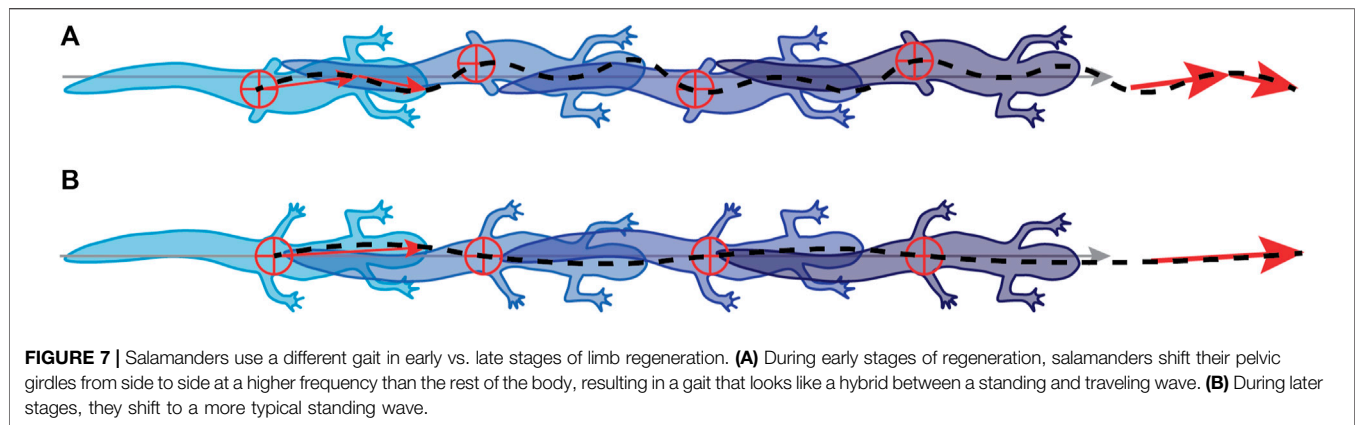


FIGURE 7 | Salamanders use a different gait in early vs. late stages of limb regeneration. **(A)** During early stages of regeneration, salamanders shift their pelvic girdles from side to side at a higher frequency than the rest of the body, resulting in a gait that looks like a hybrid between a standing and traveling wave. **(B)** During later stages, they shift to a more typical standing wave.

pectoral girdles. The amphibious fish, *Polypterus*, uses substantial pectoral fins to weight-bear when walking but lacks hind fin support. Instead, it uses an exaggerated full body and tail oscillation to push off the substrate (**Figure 5B**). We predicted, based on their similar body morphologies, that a salamander with its hind limbs removed might move like an amphibious walking fish, such as *Polypterus*. Contrary to this prediction, our data shows that, after leg amputation, salamander walking kinematics more closely resembles *Polypterus* swimming kinematics with an increase in the number of waves along the body (**Figure 6**). As limbs are more fully regenerated, there is a reduction in waves along the body and the gait more closely resembles the familiar standing wave associated with intact salamander walking as well as *Polypterus* walking. This may be the result of a universal control principle driving both salamander and *Polypterus* locomotion.

Complexity in the Swimming to Walking Model and What It Means for Overall Vertebrate Motor Control

The CPG that controls undulatory swimming in the salamander is similar to that found in more early derived animals, such as the lamprey, suggesting that the activation pattern is constrained evolutionarily (Chevallier et al., 2008; Tytell et al., 2010). Even animals that predominantly use their fins for swimming, like *Polypterus* (Standen et al., 2014) often have accompanying, subtle asynchronous body and tail undulations suggesting that the basal swimming CPG is active in the background. When *Polypterus* swim faster, they tuck their fins against the body, and the more basal undulatory CPG appears to take over.

If the neural control scheme is similar between salamanders and walking fishes, models that explain the transition from swimming to walking in salamander (Ijspeert et al., 2007) could also explain the speed transition in swimming fish. When salamanders transition from walking to swimming, they tuck their limbs against their bodies and increase undulation frequency and amplitude just

like a *Polypterus* increasing swim speed. The transition in *Polypterus* from swimming to walking, however, adds some complexity to the system because body oscillations increase and fin oscillation switches from synchronous oscillation to contralateral “stepping” (Standen et al., 2014; Standen et al., 2016). Similarly, salamanders switch from “synchronous” (inactive) limbs during swimming to contralateral stepping. If the underlying axial CPGs are always active, in both animals, mechanical constraints such as changes in friction and increased force regimes could be responsible for the differences in kinematics between slow swimming and walking.

Mechanical constraint may also influence the axial waveform of both *Polypterus* and salamanders as they move from an aquatic to terrestrial environment, or from having four to two limbs. In a salamander, limbs are used to lift the body away from ground frictional forces, focusing force constraints at the girdles, and driving the standing wave gait. In *Polypterus*, pectoral fins have limited ability to lift the body, thus frictional forces are experienced strongly by both fins and body, causing “stepping” in the pectoral fins and an increased axial oscillation in the tail. Even if the base signal from the brain to the axial CPGs remains a traveling wave, mechanical constraints at the pectoral and pelvic girdles in a salamander, and at the pectoral girdle and the tail in the fish, could constrain the traveling wave and cause a shift to a more standing form. In the salamander this becomes a true standing wave, while in the *Polypterus*, the posterior force concentration is more spread out and closer to the tail, resulting in a hybrid body wave that has both standing and traveling wave components. When the salamander lacks hind limbs, it too has a less concentrated posterior constraint. The elevation ability of the forelimbs reduces the impact of this change and the result is an increase in body waves that resemble the waves seen along the body during *Polypterus* swimming rather than walking. Interestingly, underwater walking in *S. lacertina*, a salamander that lacks hind legs, also shows a traveling axial body wave that accompanies forelimb stepping (Azizi and Horton, 2004). All of this together could mean that the axial CPG is always active as the base

controller for locomotion in vertebrates. The changes we see are only a result of changes in loading regimes which cause spikes in sensory feedback from various appendages and body parts.

Insights for the Control of Limbed Robots

In nature, salamanders deal with perturbations, including limb loss, quickly and seamlessly enough to survive. Currently, there are few robots that can deal with such an extreme perturbation as the loss of two out of four limbs without pre-programmed or computationally expensive control regimes. When a salamander loses its limbs, the entire gait changes from a standing wave in intact salamanders, to a hybrid traveling-standing wave in amputated animals. The addition of these undulations at the nose and pectoral girdle seems to keep the center of mass of the animal moving forward (Figure 7). So, rather than focus on exact limb placement, the animal is prioritizing overall forward movement.

Limbed robots could use the same strategy to deal with damaged or lost limbs. Rather than pre-programming exact leg placements, there could be a greater focus on center of mass movement. Some robots, such as Salamander Robotica (Crespi et al., 2013) already have the ability to transition to a new gait when moving from land to water using sensory feedback and an increase in axial CPG frequency. A similar control scheme could be implemented when limbs are lost. Perhaps an inertial measurement unit (IMU) placed at the center of mass could drive rotations and undulations at key points, such as the nose, pectoral, and pelvic regions. Feedback from these points in conjunction with current advances in control algorithms (Santos and Matos, 2012; Koos et al., 2013; Kano et al., 2019) could allow the robot to tune a baseline axial CPG into a hybrid gait suitable for whatever force environment it's in. Then, the robot could not only transition from aquatic to terrestrial locomotion but also deal with a range of perturbations from bumps in the road to loss of body parts. A robot with such a controller could be deployed to a much larger range of terrains, making it ideal for exploration of unknown environments.

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DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the University of Ottawa aquatic animal facility under Animal Care Protocol number BL-1926.

AUTHOR CONTRIBUTIONS

CD analyzed the data, made the figures, wrote the initial draft, and finalized the submission. KL collected salamander and polypterus data, did the statistical analysis, and edited the final draft. KG collected salamander data. ES supervised the project, collected salamander data, lead the writing of the discussion section, and edited the final draft.

FUNDING

This work was funded by the Human Frontier Science Program (No. HFSP-317 RGP0027/2017) and the University of Ottawa Undergraduate Research Opportunity Program 318 (UROP).

ACKNOWLEDGMENTS

We would like to thank Martin De Langy and Linfang Han for their help in organizing data for this work. We would also like to acknowledge the Human Frontier Science Program (HFSP-RGP0027/2017) and the University of Ottawa Undergraduate Research Opportunity Program (UROP) for funding this research.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Hybrid Parallel Compliance Allows Robots to Operate With Sensorimotor Delays and Low Control Frequencies

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OPEN ACCESS

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Specialty section:

This article was submitted to
Computational Intelligence in Robotics,
a section of the journal
Frontiers in Robotics and AI

Received: 23 December 2020

Accepted: 26 May 2021

Published: 16 June 2021

Citation:

Ashtiani MS, Aghamaleki Sarvestani A
and Badri-Spröwitz A (2021) Hybrid
Parallel Compliance Allows Robots to
Operate With Sensorimotor Delays and
Low Control Frequencies.
Front. Robot. AI 8:645748.
doi: 10.3389/frobt.2021.645748

Animals locomote robustly and agile, albeit significant sensorimotor delays of their nervous system and the harsh loading conditions resulting from repeated, high-frequent impacts. The engineered sensorimotor control in legged robots is implemented with high control frequencies, often in the kilohertz range. Consequently, robot sensors and actuators can be polled within a few milliseconds. However, especially at harsh impacts with unknown touch-down timing, controllers of legged robots can become unstable, while animals are seemingly not affected. We examine this discrepancy and suggest and implement a hybrid system consisting of a parallel compliant leg joint with varying amounts of passive stiffness and a virtual leg length controller. We present systematic experiments both in computer simulation and robot hardware. Our system shows previously unseen robustness, in the presence of sensorimotor delays up to 60 ms, or control frequencies as low as 20 Hz, for a drop landing task from 1.3 leg lengths high and with a compliance ratio (fraction of physical stiffness of the sum of virtual and physical stiffness) of 0.7. In computer simulations, we report successful drop-landings from 3.8 leg lengths (1.2 m) for a 2 kg quadruped robot with 100 Hz control frequency and a sensorimotor delay of 35 ms.

Keywords: legged robots, parallel and passive compliance, hybrid actuation and leg design, sensorimotor delay, Feedback, latency, parallel elastic actuation

1 INTRODUCTION

Animals use muscle-tendon networks, which they control by spinal circuits, the brainstem, and with sensory feedback to produce joint torque and work for legged locomotion (Forssberg et al., 1977; Grillner and Wallen, 1985; Biewener, 1989; Ijspeert, 2008; Takakusaki et al., 2016; Stratmann et al., 2018). The response time for muscle action caused by an external stimulus is related to axonal conduction velocity and animal body weight, and the resulting sensorimotor delay can be as slow as 41 ms in a 4 kg, cat-sized animal (More et al., 2010; Franklin and Wolpert, 2011; More and Donelan, 2018). House cats run with up to 5 Hz locomotion frequency (Bertram et al., 2014). At an assumed duty cycle of 0.4 the stance phase lasts 80 ms, and the animal would be sensor-blind for half its stance phase, i.e., during the entire force ramp-up time. We often assume feedback to be critical in challenging conditions like in rough terrain locomotion. However, running birds and other animals traverse hidden perturbations with ease, albeit limited sensorimotor capabilities (Daley et al., 2006; Ernst et al., 2018).

Animal locomotion control is simplified by a morphology with tendons and muscles with intrinsic physical stiffness (Alexander, 1990; Blickhan et al., 2007a). Physical elasticities mounted serially like tendons can lead to under-actuation and reduced controllability. However, animals show no obvious signs of decline in robustness, responsiveness, or agility. Many muscle-tendons are part of

more extensive networks with parallel muscle-tendon units, requiring sensorimotor coordination (Lombard, 1903; Hutchinson et al., 2005). This raises two questions: For parallel mounted active and passive stiffness, how do animals deal with significant sensorimotor delays (**Figure 1A**)? And how are legged robots impacted (**Figure 1B**)? This section briefly reviews concepts from biomechanics and legged robotics dealing with sensorimotor delays, the control of leg forces, especially at leg impacts, and active and passive joint stiffness. In the main part of this work we present a robotic proof-of-concept characterizing parallel active and passive stiffness as one source of robustness against adverse conditions for feedback controllers.

Inspired by animal morphology and passive and active leg stiffness, legged robot designs often include mechanical springs (Nasiri et al., 2016; Ambrose and Ames, 2020). Series elastic actuation (SEA) can simplify control, improve robustness and interaction safety, and protect actuators from overloads (Raibert et al., 1984; Robinson et al., 1999; Pratt and Krupp, 2004; Hutter et al., 2011; Calanca et al., 2015; Hutter et al., 2016; AhmadSharbafi et al., 2020). Designs with parallel mounted springs and actuators (parallel elastic actuation, PEA) can increase leg forces, improve locomotion energy efficiency, and reduce actuator loading (Gunther et al., 2015; Niehues et al., 2015; Plooi et al., 2016; Yesilevskiy et al., 2016; Liu et al., 2018; Toxiri et al., 2018; Yesilevskiy et al., 2018; Roozing et al., 2019; Ambrose and Ames, 2020). Combined parallel and serial elastic designs have been proposed, leading to reduced peak torques and improved locomotion applicability (Grimmer et al., 2012). Leg stiffness is altered mechanically in several ways; decoupling actuator and spring action during the locomotion cycle can simplify control and improve energy efficiency (Wiggin et al., 2011; Spröwitz et al., 2013). Variable elastic mechanisms augment physical stiffness for efficient actuation (Choi et al., 2011; Mathijssen et al., 2014; Braun et al., 2016). Until today, it remains challenging to effectively alter and rapidly manipulate compliance under high loads while keeping the mechanisms compact, robust, and lightweight.

Serial and parallel elastic-legged robots can locomote by feed-forward control and without system state knowledge from feedback (Iida and Pfeifer, 2004; Narioka et al., 2012; Spröwitz et al., 2018; Ruppert and Spröwitz, 2019). However, passive, compliant designs are under-actuated and show limited controllability. Parallel elastic designs can maintain good control authority; when controllability is more needed than spring-based natural dynamics, the actuator overrides the spring's action (Verstraten et al., 2016). Usually, parallel elastic legs are designed with strong springs providing all essential torques and forces. Consequently, strong, relatively heavy, and fast actuators are required to override springs.

Legged robots with proprioceptive actuation and sensing and quasi-direct drives feature the highest control authority, compared to passive and partially actuated designs (Seok et al., 2012; Ding and Park, 2017; Park et al., 2017). These legged machines are agile and fast, they jump high, and land robustly (Park et al., 2017; Grimmering et al., 2020). From a sensorimotor perspective, proprioceptive actuators require 1) low communication and control delays in the range of a few

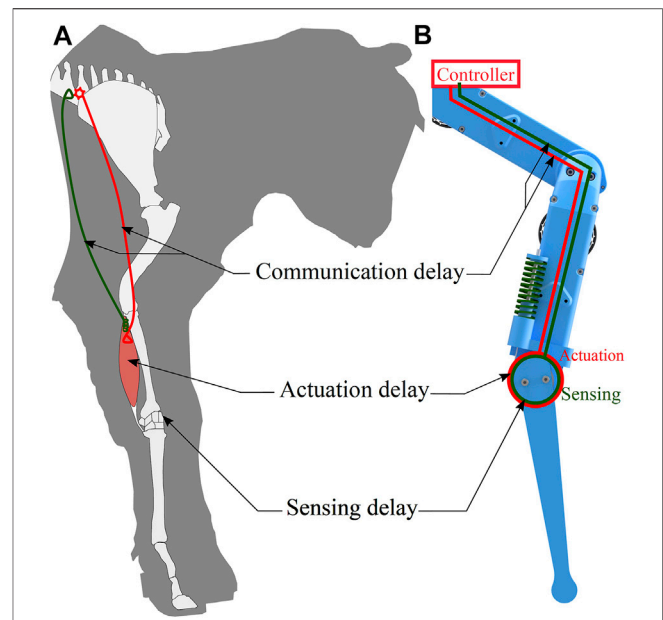


FIGURE 1 | (A) Animal locomotion control is subject to sensorimotor delays from sensing, communication, and actuation. The drawing is loosely inspired by Figure 1 of More and Donelan (2018). **(B)** Robots typically have lower intrinsic delays from electronic sensing and communication. Instead, delays are caused, for example, by filtering noisy data. We systematically tested robot controllers with varying sensorimotor delay and control frequency. We hypothesized that a hybrid system comprised of passive joint elasticity and parallel active joint stiffness can reject sensorimotor delays robustly, for appropriate compliance ratios.

milliseconds allowing 2) high-frequency control above 500 Hz, 3) accurate force and joint speed sensing, 4) and precise touch-down sensing (Bledt et al., 2018; Grimmering et al., 2020; Li et al., 2020). Not all conditions are always met, especially in unknown terrain and during harsh touch-downs, when actuator gains are changed, and when sensor noise indirectly causes feedback delays (Hubicki et al., 2016; Hammoud et al., 2020).

Robot force sensors are affected by leg impacts loading legs from zero to multiple body weights in a few ten milliseconds, and leading to wobbling masses (Günther et al., 2003; Mo et al., 2020). Impact vibrations transfer to the sensor's mechanics and appear as sensor noise requiring processing (Spröwitz et al., 2018; Grimmering et al., 2020). Low-noise leg force sensors are being developed, yet there remains a trade-off between sensitivity and specificity, sensor noise from impacts, and sensor weight and complexity (Ananthanarayanan et al., 2012; Hutter et al., 2014; Grimmering et al., 2020; Ruppert and Badri-Spröwitz, 2020). Noisy force data can be filtered to identify touch-down and leg loading uniquely, but filtering adds to the overall sensorimotor delay; for example, delays of 31 ms are documented to uniquely identify touch down with proprioceptive sensing (Grimmering et al., 2020). Monitoring the deflection of physical joint elasticity provides alternative leg loading information, for example, for virtual model control (Pratt et al., 1997). Virtual damping assumes precise speed estimation, but numerically differentiating noisy signals

requires filtering for sufficiently smooth signals, leading to feedback delay (Flacco et al., 2012; Hammoud et al., 2020).

Robot-internal electrical communication is limited only by the speed of light, and with relatively short wire lengths communication delays are minimal. Contrary, teleoperation between operator and legged robot over long-distance can lead to significant feedback delays (Varkonyi et al., 2014). Dedicated force feedback control can robustly deal with limited delays; beyond that, control destabilizes (Lee and Spong, 2006; Shafiee-Ashtiani et al., 2017; Shafiee et al., 2019). The applicability of high-level locomotion planners is related to control frequency and therefore also to sensorimotor delay; current planners run on time for control frequencies above 100 Hz (Ponton et al., 2018; Mastalli et al., 2020). Legged robots intrinsically tolerating low control frequencies are therefore good candidates for complex online locomotion planners.

Besides virtual and physical springs, both virtual and physical damping have been applied to control legged locomotion, also as part of impedance control (Seok et al., 2012; Boaventura et al., 2013; Nagayama et al., 2016; Park et al., 2017; Heim et al., 2020; Mo et al., 2020). By dissipating excess potential and kinetic energy and producing damping forces, leg reaction forces are adapted, and post-impact oscillations are reduced (Blickhan et al., 2007a; Haeufle et al., 2014; Semini et al., 2015). Virtual damping control requires precise speed estimation, which makes the method brittle in the presence of sensor noise (Bledt et al., 2018; Hammoud et al., 2020). Mechanical leg dampers are immune to feedback delays and sensor noise but must actively be switched off when not required (Mo et al., 2020).

In animals, upper limb control is subject to sensorimotor delays, like during manipulation tasks. Humans and other animals manipulate objects by exploiting muscle-tendon elasticities, effectively changing joint stiffness (Franklin et al., 2004). Antagonistic pairs of muscle-tendons can be prestressed by feed-forward ('preflex') control, leading to increased joint stiffness for a given posture independent from feedback delay, but with limited movement range (Hogan, 1984; Crevecoeur and Scott, 2014). Alternatively, reflexes can alter joint stiffness. Mouel and Brette (2019) show that increased joint stiffness should be compensated for by reduced sensorimotor gains; otherwise, delayed feedback leads to unstable behavior. Setting joint impedance through feed-forward sensorimotor commands might allow stable upper limb postures with noisy state estimation (Berret and Jean, 2020). Upper limb manipulation and lower limb locomotion tasks differ in their respective loading scenarios. Most manipulation tasks are continuous, while legged locomotion is always hybrid and non-continuous. Leg forces and loading times depend on body weight and drop height. The leg forces in this work ramp up from zero to body weights within 0.1 s and lead to joint angle changes above 45°. End-effector forces during manipulation are typically within the range of the object's weight instead of the user's body weight (Crevecoeur and Scott, 2014).

In this work, we aim to merge two diametrical principles while maintaining their best properties; 1) Passive leg joint compliance that works without feedback and at low control frequency, and 2)

active joint compliance providing control authority. We hypothesize that, for a given robot design and locomotion task, there exists a range of compliance ratios—a 'hybrid' range—that works best despite significant feedback delays and low control frequencies.

This work uniquely contributes as follows; We systematically characterized the full range of active-to-passive parallel compliance ratios for a given total leg joint compliance. We simulate adverse controller conditions in simulated and hardware drop landings, including significant feedback delays, low control frequencies, and varying duty cycles. Previous work in parallel-elastic legged robotics typically investigated parallel compliance with high-frequency and low delay actuation (Mazumdar et al., 2016).

In **Section 2**, we present a stability analysis of a simplified model in the presence of sensorimotor delays, for two ratios of parallel compliance. We then present computer simulations and hardware experiments and investigate the effect of control frequencies, sensorimotor delays, and duty cycles on a robot leg with varying ratios of parallel compliance, for drop-landings (**Section 3**). We also characterize a simulated quadruped robot made of four of these legs, for multiple drop-landing heights. We discuss the work in **Section 4**, and conclude in **Section 5**.

2 MATERIALS AND METHODS

We quantify the total (sum of) system compliance as active compliance in parallel to passive (spring-based) compliance, acting at the knee joint (**Figure 1B**):

$$K_{\text{total}} = K_{\text{active}} + K_{\text{passive}} \quad (1)$$

where K_{passive} [Nm/rad] is the joint's passive rotational stiffness, K_{active} [Nm/rad] is the joint's active, virtual, rotational stiffness produced by the actuator. K_{total} [Nm/rad] is the summed up rotational joint stiffness. We define a 'compliance ratio' λ_{passive} as the ratio of passive stiffness and total stiffness:

$$\lambda_{\text{passive}} = K_{\text{passive}} / K_{\text{total}} \quad (2)$$

Hence, for a compliance ratio $\lambda_{\text{passive}} = 0.1$ the knee spring supplies 10% of the knee torque to carry the robot, and the knee actuator supplies the remaining 90%. A λ_{passive} of 1.0 indicates a knee joint with a physical spring and no motor.

2.1 Theoretical Analysis of a Simplified, Reduced Model of an Actuated Pendulum

We analyzed a simplified system with parallel compliance, to analytically quantify the effects of sensorimotor delays. The reduced order model consists of a strut-like leg mounted as a single degree-of-freedom pendulum and represents a simplified robot lower leg (**Figure 4A**). The equations governing the pendulum motion are:

$$I\ddot{\theta} + mgL \cdot \sin(\theta - \theta_0) + K_{\text{passive}}(\theta - \theta_0) + D\dot{\theta} = \tau_m \quad (3)$$

where $D = 0.14 \text{ Nms/rad}$ is the system damping, K_{passive} is the stiffness of the parallel compliant element, $L = 0.16 \text{ m}$ is the center of mass distance to the pivot point, $m = 0.5 \text{ kg}$ is the mass, $I = mL^2$ is the moment of inertia, g is the standard gravity, and θ_0 is the equilibrium joint angle of the relaxed spring. We set a total stiffness of $K_{\text{total}} = 1.15 \text{ Nm/rad}$. The instantaneous joint angle is θ , and τ_{knee} is the knee joint control torque input, implemented as active compliance:

$$I\ddot{\theta} + mgL \cdot \sin(\theta - \theta_0) + K_{\text{passive}}(\theta - \theta_0) + D\dot{\theta} = -K_{\text{active}}(\theta_{\text{feedback}} - \theta_0) \quad (4)$$

where K_{active} is the active motor compliance. The sensor reads the joint angle θ_{feedback} . We assume a small enough angular deviation of the pendulum around the equilibrium point: $\sin(\theta - \theta_0) \approx (\theta - \theta_0)$, which allows to write Eq. 4 as a linear differential equation. We converted Equation 4 to the Laplace domain and incorporated a fixed feedback time delay t_d of the control input (active compliance). The resulting closed-loop system transfer function can be presented in the frequency domain as:

$$\frac{\Theta_s}{\Theta_{ds}} = \frac{K_{\text{active}}e^{-t_d s} + mgL + K_{\text{passive}}}{s^2 I + Ds + K_{\text{active}}e^{-t_d s} + K_{\text{passive}} + mgL} \quad (5)$$

We linearized the system's exponential time delay term with a third-order Padé approximation. A system pole analysis of this simple system provides an intuitive understanding of the effects of two compliance ratios for a given total joint stiffness on closed-loop stability, and for given sensorimotor delays.

2.2 Computer Simulation of Articulated Robot Legs

We characterized a single, articulated robot leg with hybrid joint compliance. Drop landings are one of the most challenging tasks due to high, impulse-like ground reaction forces, and nonlinear and hybrid leg loading. Drop landing is similar to a step response perturbation, which is a conventional control theory tool to characterize black box systems. We computer simulated the robot leg in PyBullet (Coumans and Bai, 2019), and performed extensive drop-landing simulations for a broad range of sensorimotor delays, duty cycle frequencies, and λ_{passive} . We simulated a single leg and a quadruped robot, both modified from the open-source quadruped robot Solo (Griminger et al., 2020).

In Figure 2, we show the control and sensorimotor strategies tested. The black curve is the schematic, desired knee motor torque trajectory. The control frequency (step-like, brown line) is measured in commands per second. For reference, the control frequency of proprioceptive actuation in legged robots is often around 1 kHz, i.e., a cycle period takes $dt_{\text{control}} = \frac{1}{f} = 1 \text{ ms}$. We are especially interested in investigating scenarios with control frequencies well below 1 kHz.

Torque is applied with three strategies; First, the activation duration $dt_{\text{activation}}$ is defined as the time period between control

commands, i.e., $dt_{\text{activation}} = DC \times dt_{\text{control}}$. The activation duration lasts at least 1 ms and at most $\frac{1}{f}$. For $dt_{\text{activation,min}}$, the control command is applied for a period of 1 ms and then reset to zero. For $dt_{\text{activation,max}}$, the actuator will maintain its value until the control command is updated (Figure 2A, brown line). Second, we applied a sensorimotor delay to the control command (Figure 2B). Third, the force-activity relationship of muscles is not fully understood (Roberts and Gabaldón, 2008), and we included tests with varying duty cycles, defined as the fraction of dt_{control} with a non-zero actuator torque (Figure 2C).

The active compliance controller knee joint input is:

$$\tau_{\text{knee,motor}} = K_{\text{total}}(1 - \lambda_{\text{passive}})(\theta_{\text{feedback,knee}} - \theta_{0,\text{knee}}) \quad (6)$$

To simulate the spring in PyBullet, we implemented a knee joint spring torque:

$$\tau_{\text{knee,spring}} = K_{\text{total}}(\lambda_{\text{passive}})(\theta_{\text{knee}} - \theta_{0,\text{knee}}) \quad (7)$$

2.3 Setup Hardware Experiments

We modified a single leg of the eight degree-of-freedom (8-DOF), open-source, quadruped robot 'Solo' (Griminger et al., 2020). The leg has two active degrees of freedom, one at the hip and one at the knee. Both leg segments are 0.16 m long, the lower leg mounts a semi-circular foot of 15 mm radius. A brushless motor (Antigravity MN4004-kv380, T-Motor) drives a two-stage belt transmission with an overall 9:1 gear ratio for each active joint. An optical encoder (AEDT-9810-T00, Avago) measures the motor's rotor position, which is recalculated into joint angles. We mounted physical springs in parallel to the knee joint (SWY 16.5–30 for $\lambda_{\text{passive}} = 1.0$, SWY 16.5–45 for $\lambda_{\text{passive}} = 0.67$, SWY 16.5–80 for $\lambda_{\text{passive}} = 0.37$, Misumi). The spring's tendon inserts into a knee joint pulley with radius 18.9 mm (Figure 3B). The spring mount allows rapid exchange of springs between experiments.

To simplify the touch-down scenario, the robot leg was dropped guided by a vertical rail (Figure 3A). The hip joint was constrained to follow half of the knee joint angle at all times, controlled by a position controller creating foot contact vertically below the hip joint. We recorded the vertical hip position with two draw-wire sensors (LX-PA-40, WayCon) mounted above and below the robot, to cancel out single sensor force bias. The hip position allows quantifying the robot's landing behavior and characterizing hybrid compliance. The hip position was sampled by an analog-to-digital (A/D) converter on the brushless motor driver board. The motor board sends motor position and vertical position data to the PC communication board, via a serial peripheral interface (SPI). The PC communication board connects the motor driver board via EtherCAT to a PC (Intel Xeon(R) W-2145 CPU, 3.7 GHz, 16 cores, 64 bit, 62.5 GB Ram, Ubuntu 18.04). We wrote a Python wrapper to control the robot. The Python wrapper timestamps and saves joint angles, motor currents, and hip height into a text file. We analyzed and plotted data in Matlab.

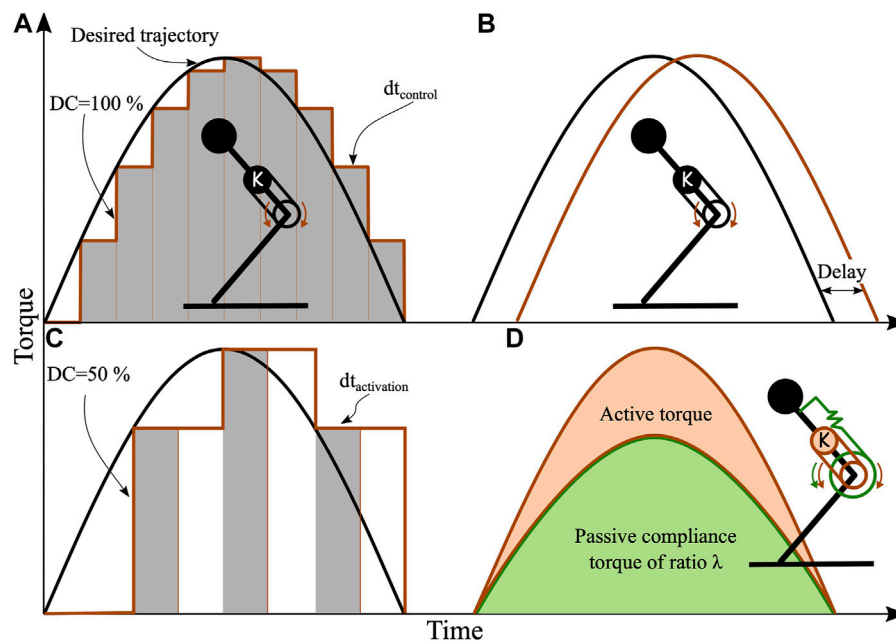


FIGURE 2 | Knee motor command for different combinations of control frequency, duty cycle, and sensorimotor delay. **(A)** A 100% duty cycle at low control frequency. **(B)** A set sensorimotor delay between the desired knee output torque, and the commanded output torque. **(C)** A 50% duty cycle. **(D)** An example for a compliance ratio of $\lambda_{passive} \approx 0.75$ is shown. The mechanical knee spring produces three quarter of the total knee torque (green). The knee actuator is programmed as a virtual spring producing the remaining torque (brown).

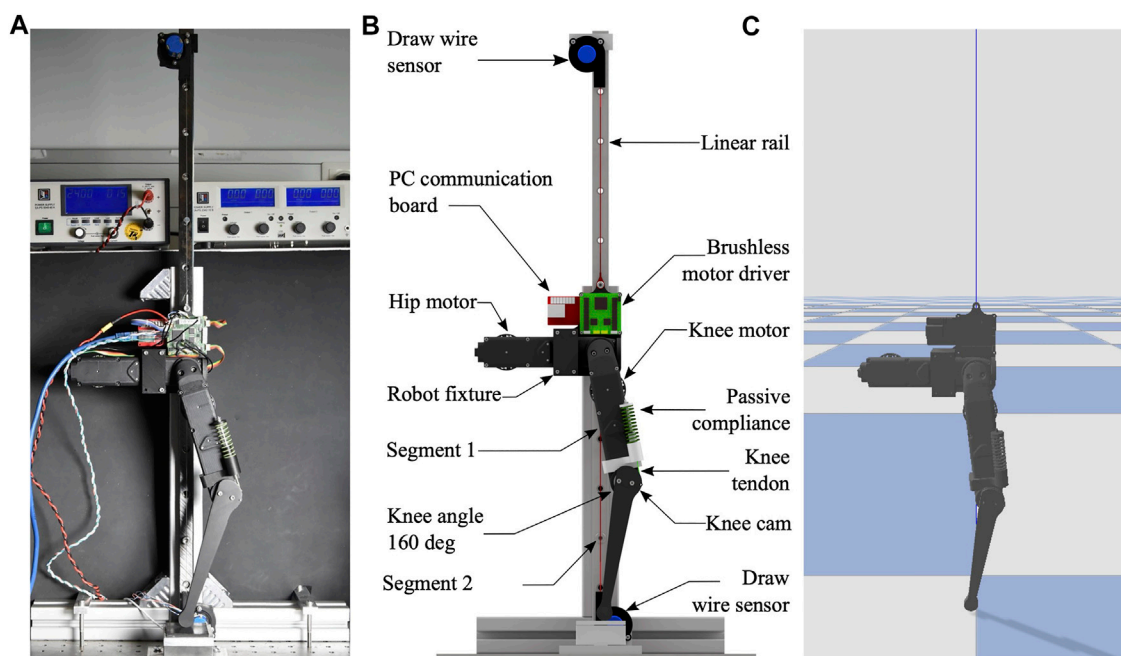


FIGURE 3 | Experimental setup. **(A)** The 2-DOF hybrid compliant leg. The one-directional spring (passive compliance) extends the knee joint via a knee tendon and a knee pulley. Knee springs with varying stiffness were mounted during the experiments, supporting between 0 and 100% robot's weight. A rail guides the robot's vertical drop, and a pair of potentiometers measures the robot's height. The knee motor produces torques in parallel to mounted knee spring. **(B)** Setup details, computer aided drawing. **(C)** The Unified Robot Description Format (URDF)-based model of the hybrid compliant robot leg, simulated in PyBullet.

3 RESULT

This section initially presents results from the pendulum task. We then show computer simulation results with a single robot leg and hybrid joint compliance. We simulated quadruped-robot drops from multiple heights, and we present hardware experiment results with a single leg mounted to a vertical slider.

3.1 Hanging Pendulum Analysis, Simplified Model

The pendulum pole analysis shows that for $\lambda_{\text{passive}} = 0$ and with increasing feedback delay, the dominant system poles move from their stable region toward the unstable region at the imaginary axis (**Figure 4B**). For medium compliance ratios, the rate of divergence is lower. The step response indicates that increasing the sensorimotor delay with active control ($\lambda_{\text{passive}} = 0.0$) leads to continuous oscillations, and resonance eventually destabilizes the system (**Figure 4C**). For hybrid passive compliance and a feedback delay of 20 ms, the closed-loop response is stable and smooth (**Figure 4D**).

The pendulum example is a simplification allowing a pole analysis with few parameters, but with an intuitive interpretation; **Figure 4B** shows when parameters lead to destabilization, with a clear cross-over into the unstable regime. The robot leg computer simulations in the following sections require more elaborate interpretation, but are more precise in terms of mechanics, and less simplified. Instead of continuous time analyses, time-discrete analyses are also applied for simplified systems, and we briefly provide results of a time-discrete analysis of the pendulum example in the **Supplementary Material** section for the interested reader.

3.2 Single-Leg Computer Simulation

We studied the effects of varying combinations of sensorimotor delay, control frequency, and compliance ratio λ_{passive} on controller performance during landing. We initially recorded a reference hip height trajectory dropping the robot leg with $\lambda_{\text{passive}} = 1.0$, which settled after 0.35 s at a hip height of 33 cm (**Figure 5**).

We then performed computer simulations to quantify the viability of the landing task, varying λ_{passive} from 0.0 to 1.0 in steps of 0.05, the sensorimotor delay from 0 to 60 ms in steps of 5 ms, and sensorimotor control frequencies of 20, 50, 100, 250, and 1,000 Hz. We tested duty cycles of 25, 50, and 100%.

In PyBullet, we set joint damping values of 0.01 Nms/rad and 0.05 Nms/rad for hip and knee, respectively. A single leg weighs 0.6 kg, and the quadruped robot 2.0 kg. We chose the total knee joint stiffness so that leg length changed by 10% during the first mid-stance, after dropping it from 42.5 cm. We implemented a $\lambda_{\text{passive}} = 1.0$ with a spring of stiffness $K = 4680$ N/m acting on the knee pulley of radius $r = 18.9$ mm, leading to a rotational stiffness of $Kr^2 = 1.67$ Nm/rad. We defined settling time as the difference between the initiated drop time and the hip position stabilizing within a $\pm 1\%$ margin of the settling hip height after 3 s simulation time. We applied the Matlab function *stepinfo* for this analysis. We used twice the $\lambda_{\text{passive}} = 1.0$ value as the global settling time

(0.7 s) and defined 90% of the passive compliant $\lambda_{\text{passive}} = 1.0$ settling hip height as minimum final hip height (30 cm).

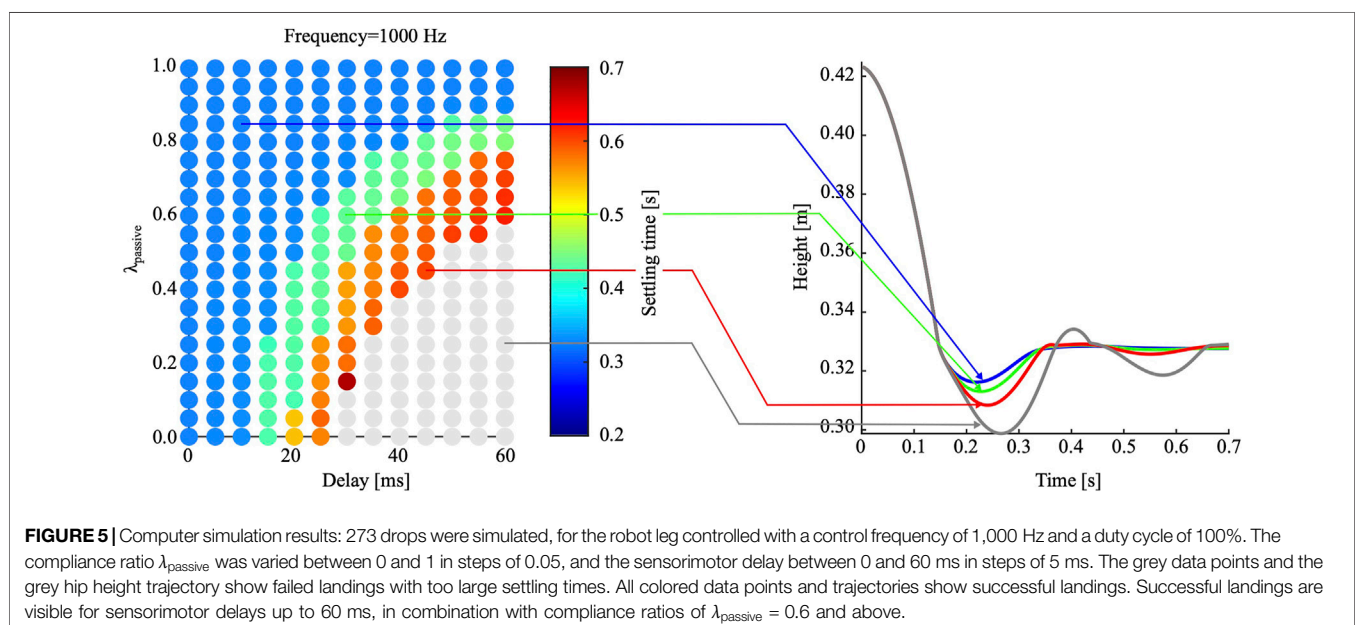
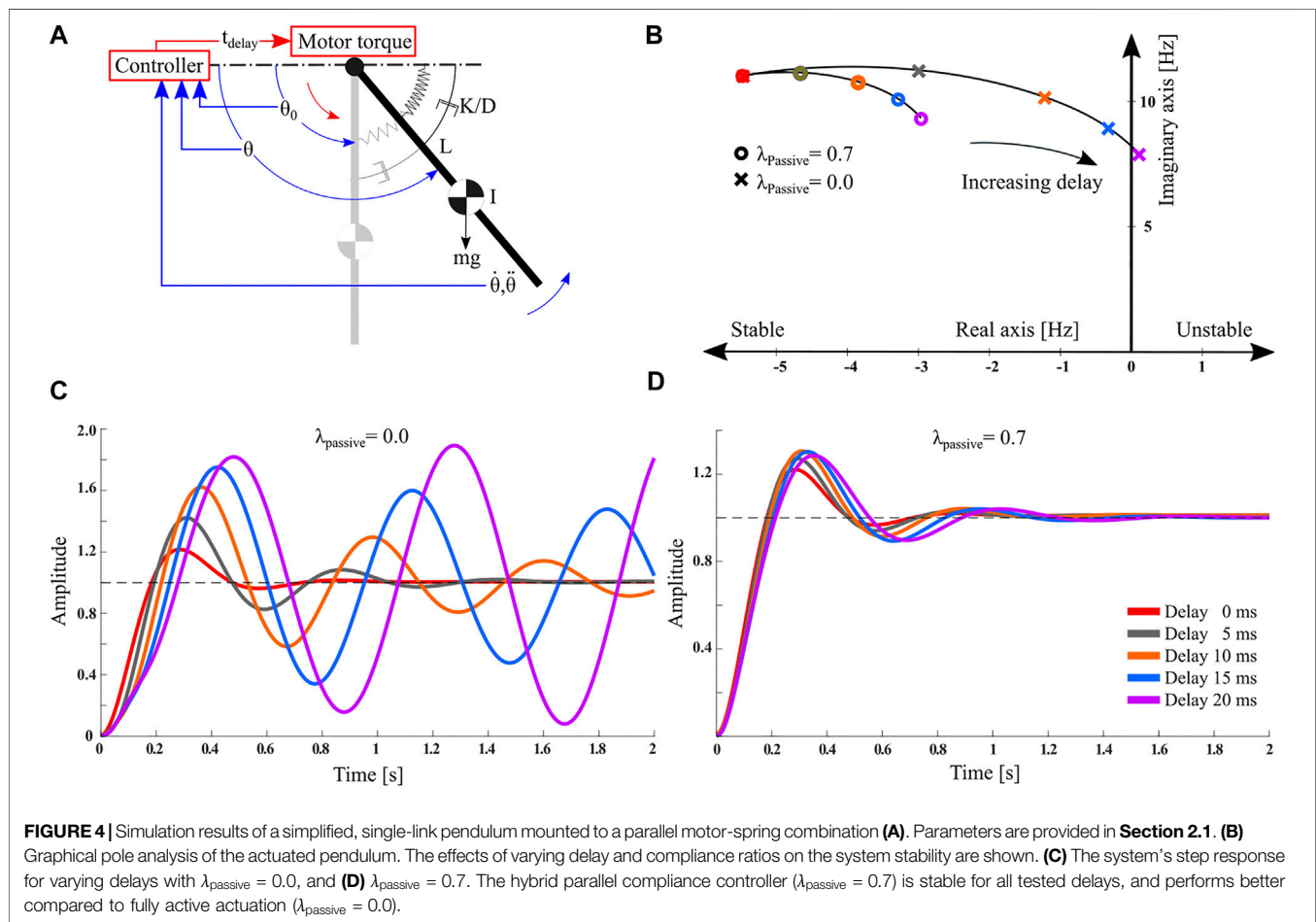
In **Figure 5**, the results of 273 drop-landing simulations are shown, with varying sensorimotor delays and λ_{passive} settings, a 100% duty cycle, and a control frequency of 1 kHz. Grey data points represent failed landings with a settling time higher than 0.7 s or too low settling hip heights. For full active actuation ($\lambda_{\text{passive}} = 0.0$), and when increasing the sensorimotor delay above 25 ms, all landings fail. For $\lambda_{\text{passive}} > 0.4$, the leg lands successfully in the presence of 40 ms delays. Results show that the hybrid compliant leg has successful intermediate regimes allowing for relatively large sensorimotor delays, with an appropriate combination of passive and active compliance.

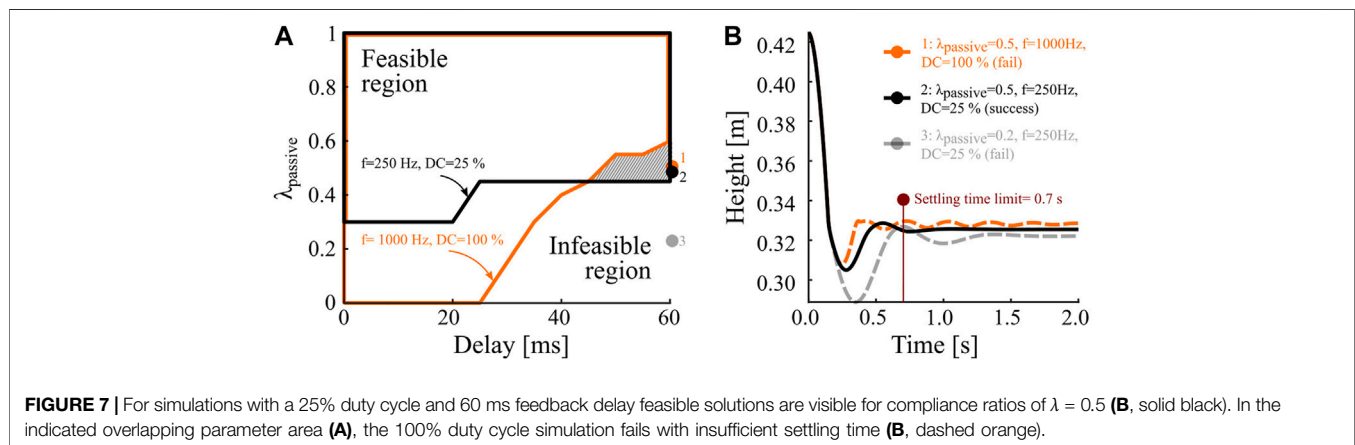
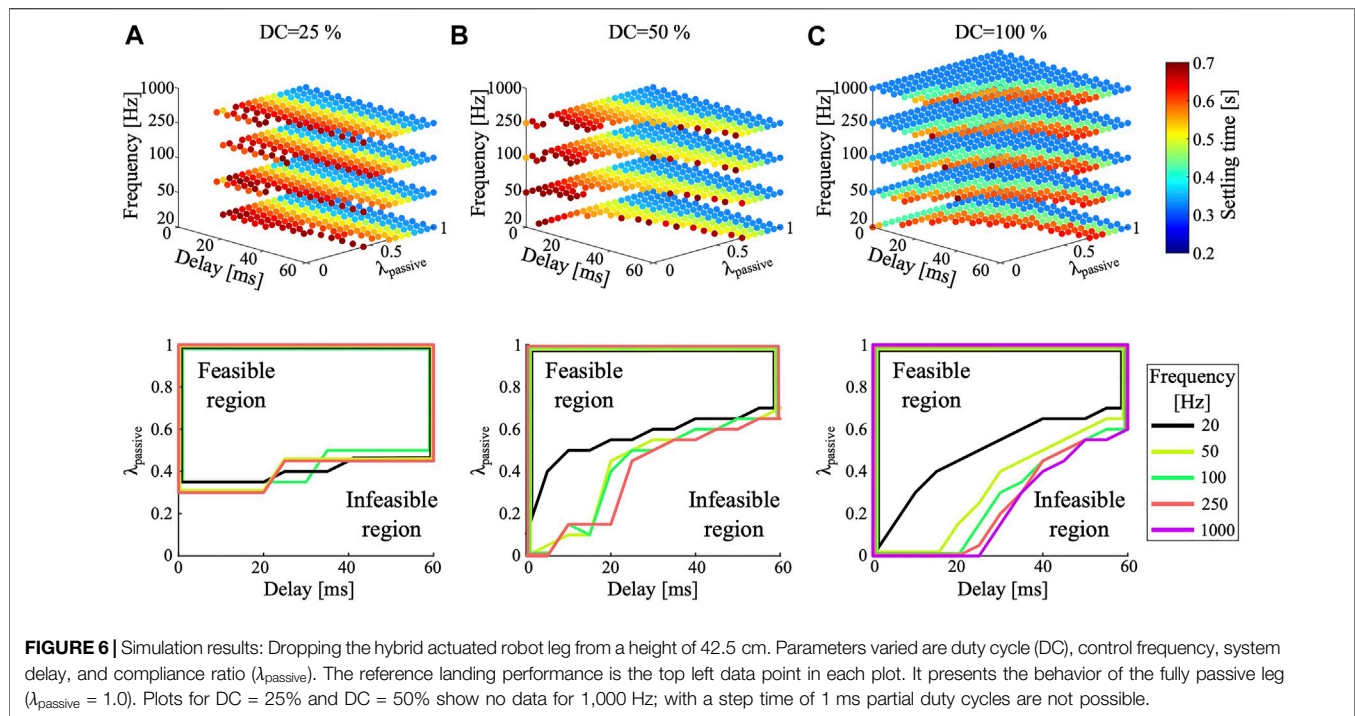
We then investigated the effect of varying control frequency (20, 50, 100, 250, and 1,000 Hz) and duty cycle (25, 50, and 100%, **Figure 6**). Most visible is a decreasing feasible area for all three duty cycles at reduced control frequencies. Comparing duty cycles of 25 and 100% (**Figures 6A,C**) shows that the feasible area did change with reduced duty cycles. Low compliance ratios ($\lambda_{\text{passive}} \approx 0.2$) lead to successful landings combined with a duty cycle of 50% or the highest control frequency (1 kHz). **Figure 6C** shows that duty cycles of 100% at control frequencies of 100, 250, and 1,000 Hz have a similar-sized feasible region. When switching to a low control frequency (20 Hz, black line) the feasible area reduces much. For a 50% duty cycle, the feasible area changes slightly when switching between 50 and 250 Hz control frequency (**Figure 6B**). The biggest changes are visible when changing from 1,000 Hz to 250 Hz, and from 50 to 20 Hz. Typically, higher duty cycle values led to better results, for otherwise identical parameters. An exception is found when comparing duty cycles of 25 and 100%. The hatched area in **Figure 7A** indicates successful landings at low duty cycles, where high duty cycle landings failed because of hip height oscillations beyond the settling time limit (**Figure 7B**). For most compliance ratios above 0.6, we observe successful landings, including critical combinations of 60 ms delay and 20 Hz control frequency. All results indicate successful landing for compliance ratios equal and higher than 0.7.

3.3 Quadruped Computer Simulation

The previous single leg simulation results indicate that with high compliance ratio, robot performance becomes largely independent of sensorimotor delay, and control frequency. But fully passive compliance reduces control authority. In seven drop-landing scenarios, we altered drop height and passive and active stiffness of a quadruped robot, to characterize system and controller performance, but also to emphasize the importance of control authority (**Figure 8**). The duty cycle was set to 100% in all quadruped robot simulations. The simulation parameters are provided in **Table 1**.

The case-1 robot simulated a compliance ratio of 1.0, i.e., fully passive elastic knee joints. The robot was dropped from a height of 0.7 m and landed successfully. The case-2 robot used identical control parameters, was dropped from 1.0 m height, and failed to land successfully. At close observation it becomes visible that its knee joints inverted after the first landing rebound, and the robot landed with inverted knee angles and without spring support.





Case-2 emphasizes the drawback of passive compliance; without control, the knee joint orientation cannot be adjusted prior to rebounding. The case-3 configuration featured a controller with full, bi-directionally active compliance (no passive compliance), and without sensorimotor delay. The controller ran at 1 kHz and successfully guided the landing. In case-4, a fully active compliant robot with 17 ms sensorimotor delay failed to land properly, which shows the vulnerability of active compliance in the presence of sensorimotor delay. Case-5 shows a successful landing scenario by combining passive and active compliance ($\lambda_{\text{passive}} = 0.67$), with 27 ms sensorimotor delay, and reduced control frequency (200 Hz). Case-6 was also configured with a $\lambda_{\text{passive}} = 0.67$, a control frequency of 100 Hz, and failed landing the robot. For case-7, we decreased the compliance ratio to

$\lambda_{\text{passive}} = 0.59$, and the robot landed successfully from a height of 1.2 m, and with a sensorimotor delay of 35 ms at a control frequency of 100 Hz. Case-7 shows how an appropriate combination of active and passive compliance at low control frequency maintains good control authority and robustness in the presence of sensorimotor delay.

3.4 Hardware Experiments

We validated the previous single-leg simulations with hardware experiments. We chose compliance ratios of $\lambda_{\text{passive}} = [0, 0.37, 0.67, 1]$ and a total rotational knee stiffness of $K_{\text{total}} = 1.67 \text{ Nm/rad}$. We then varied control frequencies ($[1000, 100, 10] \text{ Hz}$) and sensorimotor delays ($[0, 10, 20, 30, 50] \text{ ms}$). The duty cycle was set to 50% for 10

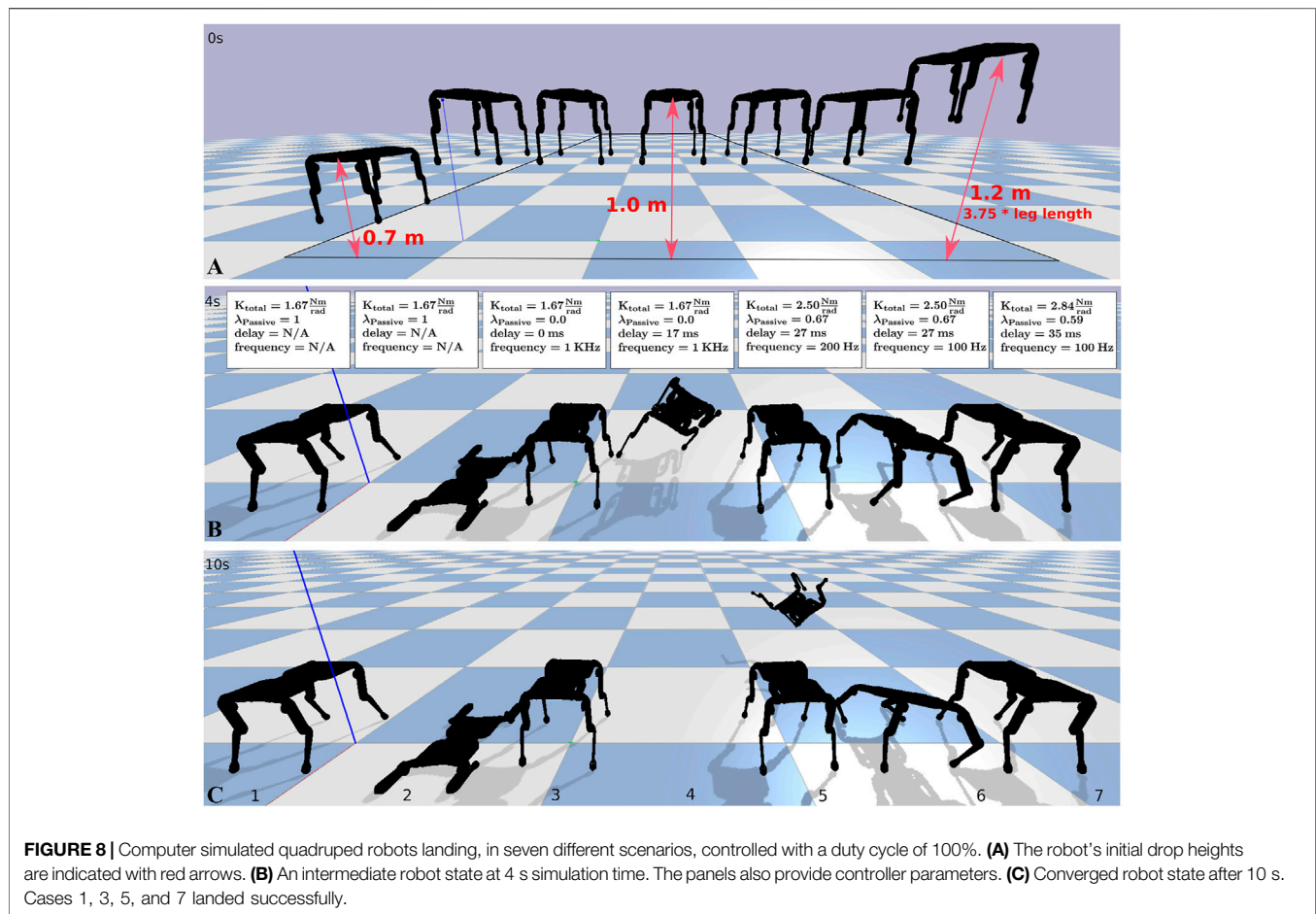


TABLE 1 | Simulation parameters of the quadrupedal robot, with a duty cycle of 100%.

Case	Total compliance (Nm/rad)	$\lambda_{passive}$ (%)	Control frequency (Hz)	Delay (ms)
1	1.6717	100	1,000	0
2	1.6717	100	1,000	0
3	1.6717	0	1,000	0
4	1.6717	0	1,000	17
5	2.5076	67	200	27
6	2.5076	67	100	27
7	2.8419	59	100	35

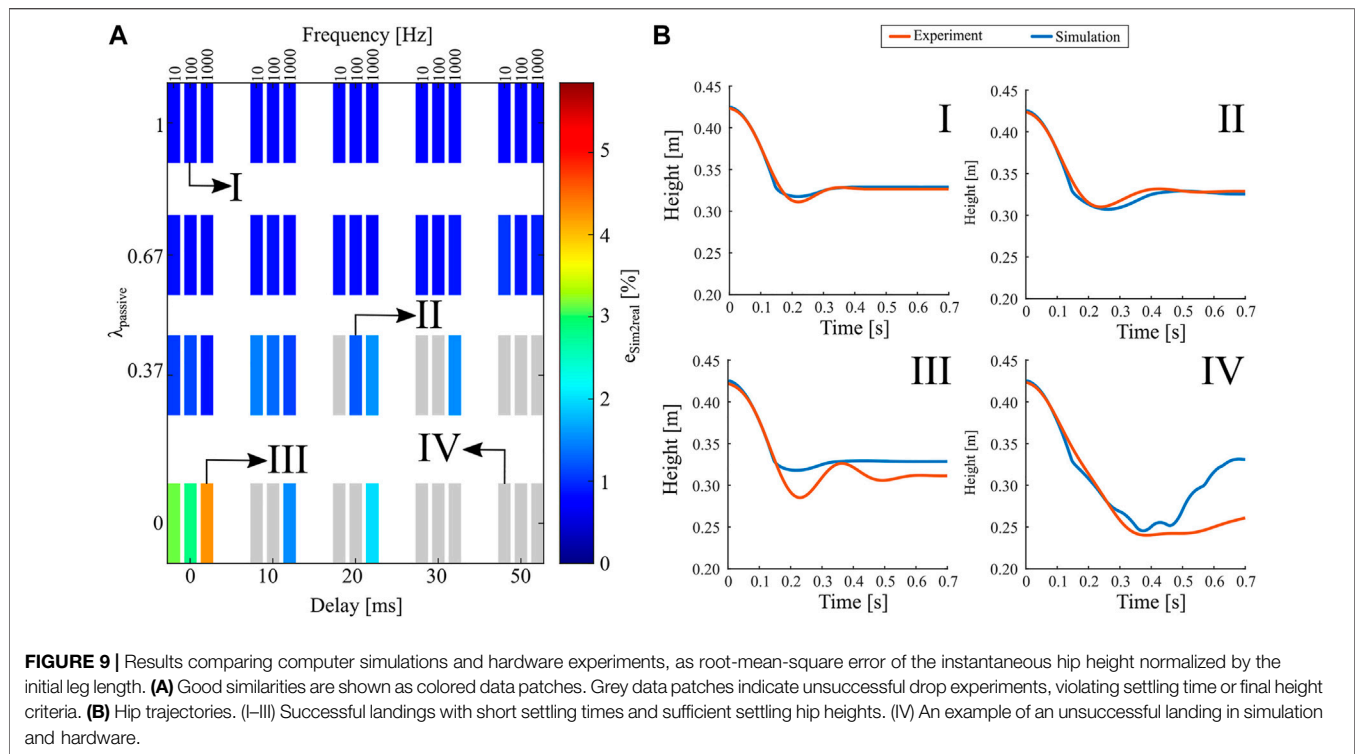
and 100 Hz control frequency, and 100% for 1,000 Hz control frequency.

In **Figure 9**, we assess the difference $e_{sim2real}$ between computer simulations and hardware experiments, as the root-mean-square error (RMSE) between two resulting hip trajectories, normalized by the maximum leg length, measured during the settling duration of 0.7 s. The criteria for successful drop landings in hardware and computer simulation are identical (**Section 3.2**). Grey colored data shows failure cases in both experiments and simulations. Viable cases with an RMSE of less than 6% (**Figure 9**) indicate good consistency between hardware experiment and computer simulation. We show four exemplary hip trajectories for varying compliance ratios

(**Figure 9, I–IV**). The first two cases are feasible landings with good consistency between simulation and experiments. In case III, the hardware experiment stabilized at a lower-than-simulation hip height but still within the required margin. Case IV is a failed drop, and neither the hardware experiment nor the simulated robot leg showed the necessary settling behavior.

4 DISCUSSION

The single-leg drop results in **Figure 5** show a continuous and gentle decrease of system robustness with increasing feedback



delay when transitioning from a fully physically springy leg toward a fully actuated leg controlled by a virtual-spring controller. Hence, parallel structures of active compliance with the correct amount of passive compliance offer one possible answer to the question of how animals counteract perturbations in the presence of large sensorimotor delays. The ratio of passive to active compliance could be permanently set genetically, formed over a lifetime by training (Fouré et al., 2012), or set when required by partial or full recruitment of slacked muscle-tendon structures (Hogan, 1984). Legged robots equally benefit from intrinsic robustness against feedback delay. We believe that compliance ratios for other designs will depend on the specific leg and controller design parameters, the locomotion task, and the required controllability. If the available control frequency is limited or high delays are expected, a higher compliance ratio can be used. In the future, we are especially interested in exploring compliance ratios of $\lambda_{\text{passive}} > 0.5$. One early design choice to consider is the effective spring deflection. Typically, stiffer springs feature a smaller deflection range possibly leading to limited joint movement range, compared to softer springs. We used springs designed for large deflections. One can also balance the knee cam radius with the spring's movement range and stiffness. We suggest the following, general procedure to establish a compliance ratio for a given task and robot:

1. Select a total joint stiffness based on the required steady state leg length, the maximum leg deflection, and the leg geometry (segment lengths, robot mass, cam radius). This step can be executed by test-mounting a $\lambda = 1$ spring (no actuator) with

given stiffness and spring slack position, dropping the robot leg, and observing its joint angles.

2. Alternatively, a simplified kinematic model can provide an estimate of the steady-state leg length (**Supplementary Material Section 3**).
3. Select a desired compliance ratio. In the examples shown, compliance ratios between 0.5 and 0.7 worked well. Low compliance ratios provide higher controllability, as long as control frequencies are high and feedback delays are low, and vice versa. Duty cycles should be set to maximum (100%), unless they are specifically exploited.
4. Check that the parallel mounted actuator has the capacity to supply the required torque and speed. Low compliance ratios (≈ 0.5) require an actuator providing a higher work and power output throughout the task. With higher compliance ratios (> 0.7) the parallel spring carries more base load. When spring dynamics must be overwritten, high actuator torques are required but typically for shorter time. For a motor-gearbox design methodology we refer to Roos et al. (2006).

This work centers around adjusting the ratio of physical, passive compliance for a given total joint compliance. Online-adjustable spring stiffness mechanisms have been proposed, but many are still bulky and heavy (Yamaguchi and Takanishi, 1997; Vanderborght et al., 2013; Wolf et al., 2015). If a locomotion task requires large changes of total joint stiffness with a constant ratio of passive compliance (Ferris et al., 1998), robust and light-weight adjustable stiffness designs will be needed. For versatile locomotion sequences like jumping, landing and fast running, learning-based

methods could extract a ‘best’ range of compliance ratios from large locomotion data sets.

We see at least three applications for hybrid compliance ratios in legged robots; 1) For legged robots which exploit natural dynamics of mechanical springs but require intermittent, high controllability for tasks like jumping or acceleration (Spröwitz et al., 2013; Lakatos et al., 2017). 2) For legged robots without access to high-frequency control or low-noise and low-latency sensors, which are expensive and time-consuming to develop (Nam et al., 2020). 3) For motion planners featuring update frequencies in the low sub-kilohertz range, in need of a legged robot with intrinsic robustness when controlled at these frequencies (Ponton et al., 2018).

5 CONCLUSION AND SUMMARY

We systematically characterized combinations of parallel mounted passive and active joint compliance for their ability to control the robot’s leg length after landing. We tested against detrimental effects of significant feedback delays, low control frequencies, and low duty cycles in the full range of compliance ratios. Our goal was to find a compliance ratio for one given total knee compliance that works well with the above controller limitations. In comparison, previous work in parallel-elastic legged robotics typically investigated parallel compliance with high-frequency and low delay actuation (Batts et al., 2016; Mazumdar et al., 2016).

Our computer simulations show successful single-leg drop-landings for sensorimotor delays up to 60 ms, and control frequencies as low as 20 Hz in combination with a compliance ratio of $\lambda_{\text{passive}} = 0.7$. For a ‘hybrid’ setting between λ_{passive} 0.4 and 0.7; the partially active compliance ensures good control authority, and the remaining passive, spring-based compliance reacts immediately and independently from the controller. We verified single-leg computer simulations with hardware experiments for a range of parameters and showed good agreement between both.

We ran computer simulations of quadruped robots with varying total leg stiffness values when landing from multiple

drop heights. Compliance ratios in the hybrid range (around 0.5) worked better in the presence of adverse controller settings (delays, control frequency) than active compliance, and allowed for the necessary amount of controllability compared to pure passive compliance. We finally note that the engineered compliance ratios were robustly handling feedback delays similar to the neuromuscular sensorimotor delays reported of running animals of equal size to the presented hybrid robot leg.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MA and AS contributed to the concept, robot design, experimental setup, simulation, and experimentation. AB-S developed the original hybrid active/passive compliant concept. All authors discussed the data, agreed with the presented results, and contributed to the writing.

ACKNOWLEDGMENTS

The authors thank the International Max Planck Research School for Intelligent Systems (IMPRS-IS) for supporting AAS. We thank Felix Grimminger and Jad Saud for support developing the robot leg and the spring mechanism, the Robotic ZWE for prototyping support, and Julian Viereck for providing the quadruped robot URDF file.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frobt.2021.645748/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Spontaneous Gait Transitions of Sprawling Quadruped Locomotion by Sensory-Driven Body-Limb Coordination Mechanisms

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OPEN ACCESS

Edited by:

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Received: 23 December 2020

Accepted: 09 June 2021

Published: 30 July 2021

Citation:

Suzuki S, Kano T, Ijspeert AJ and
Ishiguro A (2021) Spontaneous Gait
Transitions of Sprawling Quadruped
Locomotion by Sensory-Driven
Body-Limb Coordination
Mechanisms.
Front. Neurobot. 15:645731.
doi: 10.3389/fnbot.2021.645731

Deciphering how quadrupeds coordinate their legs and other body parts, such as the trunk, head, and tail (i.e., body-limb coordination), can provide informative insights to improve legged robot mobility. In this study, we focused on sprawling locomotion of the salamander and aimed to understand the body-limb coordination mechanisms through mathematical modeling and simulations. The salamander is an amphibian that moves on the ground by coordinating the four legs with lateral body bending. It uses standing and traveling waves of lateral bending that depend on the velocity and stepping gait. However, the body-limb coordination mechanisms responsible for this flexible gait transition remain elusive. This paper presents a central-pattern-generator-based model to reproduce spontaneous gait transitions, including changes in bending patterns. The proposed model implements four feedback rules (feedback from limb-to-limb, limb-to-body, body-to-limb, and body-to-body) without assuming any inter-oscillator coupling. The interplay of the feedback rules establishes a self-organized body-limb coordination that enables the reproduction of the speed-dependent gait transitions of salamanders, as well as various gait patterns observed in sprawling quadruped animals. This suggests that sensory feedback plays an essential role in flexible body-limb coordination during sprawling quadruped locomotion.

Keywords: salamander locomotion, body-limb coordination, gait transition, decentralized control, sensory feedback control

1. INTRODUCTION

Quadruped animals exhibit a high agility and adaptability to terrestrial environments. These locomotor abilities are achieved by coordinating their legs and other body parts, such as the trunk, head, and tail (i.e., through body-limb coordination). For instance, the bending of a cheetah's body improves its speed (Hildebrand, 1959), a horse's nodding reduces metabolic costs (Loscher et al., 2016), and the undulation of a salamander's tail facilitates dynamic balance (Bicanski et al., 2013b). These examples suggest that the body-limb coordination mechanisms play an essential role in animal locomotor skills. Decoding the body-limb coordination mechanisms will contribute to the design of highly functional legged robots and help understand the motor control of legged animals.

The salamander is an amphibian and is well-suited for investigating the body-limb coordination mechanisms because it exhibits a flexible body-limb coordination dependent on locomotion speed

(Ashley-Ross, 1994). At slow speeds, salamanders show lateral-sequence walking gait (L-S walk) with standing waves of lateral body undulation in which the body oscillates synchronously while some points act as “nodes” and do not move. At higher speeds, they exhibit a walking trot gait with first standing waves (at medium speeds) and then traveling waves (at high speeds) of lateral undulation in which all body parts oscillate laterally, propagating the waves rostrocaudally. Despite this flexible body–limb coordination, the locomotor nervous systems of salamanders are simpler than those of mammals in that they have fewer neurons and less differentiated structures (Chevallier et al., 2008; Bicanski et al., 2013b). Therefore, salamanders likely possess flexible and simple body–limb coordination mechanisms.

The locomotion of salamanders and other vertebrate animals is controlled by distributed neural networks, called central pattern generators (CPGs), and sensory feedback from peripheral nerves (Cabelguen et al., 2003; Ryczko et al., 2020). In particular, decerebrate salamander experiments showed that neural communication between CPGs is responsible for coordinating axial and limb movements. Based on these findings, CPG networks have been modeled, and salamander locomotion investigated through numerical simulations and robot experiments (Ijspeert, 2001, 2020; Ijspeert et al., 2007; Harischandra et al., 2010, 2011; Bicanski et al., 2013a; Crespi et al., 2013; Liu et al., 2018). Most previous studies used an oscillator model with inter-oscillator couplings in which oscillators represent CPGs and inter-oscillator couplings represent neural communications between CPGs. These studies designed inter-oscillator couplings to coordinate axial and limb movements and reproduced various behaviors, such as walking, swimming, and turning (Ijspeert, 2001; Ijspeert et al., 2007; Bicanski et al., 2013a; Crespi et al., 2013; Liu et al., 2018). These studies intensively investigated the body–limb coordination mechanisms based on inter-oscillator couplings, and less attention was paid to the role of sensory feedback in body–limb coordination. Harischandra et al. (2011) proposed a CPG model with stretch sensory feedback and showed that sensory feedback contributes to gait generation and transition. However, the main focus of this study is interlimb coordination, as opposed to body–limb coordination. The role of sensory feedback in body–limb coordination remains elusive.

We aim to understand the contribution of sensory feedback to body–limb coordination. We previously proposed a decentralized control model with cross-coupled sensory feedback from the body to limb, and vice versa, in simulated and real sprawling quadruped robots (Suzuki et al., 2019, 2021). Body–limb coordination was successfully established by sensory couplings without inter-oscillator couplings. These studies also suggested that sensory feedback provides rapid convergence to a stable gait, easy parameter tuning, and high robustness against leg failure and morphological changes. However, the results cannot explain the body–limb coordination mechanisms responsible for gait transition because of the simplified body structure in which the body trunk had only one degree of freedom.

In this study, we investigate the mechanisms for coordination between the legs and a flexible elongated trunk and aim to reproduce the speed-dependent gait transition of salamanders. To this end, we extend our previous model to simulate a

salamander robot with a multi-segmented trunk. The simulation results show that the proposed model can reproduce the gait transition between a standing wave pattern at low speed and a traveling wave pattern at high speed, by changing only one parameter related to the command from the brain. The model also reproduces several gait patterns observed in other sprawling quadruped animals by changing the sensory feedback strength. These results suggest that, in addition to inter-oscillator couplings (which are known to exist in the salamander spinal cord), sensory feedback could play an essential role in flexible body–limb coordination underlying sprawling quadruped locomotion.

The remainder of this paper is structured as follows. Section 2 contains a description of a decentralized control for body–limb coordination and details the effects of sensory feedback rules. Section 3 contains an outline of the simulation experiments and the results. In section 4, the potential role of sensory feedback in body–limb coordination is discussed, and recommendations for future studies are presented.

2. MODEL

2.1. Body

The body consists of n trunk segments and four legs, as shown in **Figure 1**. The segments are concatenated via yaw hinge joints with a parallel combination of a rotary actuator, passive spring, and passive damper. The fore- and hind-legs are attached on both sides of the k -th and l -th segments, respectively. Each leg has two rotary actuators in the yaw and roll directions, controlled by phase oscillators.

Each foot tip has a force sensor that detects the normal force from the ground, and each trunk joint has angle and torque sensors. The angle sensors detect the angle θ_j^b of the j -th trunk joint from the head. Here, the j -th trunk joint connects the j -th and $j + 1$ -th segments from the head. The variable θ_j^b is positive when the trunk joint bends to the right, as shown in **Figure 1**. The torque sensors detect the torque generated by the rotary actuators at the trunk joint.

2.2. Control Algorithm

The proposed decentralized control algorithm is an extension of our previous study (Suzuki et al., 2019). The controller is composed of oscillators, which represent CPGs. In order to focus on the potential role of sensory feedback as synchronization mechanism, inter-oscillator couplings are not modeled here; instead, nearby body parts are coupled through sensory feedback (**Figure 2**). The sensory feedback consists of the following four feedback rules:

1. Force feedback from limb to limb
2. Torque feedback from body to limb
3. Force feedback from limb to body
4. Angle feedback from body to body

The first rule is responsible for coordinating the four legs as they move forward while supporting the body. The second and third rules comprise the cross-coupled feedback that establishes self-organized body–limb coordination. The fourth rule coordinates

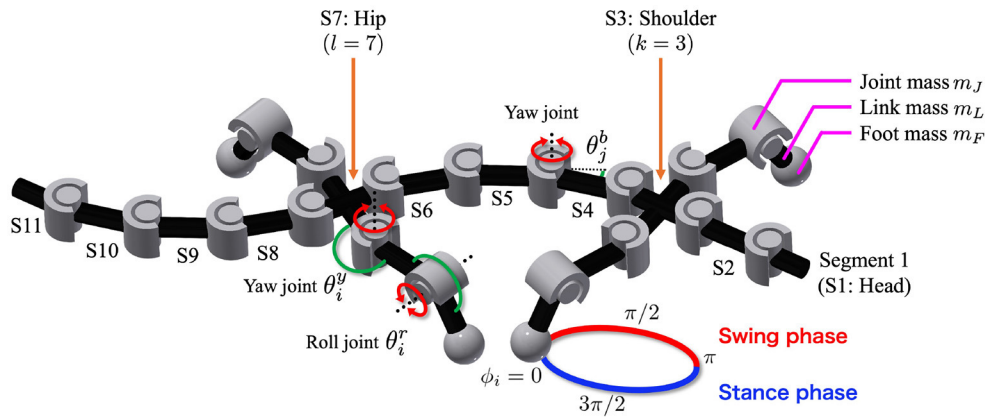


FIGURE 1 | Body model. The trunk has $n - 1$ actuated degrees of freedom (DoFs), and θ_j^b denotes the angle of the j -th DoF from the head. The fore- and hind-legs are attached on both sides of the k -th and l -th segments, respectively (in the figure, $n = 11$, $k = 3$, and $l = 7$). Each leg has two DoFs controlled by phase oscillators. The subscript i denotes the leg identifier: (1, left fore; 2, right fore; 3, left hind; and 4, right hind), and θ_i^y and θ_i^r are the angles of the leg joints in the yaw and roll directions, respectively. The circle around the right foreleg shows the leg trajectory based on the oscillator phase ϕ_i . Variables m_J , m_L , and m_F are the masses of each joint, link, and foot, respectively.

the lateral undulations of the multi-segmented body trunk. Through the interplay of these rules, it is expected that the model will generate flexible locomotion patterns. The following section describes each sensory feedback control in detail.

2.2.1. Leg Control

A phase oscillator is implemented in each leg, and its phase determines the target angle of the rotary actuators in the yaw and roll directions as follows:

$$\begin{aligned}\bar{\theta}_i^y &= C_0^y - C_{amp}^y \cos \phi_i, \\ \bar{\theta}_i^r &= C_0^r - C_{amp}^r \sin \phi_i,\end{aligned}\quad (1)$$

where $\bar{\theta}_i^y$ and $\bar{\theta}_i^r$ denote the target angles, C_0^y and C_0^r represent the neutral angles, C_{amp}^y and C_{amp}^r represent the amplitudes of the yaw and roll actuators, respectively (**Figure 1**); ϕ_i is the oscillator phase and the subscript i denotes the leg identifier (1: left fore, 2: right fore, 3: left hind, and 4: right hind). When $0 < \phi_i < \pi$, the leg tends to be in the swing phase; otherwise, it tends to be in the stance phase. The time evolution of the phase is described as follows:

$$\dot{\phi}_i = \omega + f_{LL,i} + f_{BL,i}, \quad (2)$$

$$f_{LL,i} = -\sigma_{LL} \tanh(\rho_{LL} N_i) \cos \phi_i, \quad (3)$$

$$f_{BL,i} = \begin{cases} +\sigma_{BL} \tanh(\rho_{BL} \tau_k^b) \cos \phi_i & (i = 1) \\ -\sigma_{BL} \tanh(\rho_{BL} \tau_k^b) \cos \phi_i & (i = 2) \\ +\sigma_{BL} \tanh(\rho_{BL} \tau_l^b) \cos \phi_i & (i = 3) \\ -\sigma_{BL} \tanh(\rho_{BL} \tau_l^b) \cos \phi_i & (i = 4), \end{cases} \quad (4)$$

where ω [rad/s] denotes the intrinsic angular velocity of the phase oscillators; and σ_{LL} [rad/s], ρ_{LL} [1/N], σ_{BL} [rad/s], and ρ_{BL}

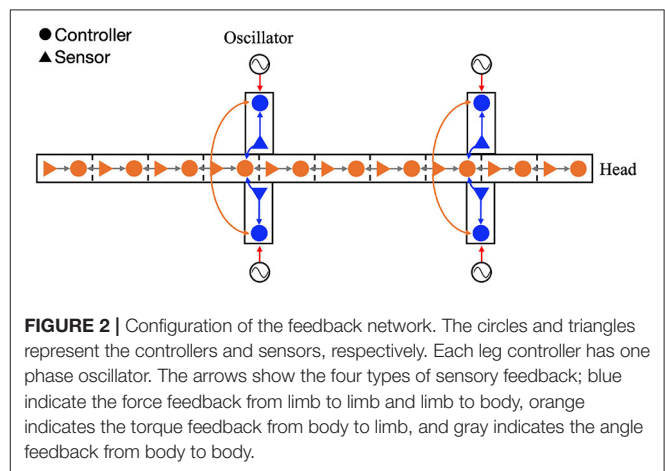
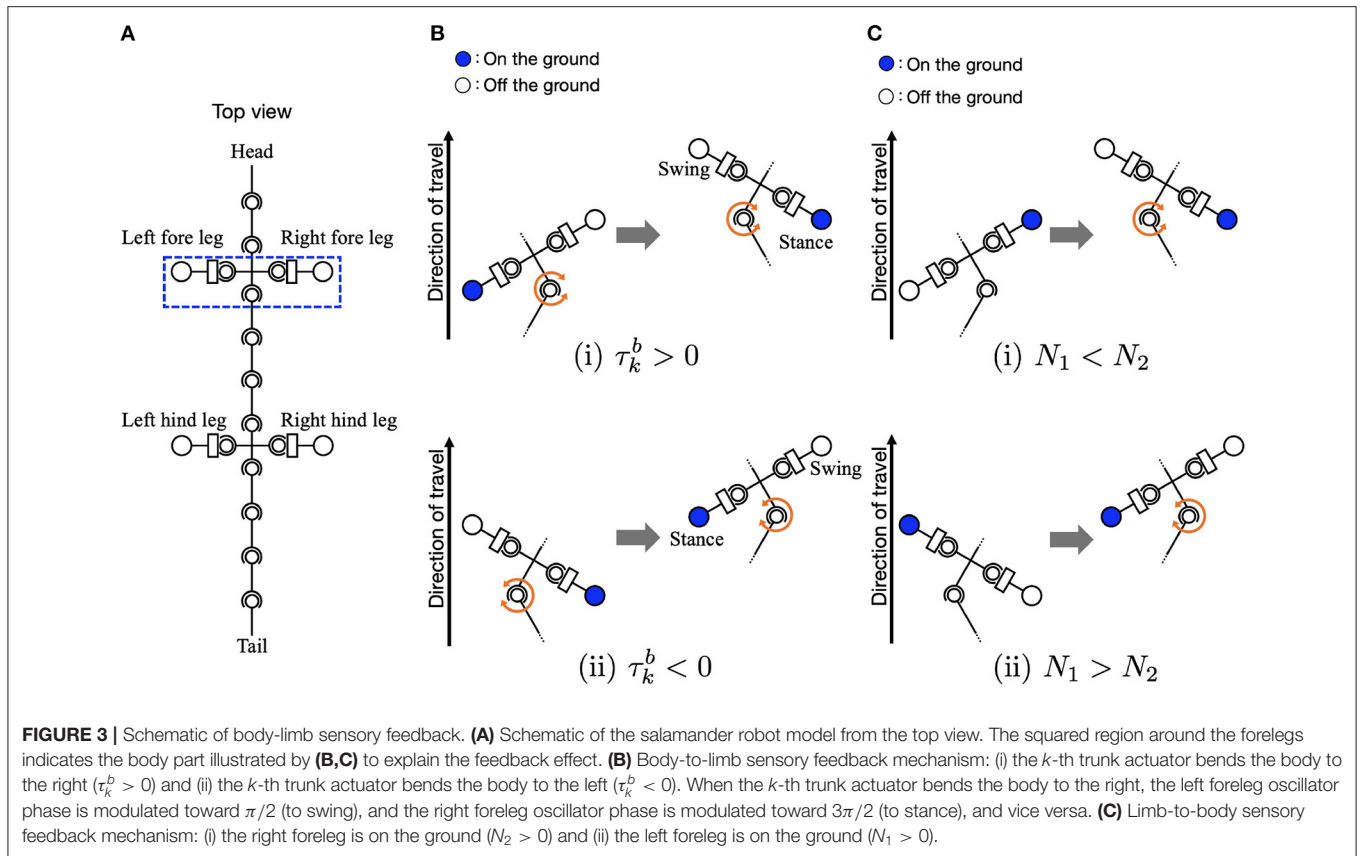


FIGURE 2 | Configuration of the feedback network. The circles and triangles represent the controllers and sensors, respectively. Each leg controller has one phase oscillator. The arrows show the four types of sensory feedback; blue indicate the force feedback from limb to limb and limb to body, orange indicates the torque feedback from body to limb, and gray indicates the angle feedback from body to body.

$[1/(\text{N}\cdot\text{m})]$ are the weights of the sensory feedback terms; and N_i [N] represents the normal force detected at the foot tip. Further, τ_k^b and τ_l^b [N·m] represent the torque generated by the k -th and l -th trunk actuators, respectively.

Equation (3) relates to the limb-to-limb feedback. The local feedback rule was proposed by Owaki et al. (2013). It generates adaptive interlimb coordination in response to the speed and physical properties of the robot (Owaki et al., 2013; Owaki and Ishiguro, 2017). Based on the sensory feedback effect, the oscillator phase is modulated to $3\pi/2$ when $N_i > 0$. When the leg supports the body, the foot obtains a higher ground reaction force, that is, a higher N_i . Thus, this feedback implies that the leg remains on the ground when it supports the body. The local sensory information, denoted by N_i , describes the extent to which a specific leg provides support to the body, and it also indicates how much other legs are currently contributing to supporting the body. Using such sensory information, this feedback can generate



adaptive interlimb coordination without neural communication between the legs.

Equation (4) relates to the body-to-limb feedback (**Figures 3A, B**). When the k -th trunk actuator bends the body to the right ($\tau_k^b > 0$), the oscillator phase of the left foreleg is modulated to $\pi/2$ to lift the legs, and the oscillator phase of the right foreleg is modulated to $3\pi/2$ to place the legs on the ground. By phase modification, the left foreleg lifts from the ground, and the right foreleg is anchored to the ground. This facilitates the k -th trunk actuator to bend the body to the right ($\theta_k^b > 0$), and the robot moves forward when the anchored legs serve as a pivot. Similarly, the oscillator phases of the hind legs are modulated by the torque of the l -th trunk actuator.

2.2.2. Body Control

The torques at the trunk actuators are described as follows:

$$\tau_j^b = f_{LB,j} + f_{BB,j}, \quad (5)$$

$$f_{LB,j} = \begin{cases} \sigma_{LB} \tanh\{\rho_{LB}(N_2 - N_1)\} & (j = k) \\ \sigma_{LB} \tanh\{\rho_{LB}(N_4 - N_3)\} & (j = l) \\ 0 & \text{otherwise,} \end{cases} \quad (6)$$

$$f_{BB,j} = -\sigma_{BB} \tanh\{\rho_{BB}(\theta_j^b - \theta_{j-1}^b)\}, \quad (7)$$

where θ_j^b is the actual angle of the trunk actuator. The variables σ_{LB} [N·m] and ρ_{LB} [1/N], σ_{BB} [N·m], and ρ_{BB} [1/rad] represent the weights of the sensory feedback.

Equation (6) relates to the limb-to-body feedback. The sensory feedback effect is such that the k -th and l -th trunk segments bend in response to ground contacts, as shown in **Figures 3A, C**. When the left foreleg is on the ground ($N_1 > 0$), the k -th actuator bends the body to the left ($\tau_k^b < 0$). Similarly, when the right foreleg is on the ground ($N_2 > 0$), the k -th trunk actuator bends the body to the right ($\tau_k^b > 0$). The interactions of the sensory feedback from body to limb and limb to body establish the relationship between the legs and trunk, providing longer strides and more powerful pushing-off against the ground. The interactions of the body-to-limb and limb-to-body feedback establish the relationship between the legs and trunk, providing longer strides and more powerful pushing-off against the ground (Suzuki et al., 2019, 2021).

Equation (7) relates to the body-to-body feedback. The local feedback rule is based on the curvature derivative control proposed in a previous study for snake-like locomotion (Date and Takita, 2007). It generates a torque proportional to the curvature derivative of the body curve such that the lateral body undulation propagates posteriorly. As reported in a previous study (Kano and Ishiguro, 2020), the control with additional sensory feedback can generate versatile undulation patterns. Therefore, it can potentially generate flexible, sensory-driven,

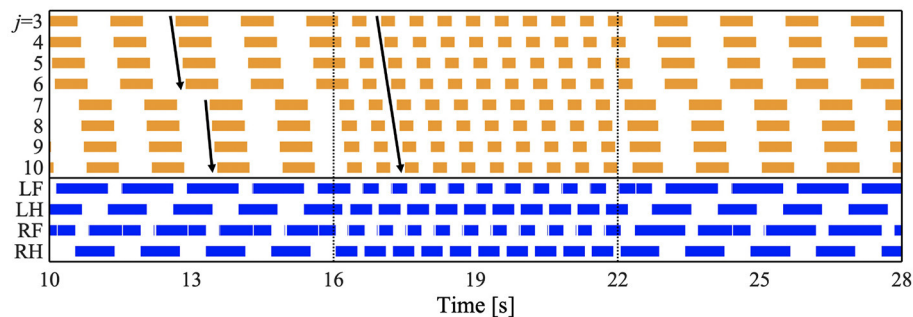


FIGURE 4 | Spontaneous gait transition from L-S walk with standing waves to walking trot with traveling wave and vice versa. The upper graph represents the lateral flexion of the trunk joint, wherein the colored region denotes the period when the trunk joint bends to the right ($\theta_j^b > 0$). The lower graph represents the gait diagram, wherein the colored region denotes the period when the foot is in contact with the ground ($N_i > 0$). We set the parameter ω from 1.8π to 3.8π [rad/s] at period 16 [s], and from 3.8π to 1.8π [rad/s] at period 22 [s]. We confirmed that the gait transition was observed for any initial oscillator phase (for all 10 trials).

intersegmental coordination, as an alternative to inter-oscillator couplings (as modeled in Ijspeert et al. (2007) for instance). The interplay between limb-to-body and body-to-body feedback arranges the waveform of the lateral body undulations.

3. SIMULATION RESULTS

We conducted simulation experiments using the Open Dynamics Engine, which is an open-source library for simulating rigid body dynamics (Smith, 2005). Each trial was conducted on flat terrain for 60 s, with the oscillator phases initially set to random. The body size and weight were determined by considering those of a salamander robot developed as a prototype in our previous study (Suzuki et al. 2019b). The angular frequency and amplitude of the legs were chosen with physically plausible values. The other parameters were determined by trial and error, referring to the parameter sets of our previous simulation study [Suzuki et al., 2019]. The simulation time step was set to 0.01 s, and the control commands were updated at each time step. The results are provided in the following sections. We first show that the speed-dependent gait transition of salamanders can be successfully reproduced (section 3.1). Next, we demonstrate that two other gait patterns observed in other sprawling quadruped animals can be reproduced (section 3.2). Finally, we clarify which parameters affect the exhibited gait pattern by changing the feedback strength (section 3.3) and body parameters (section 3.4).

3.1. Speed-Dependent Gait Transition of Salamanders

To investigate whether the proposed model can reproduce the speed-dependent gait transition of salamanders, we performed a simulation by changing the parameter ω from 1.8π to 3.8π [rad/s] at period 16 [s] and from 3.8π to 1.8π [rad/s] at period 22 [s]. **Figure 4** and **Supplementary Video 1** show the results. The upper graph represents the lateral flexion of the trunk joint, wherein the colored region denotes the period when the trunk joint bends to the right ($\theta_j^b > 0$). The lower graph represents

the gait diagram, wherein the colored region denotes the period when the foot is in contact with the ground ($N_i > 0$).

For $\omega = 1.8\pi$, the bending of the body trunk ($j = 3 - 6$) is antiphase to that of the tail ($j = 7 - 10$), as shown in **Figure 4**. This pattern is a standing wave with nodes at the shoulder and the hip, similar to that of a salamander walking (Ashley-Ross, 1994). Next, the feet touched down in the following order: right hind (RH), right fore (RF), left hind (LH), and left fore (LF). The mean and standard deviation (SD) of the duty factor were 69.3 and 0.55%, respectively. The mean and SD of the diagonality were 21.9 and 1.26%, respectively. These values were calculated within 10–16 [s] for each of the 10 trials. The duty factor is the time percentage at which one foot spends in the stance phase during a gait cycle, and diagonality is the percentage of the cycle period by which the left/right hind footfall precedes the left/right fore-footfall. Thus, the gait was classified as a lateral-sequence (L-S) walk, according to Hildebrand's gait classification (Hildebrand, 1965; Cartmill et al., 2002). This gait was observed in salamander's slow-speed walking (Ashley-Ross, 1994). In conclusion, for $\omega = 1.8\pi$, the model reproduced the bending and footfall patterns of a salamander's slow-speed walking.

For $\omega = 3.8\pi$, the flexion duration moved posteriorly and continuously (**Figure 4**), indicating a traveling wave. The footfall pattern is such that the diagonally opposite feet were nearly synchronized. The mean and SD of the duty factor were 64.5% and 9.74×10^{-2} , respectively. The mean and SD of the diagonality were 48.0 and 1.97%, respectively. These values are calculated within 18–22 [s] for each of the 10 trials. Thus, the gait was classified as a walking trot according to Hildebrand's gait classification (Hildebrand, 1965; Cartmill et al., 2002). The bending and footfall patterns were observed in a salamander's high-speed walking (Ashley-Ross, 1994). Therefore, the model also reproduced the gait pattern of a salamander's high-speed walking for $\omega = 3.8\pi$.

When changing ω from 1.8π to 3.8π at period 16 [s], the gait pattern spontaneously and smoothly changed from a L-S walk with standing waves to a walking trot with traveling waves, as shown in **Figure 4**. Similarly, the reverse gait transition (from walking trot to L-S walk) was observed when changing ω from

3.8π to 1.8π at period 22 [s]. We confirmed that the gait transition was observed for any initial oscillator phase (for all 10 trials). Thus, the proposed model successfully reproduced the speed-dependent gait transition of salamanders, by simply changing the ω parameter.

We then analyzed the lateral bending waveform of each gait pattern and compared it with that of salamanders. **Figure 5** shows the comparison of the body waveform between the simulated robot and the salamander, *Dicamptodon tenebrosus* (Ashley-Ross, 1994). In **Figures 5A,B**, the stick figures were made by connecting the lateral positions of the body segments from the shoulder ($j = 3$) to the hip ($j = 7$) in the simulated robot for $\omega = 1.8\pi$ (**Figure 5A**) and $\omega = 3.8\pi$ (**Figure 5B**), respectively. All stick figures throughout one gait cycle were superimposed by lining them up on the shoulder segment. This analysis refers to Ashley-Ross's study (Ashley-Ross, 1994), and **Figures 5C,D** were adapted from the analysis of a salamander walking and trotting conducted in this study. These stick figures were made by connecting the marker point over the midline from the pectoral girdle to the pelvic girdle while walking (**Figure 5C**) and trotting (**Figure 5D**). All stick figures throughout one gait cycle were superimposed by lining them up on the anteriormost midline marker dot.

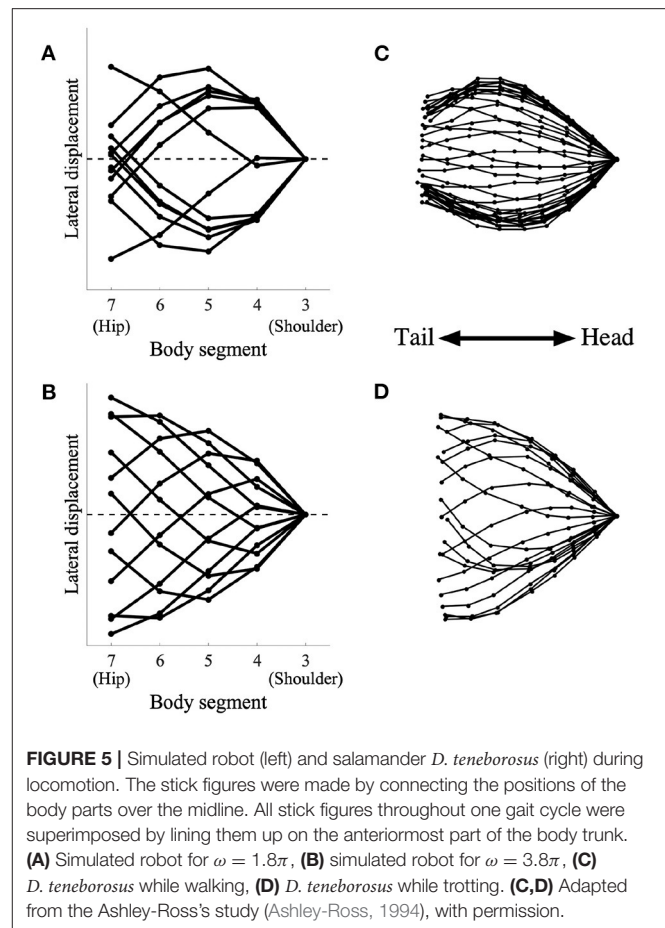
Figure 5A shows the body waveform alternate between two stable curve configurations; the curve features a half-wavelength from the shoulder and hip. This pattern is a standing wave with nodes at the shoulder and the hip, and is similar to that of a salamander's walking, as shown in **Figure 5C**. **Figure 5B** shows that the body waveform has no nodes; the trunk does not follow a simple side-to-side bending pattern (such as in **Figure 5A**). This pattern is a traveling wave, and is also similar to that of a salamander's trotting, as shown in **Figure 5D**. These results suggest that the model certainly generates two types of body waveforms, namely, standing and traveling waves; these waveforms are qualitatively similar to those exhibited by a salamander.

3.2. Reproduction of Gait Patterns Observed in Other Species

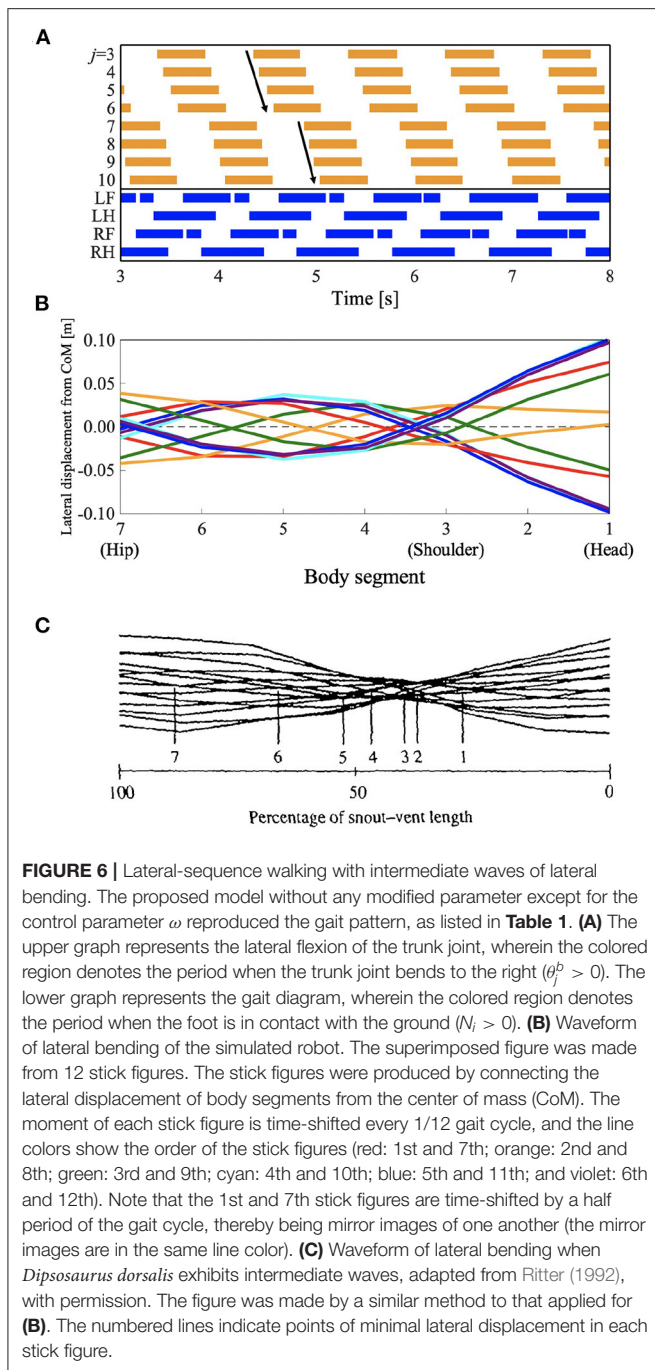
While salamanders exhibit a L-S walk with standing waves of lateral body undulation and walking trot gait with standing or traveling waves of, different gait patterns have been observed in other species that exhibit sprawling locomotion (Ritter, 1992). In this subsection, we demonstrate that the proposed model can reproduce such patterns by changing the control parameters.

L-S Walk With Intermediate Waves

Some species of lizards, such as *Dipsosaurus dorsalis*, also show speed-dependent gait transitions (Ritter, 1992). They use standing waves at lower speeds and traveling waves at higher speeds, similar to the salamander's gait. Interestingly, they also use "intermediate" waves at intermediate speeds in between the speeds for standing and traveling waves. The waveform has attributes of both standing and traveling waves. To investigate whether the proposed model can reproduce these gait patterns, we performed a simulation by setting the parameter ω to 2.3π , that is, in between standing and traveling waves; and the



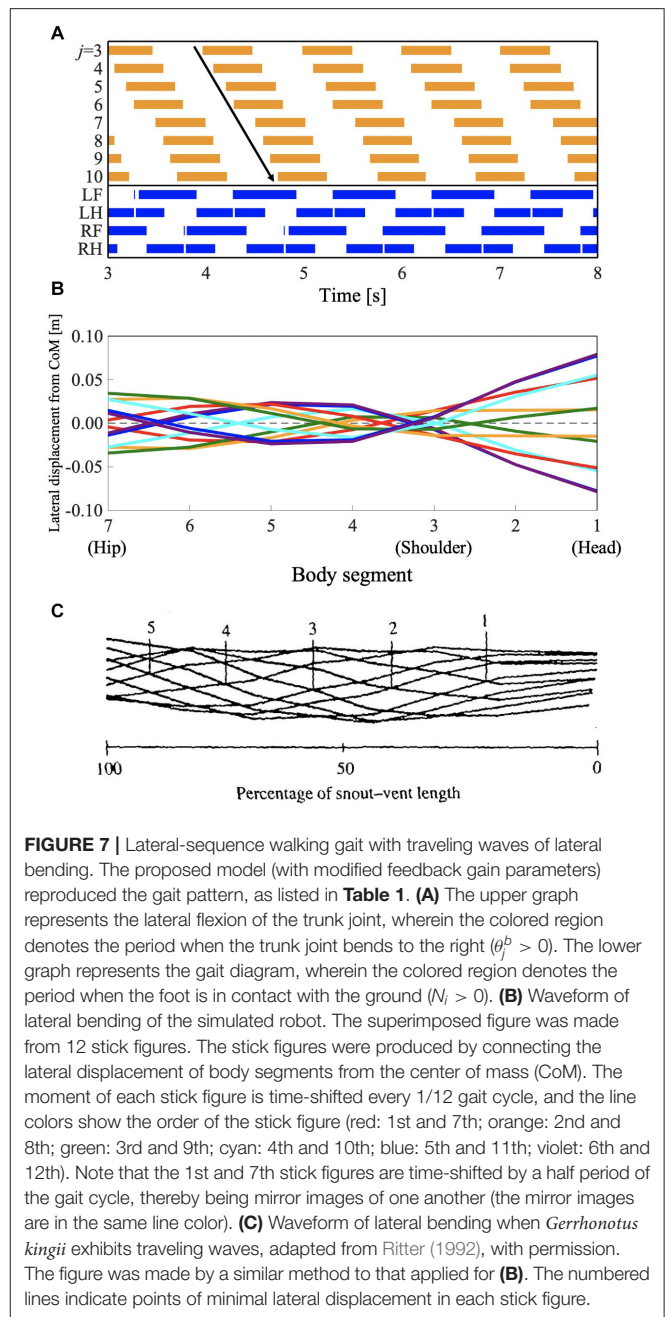
remaining parameters were the same as those used in section 3.1. **Figure 6** and **Supplementary Video 2** present the results. **Figure 6A** shows the diagram for lateral bending and the gait diagram. The footfall pattern was a L-S walk; the mean and SD of the duty factor were 66.8 and 0.23%, respectively; the mean and SD of the diagonality were 29.0 and 0.35%, respectively. These values were calculated from the 10 trials. The body flexion duration moves posteriorly but not continuously. The wave propagation has an irregular point at the hip ($j = 7$). **Figures 6B,C** show the lateral displacement of each body part toward the moving direction of the simulated robot and the lizard, *D. dorsalis*, respectively. In **Figure 6B**, the minimal lateral displacement point moves posteriorly, similar to traveling waves. However, there are several points at the same position (posterior to the shoulder) as if the nodes were present, similar to standing waves. Therefore, the waveform has attributes of both standing and traveling waves; thus, intermediate waves emerge. **Figure 6C** shows the waveform when the lizard exhibits intermediate waves. The numbered lines indicate the minimal lateral displacement points. The points moved posteriorly, and some of them were within a restricted portion of the mid-trunk. The tendency is qualitatively similar to that of the simulation results. Therefore, the proposed model without any modified parameter except for



the control parameter ω reproduced gait patterns exhibited by the *D. dorsalis*.

L-S Walk With Traveling Waves

The salamander uses a traveling wave when performing a walking trot, but they have not been found to use traveling waves when using other slower walking gaits (Edwards, 1977). However, some lizards such as *G. kingii*, exhibit traveling waves, even at the lowest speed (Ritter, 1992). To investigate whether the proposed model can reproduce such gait patterns,



we performed a simulation by setting the parameter ω to 2.3π , and the feedback gain from limb-to-body σ_{LB} and body-to-body σ_{BB} to lower values than those used in section 3.1 ($\sigma_{LB} = 4.5$ and $\sigma_{BB} = 5.0$, respectively). **Figure 7** and **Supplementary Video 3** show the results. **Figure 7A** shows the diagram for lateral bending and the gait diagram. The footfall pattern was a L-S walk; the mean and SD of the duty factor were 64.2% and 5.28×10^{-2} , respectively. The mean and SD of the diagonality were 38.7 and 0.13%, respectively. These values were calculated from the 10 trials. The body flexion duration moves posteriorly and continuously. **Figures 7B,C** show the lateral displacement of each body part toward the moving direction

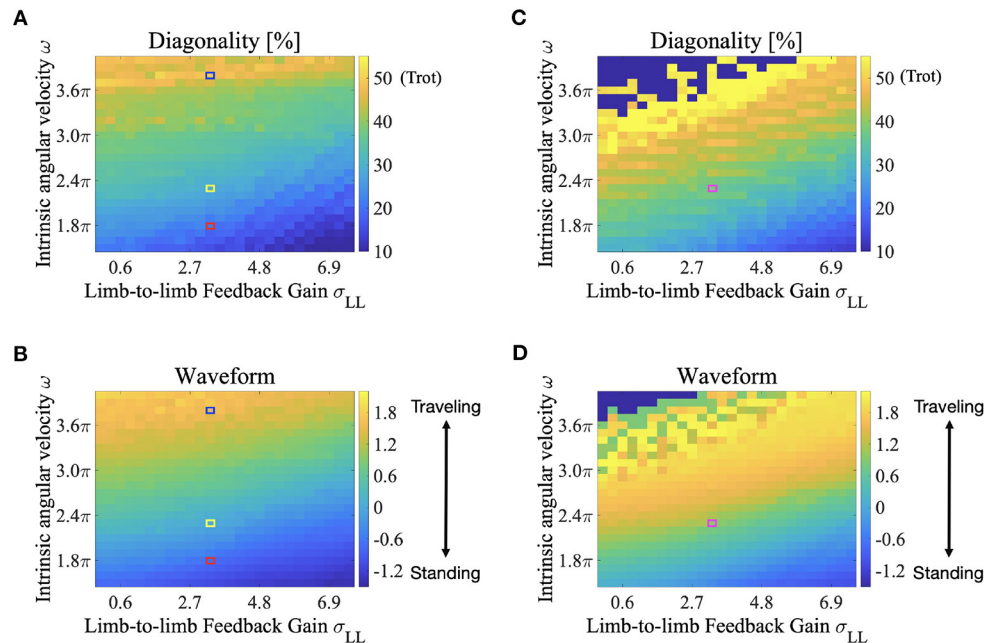


FIGURE 8 | Color maps showing the two indices; diagonality and the waveform index, when the intrinsic angular velocity ω is between 1.5π and 4.0π , and the feedback gain from limb-to-limb σ_{LL} is between 0.00 and 7.50. **(A)** diagonality ($\sigma_{LB} = 7.0$, $\sigma_{BB} = 7.7$), **(B)** waveform index ($\sigma_{LB} = 7.0$, $\sigma_{BB} = 7.7$), **(C)** diagonality ($\sigma_{LB} = 4.5$, $\sigma_{BB} = 5.0$), **(D)** waveform index ($\sigma_{LB} = 4.5$, $\sigma_{BB} = 5.0$). In **(A,C)**, the brighter region indicates a higher diagonality. In **(B,D)**, the brighter region shows that a traveling wave emerges. The fluctuation in the upper left part of **(C,D)** indicates that an unstable locomotion emerged, and the gait was not evaluated correctly. The squared regions indicate the parameter sets used in the other experiments (red: **Figure 4** for $\omega = 1.8\pi$ described in section 3.1; blue: **Figure 4** for $\omega = 3.8\pi$ described in section 3.1; yellow: **Figure 6** described in section 3.2; and purple: **Figure 7** described in section 3.2).

of the simulated robot and the lizard, *G. kingii*, respectively. In **Figure 6B**, the minimal lateral displacement point moves posteriorly and continuously. The waveform is a traveling wave in which no node is present. **Figure 6C** shows the waveform when the lizard exhibits a traveling wave. The numbered lines indicate the minimal lateral displacement points. The figure shows that the points move posteriorly and continuously. The tendency is qualitatively similar to that of the simulation results. Therefore, the proposed model (with modified feedback gain parameters) reproduced the gait patterns exhibited by the *G. kingii*.

3.3. Effect of Sensory Feedback Strength on Gait Patterns

We performed simulations by changing various parameter sets, particularly, the feedback strengths, to specify the determinants of the gait patterns. For a quantitative gait evaluation, we used the two indices: diagonality and waveform index. The waveform index W was derived based on the gait evaluation method proposed by Kano et al. (2014) as follows:

$$W = D_{std} - D_{trv}, \quad (8)$$

$$D_x = \min_{\Theta \in [0, 2\pi]} |\mathbf{r} - e^{i\Theta} \mathbf{r}_x|, \quad (9)$$

$$\mathbf{r} = \{e^{i\Phi_3}, e^{i\Phi_4}, e^{i\Phi_5}, e^{i\Phi_6}, e^{i\Phi_7}, e^{i\Phi_8}, e^{i\Phi_9}, e^{i\Phi_{10}}\}, \quad (10)$$

$$\mathbf{r}_{std} = \{0, 0, 0, 0, e^{i\pi}, e^{i\pi}, e^{i\pi}, e^{i\pi}\}, \quad (11)$$

$$\mathbf{r}_{trv} = \{0, e^{-i\frac{\pi}{4}}, e^{-i\frac{2\pi}{4}}, e^{-i\frac{3\pi}{4}}, e^{-i\frac{4\pi}{4}}, e^{-i\frac{5\pi}{4}}, e^{-i\frac{6\pi}{4}}, e^{-i\frac{7\pi}{4}}\}, \quad (12)$$

where W denotes the waveform index. D_{std} and D_{trv} are the intergait distances of standing and traveling waves, respectively. $\mathbf{r}$, $\mathbf{r}_{std}$, and $\mathbf{r}_{trv}$ are the phase relationships between the trunk-joint angles ($j = 3 - 10$) of the exhibited wave, the standing wave, and the traveling wave, respectively. The phase of the trunk joint Φ_j can be defined by the timing of lateral flexion of the trunk joint; for example, $\Phi_j = 0$ is the timing when the trunk joint bends to the right from the neutral angle ($\theta_j^b = 0$). Intergait distance is a measure for gait evaluation proposed by Kano et al. (2014). The distance shows the similarity of the specific gaits. For example, when a standing wave emerges, D_{std} is lower and D_{trv} is higher. Conversely, when a traveling wave emerges, D_{std} is higher and D_{trv} is lower. Therefore, when the waveform index W is positive, traveling waves emerge, when W is negative, standing waves emerge; and when $W = 0$, intermediate waves emerge. For further details of the derivation process, please refer to Kano et al. (2014).

The color maps in **Figure 8** show the two indices when the intrinsic angular velocity ω is between 1.5π and 4.0π and the feedback gain from limb-to-limb σ_{LL} is between 0.00 and 7.50. In **Figures 8B,D**, the control parameters σ_{LB} and σ_{BB} are 7.0 and 7.7, respectively. In **Figures 8C,D**, the control parameters σ_{LB} and σ_{BB} are 4.5 and 5.0, respectively. The fluctuation in the upper left part of **Figures 8C,D** indicates

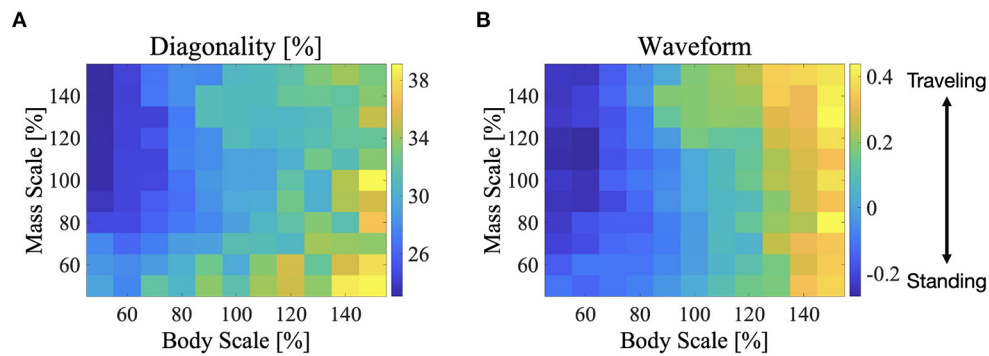


FIGURE 9 | Color maps showing the two indices; diagonality and the waveform index, when the body size and mass are between 50 and 150%, **(A)** diagonality, **(B)** waveform index. In **(A)**, the brighter region indicates a higher diagonality. In **(B)**, the brighter region shows that the waveform is relatively similar to the traveling waves. The control parameter set was used in **Figure 6** is described in section 3.2; for the L-S walk with intermediate waves.

TABLE 1 | Parameter values of employed in the simulations.

Common parameters	Body length [m]		0.60
	Shoulder/hip length [m]		0.06
	Leg length [m]		0.06
	Body mass [kg]		2.85
	Joint mass [kg]	m_J	0.10
	Link mass [kg]	m_L	0.05
	Foot mass [kg]	m_F	1.0×10^{-5}
	Spring coefficient of trunk actuators [N/m]		1.5
	Damper coefficient of trunk actuators [(N·s)/m]		0.5
	Leg amplitude in yaw direction [rad]	C_0^y	$\pi/9$
	Leg amplitude in roll direction [rad]	C_0^r	$\pi/9$
	Gain for limb-to-limb feedback [rad/s]	σ_{LL}	3.30
	Gain for limb-to-limb feedback [1/N]	ρ_{LL}	0.10
	Gain for body-to-limb feedback [rad/s]	σ_{BL}	4.00
	Gain for body-to-limb feedback [1/(N · m)]	ρ_{BL}	0.20
	Gain for limb-to-body feedback [1/N]	ρ_{LB}	0.20
	Gain for body-to-body feedback [1/rad]	ρ_{BB}	1.00
Section 3.1	Intrinsic angular velocity [rad/s]	ω	$1.8\pi \rightarrow 3.8\pi$ at 16 s $3.8\pi \rightarrow 1.8\pi$ at 22 s
	Gain for limb-to-body feedback [N·m]	σ_{LB}	7.00
	Gain for body-to-body feedback [N·m]	σ_{BB}	7.70
Section 3.2			
Lateral-sequence walk with intermediate wave	Intrinsic angular velocity [rad/s]	ω	2.3π
	Gain for limb-to-body feedback [N·m]	σ_{LB}	7.00
	Gain for body-to-body feedback [N·m]	σ_{BB}	7.70
Lateral-sequence walk with traveling wave	Intrinsic angular velocity [rad/s]	ω	2.3π
	Gain for limb-to-body feedback [N·m]	σ_{LB}	4.50
	Gain for body-to-body feedback [N·m]	σ_{BB}	5.00

that an unstable locomotion emerged, and the gait was not evaluated correctly. The squared regions indicate the parameter sets used in the other experiments (red: **Figure 4** for $\omega = 1.8\pi$ described in section 3.1; blue: **Figure 4** for $\omega = 3.8\pi$ described in section 3.1; yellow: **Figure 6**

described in section 3.2; and purple: **Figure 7** described in section 3.2).

According to **Figures 8A,B**, both the diagonality and the index W increases as ω increases. Therefore, a walking trot with a traveling wave emerges for large values of ω . Conversely, both

indices decrease as σ_{LL} increases, and a L-S walk with a standing wave emerges for large values of σ_{LL} . Intermediate waves emerge for intermediate values of ω . Meanwhile, the values of both the diagonality and index W in **Figures 8C,D** are generally larger than those in **Figures 8A,B**. Therefore, for small σ_{LB} and σ_{BB} , a walking trot with a traveling wave emerges even at a relatively small value of ω . This tendency is qualitatively consistent with the behavior of *G. kingii* using traveling waves exclusively, even at extremely slow speeds (Ritter, 1992).

3.4. Effect of Body Size and Mass on Gait Patterns

We performed simulations by changing the body size and weight, and investigated the effect of these parameters on the exhibited gait patterns. This experiment used the same parameter set used in **Figure 6** which is described in section 3.2 (i.e., for the L-S walk with intermediate waves). The color maps in **Figure 9** show the two indices; diagonality and waveform index, when the body size and weight are between 50 and 150% of those, as listed in **Table 1**. **Figure 9A** shows that the diagonality tends to be higher for a larger body size and be lower for a heavier body. **Figure 9B** shows that the waveform index tends to be higher; that is, the waveform is relatively similar to traveling waves, for a larger body size.

4. DISCUSSION

To the best of our knowledge, this is the first study to demonstrate the spontaneous gait transition from lateral sequence walking with standing body waves, to walking trot with traveling body waves, in sprawling quadruped locomotion. The gait transition was achieved by changing only one parameter ω , which is related to a command from the brain. In the previous studies, Ijspeert et al. (2007) reproduced the salamander gait transitions from walking to swimming. This study also reproduced the standing- and traveling-wave patterns by modulating the strength of the descending command. However, the traveling waves were used for swimming but not for walking, and the walking pattern was uniquely determined by inter-oscillator couplings between the limbs and body CPGs. Harischandra et al. (2011) proposed a CPG model utilizing sensory feedback based on the Ijspeert's model and showed the gait transition from walk to trot. That study suggested that sensory modulation has an essential role for gait transition. However, because the body-limb coordination patterns were predetermined by inter-oscillator couplings, the transition of the bending patterns of the body trunk was not reproduced. In contrast, we designed a CPG controller based on sensory couplings through bidirectional feedback between the limbs and body without inter-oscillator couplings, and we demonstrated that the controller can reproduce flexible body-limb coordination patterns. This result suggests that the proposed sensory feedback mechanisms could play an important role in sprawling quadruped locomotion.

The proposed model changes the footfall pattern in response to the control and body parameters. Specifically, diagonality tends to be higher when the leg phase oscillator has a higher frequency. For example, the higher the intrinsic angular velocity

of the oscillator ω , the higher the diagonality (**Figures 8A,C**). Meanwhile, the higher feedback gain of limb-to-limb σ_{LL} and body-to-limb σ_{BL} tend to have lower diagonality owing to the effect of the phase modification that decreases the phase frequency. Similarly, a heavier body tends to have a lower diagonality because a heavier body can obtain a higher reaction force N_i that enhances the limb-to-limb feedback. Furthermore, the higher feedback gain of limb-to-body σ_{LB} and body-to-body σ_{BB} tend to have lower diagonality because the feedback gain is related to the generated torque at the trunk, which enhances the body-to-limb feedback. Owing to the close interactions between the sensory feedback mechanisms, the proposed model generates flexible footfall patterns.

Sprawling quadruped animals use various body bending patterns. However, the mechanisms responsible for generating flexible bending patterns remain unclear. In this article, we presented a potential solution to generate various bending patterns. Our proposed model coordinates axial movements using curvature derivative control and sensory feedback from the legs. Curvature derivative control causes the angle of the trunk joint to follow that of the anterior trunk joint. Therefore, the control shapes a traveling wave of axial movements. Because the control gain (here is σ_{BB}) is related to the follow-up speed, the higher the feedback gain, the faster the wave speed of the traveling waves. Meanwhile, the feedback from the legs imposes bending of the trunk joint at the shoulder ($j = 3$) and hip ($j = 7$) in response to the ground contacts. Given that the footfall timings of diagonally opposite feet are roughly synchronized, the feedback tends to cause the bending of the shoulder antiphase with respect to that of the hip. As a result, a standing wave with nodes at the shoulder and hip emerges for a large feedback gain of curvature derivative control σ_{BB} , that is, when the wave speed is higher. When the σ_{BB} is lower, the wave speed is lower, and a traveling wave emerges. The intermediate wave emerges in the condition between those of the standing wave and traveling waves. Based on these mechanisms, the proposed model generates flexible bending patterns. Furthermore, increasing the body size has a similar effect of reducing the body-to-body feedback gain (**Figure 9B**) because a larger body size has a higher inertia that delays the wave speed of the body bending.

We hypothesized that a salamander possesses load and stretch sensors at each body part and that sensory information is transmitted to nearby body parts. At present, there is no definitive neurophysiological evidence for the proposed sensory feedback mechanism. However, several biological findings suggest that the proposed mechanism possibly exists. First, it has been reported that the salamander's body and limbs have mechanoreceptors (Chevallier et al., 2008; Ryczko et al., 2020). Second, similar feedback mechanisms were reported for other vertebrates. Specifically, cats utilize signals related to the force in leg muscles to initiate the transition from the stance to swing phase in each leg (Pearson et al., 2006), while lampreys utilize stretch receptors along the trunk to coordinate axial movements (Grillner, 1996). Third, the neural circuits for limb movements are located in particular vertebrae above and below the axial trunk network (Bicanski et al., 2013b). Therefore, sharing sensory signals among nearby body parts is feasible.

Further biological studies are required to prove the validity of the proposed mechanisms. In addition, direct inter-oscillator couplings are known to exist within the salamander spinal cord, in particular in the axial networks (Ryczko et al., 2010), whereas in this study we purposely removed them in order to focus on sensory-driven synchronization mechanisms. Future studies should investigate this further once the actual neural circuits of the salamander spinal cord are better known. The finding of this study suggests that the role of inter-oscillator coupling in shaping the locomotor patterns might be less important than previously thought, compared to sensory-driven mechanisms.

In the future, we aim to develop a salamander robot and verify the proposed model in the real world. We will investigate the locomotion speed and cost efficiency for various gait patterns and contribution of the proposed sensory feedback mechanisms. This will contribute to an understanding of the merits of gait transitions in sprawling locomotion. Furthermore, we will investigate the robustness of ground property changes. Although this study used flat terrain as the experimental environment, we expect that the proposed sensory feedback mechanisms have some adaptability toward various ground properties, such as a granular surface and gravel road, owing to the body–limb sensory feedback mechanisms. Finally, we would like to elucidate a common principle underlying body–limb coordination by studying other animals. We have already proposed models for body–limb coordination of sea roaches (Kano et al., 2019) and quadrupeds that exhibit cheetah-like galloping (Fukuhara et al., 2020). Based on these studies, we aim to find commonalities to various legged animals, and establish a universal control framework for legged robots with high robustness and adaptability.

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DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

SS, AIj, and AIs designed the study. AIs supervised the project. SS, TK, and AIs designed the mathematical model. SS carried out the simulation experiments and the initial draft of the manuscript. All authors are involved in revising the manuscript.

FUNDING

This work was supported by the Human Frontier Science Program (RGP0027/2017), the Grant-in-Aid for JSPS Research Fellows (No. 20J10805), and the Division for Interdisciplinary Advanced Research and Education, Tohoku University.

ACKNOWLEDGMENTS

The authors would like to thank Dr. Akira Fukuhara, Kotaro Yasui, Taishi Mikami, and Hayato Amaike of Tohoku University for their helpful suggestions.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fnbot.2021.645731/full#supplementary-material>

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Fast and Slow Adaptations of Interlimb Coordination *via* Reflex and Learning During Split-Belt Treadmill Walking of a Quadruped Robot

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OPEN ACCESS

Edited by:

Dai Owaki,
Tohoku University, Japan

Reviewed by:

Malte Schilling,
Bielefeld University, Germany
Takeshi Kano,
Tohoku University, Japan

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Specialty section:

This article was submitted to
Computational Intelligence in Robotics,
a section of the journal
Frontiers in Robotics and AI

Received: 19 April 2021

Accepted: 12 July 2021

Published: 06 August 2021

Citation:

Aoi S, Amano T, Fujiki S, Senda K and
Tsuchiya K (2021) Fast and Slow
Adaptations of Interlimb Coordination
via Reflex and Learning During
Split-Belt Treadmill Walking of a
Quadruped Robot.
Front. Robot. AI 8:697612.
doi: 10.3389/frobt.2021.697612

Interlimb coordination plays an important role in adaptive locomotion of humans and animals. This has been investigated using a split-belt treadmill, which imposes different speeds on the two sides of the body. Two types of adaptation have been identified, namely fast and slow adaptations. Fast adaptation induces asymmetric interlimb coordination soon after a change of the treadmill speed condition from same speed for both belts to different speeds. In contrast, slow adaptation slowly reduces the asymmetry after fast adaptation. It has been suggested that these adaptations are primarily achieved by the spinal reflex and cerebellar learning. However, these adaptation mechanisms remain unclear due to the complicated dynamics of locomotion. In our previous work, we developed a locomotion control system for a biped robot based on the spinal reflex and cerebellar learning. We reproduced the fast and slow adaptations observed in humans during split-belt treadmill walking of the biped robot and clarified the adaptation mechanisms from a dynamic viewpoint by focusing on the changes in the relative positions between the center of mass and foot stance induced by reflex and learning. In this study, we modified the control system for application to a quadruped robot. We demonstrate that even though the basic gait pattern of our robot is different from that of general quadrupeds (due to limitations of the robot experiment), fast and slow adaptations that are similar to those of quadrupeds appear during split-belt treadmill walking of the quadruped robot. Furthermore, we clarify these adaptation mechanisms from a dynamic viewpoint, as done in our previous work. These results will increase the understanding of how fast and slow adaptations are generated in quadrupedal locomotion on a split-belt treadmill through body dynamics and sensorimotor integration via the spinal reflex and cerebellar learning and help the development of control strategies for adaptive locomotion of quadruped robots.

Keywords: split-belt treadmill walking, quadruped robot, interlimb coordination, spinal reflex, cerebellar learning, central pattern generator

1 INTRODUCTION

Humans and animals change their locomotor behaviors depending on the environment and situation. Interlimb coordination plays an important role in such adaptive locomotion. For example, to walk along a curved path, the outer legs have a longer stride and higher speed than those of the inner legs (Courtine and Schieppati, 2003; Gruntman et al., 2007). Split-belt treadmills, which impose different speeds on the two sides of the body (Yanagihara and Udo, 1994; Prokop et al., 1995; Reisman et al., 2005; Morton and Bastian, 2006; Choi and Bastian, 2007; Frigon et al., 2013), have been used to investigate the mechanisms that control interlimb coordination. Adaptive behaviors induced by changes in the treadmill speed condition have been investigated. During the split-belt treadmill walking of humans, when the treadmill speed condition is changed from the tied configuration (belts move at the same speed) to the split-belt configuration (belts move at different speeds), the relative phase between the leg movements rapidly changes to break the antiphase relationship (i.e., asymmetric interlimb coordination appears) and the stride length and duty factor differ between the two legs (Reisman et al., 2005). However, the relative phase slowly returns to regain the antiphase relationship and to reduce the asymmetric interlimb coordination in the split-belt configuration. The stride length and duty factor remain almost unchanged and different between the two legs. Furthermore, when the treadmill speed condition is returned to the tied configuration, the stride length and duty factor quickly return, whereas the relative phase rapidly diverges from antiphase (i.e., asymmetric interlimb coordination appears even in the tied configuration) and then slowly returns to antiphase to reduce the asymmetry. Because the spinal cord and reflex contribute to rapid changes in locomotor behavior due to environmental changes (Grillner, 1975), it has been suggested that the fast adaptations in split-belt treadmill walking are induced by sensorimotor integration in the spinal cord. The slow changes in the relative phase and the quick divergence of the relative phase from antiphase upon return to the tied configuration do not appear during split-belt treadmill walking of subjects with cerebellar damage (Morton and Bastian, 2006), which suggests that these changes are induced by learning in the cerebellum. In particular, the quick divergence of the relative phase upon return to the tied configuration has been suggested to be the after-effect of learning.

Although these adaptive behaviors are observed in walking on a split-belt treadmill, locomotion is a complicated dynamical phenomenon generated through interactions between the central nervous system, the body's musculoskeletal system, and the environment, and thus it is difficult to fully understand the locomotion mechanism based on only observations and measurements of the locomotor system. To overcome this limitation, mathematical models and legged robots have been applied to study locomotion (Aoi et al., 2011, 2017; Fukui et al., 2019; Fukuoka et al., 2015; Ijspeert, 2014; Masuda et al., 2021; Otoda et al., 2009; Owaki et al., 2013; Owaki and Ishiguro, 2017; Spröwitz et al., 2013). In our previous works (Fujiki et al., 2013, 2015), we developed a locomotion control system for a biped robot based on the spinal reflex and

cerebellar learning. We reproduced the fast and slow adaptive behaviors observed in humans during split-belt treadmill walking of the robot. These behaviors were not the result of specifically designed features in our control system, but emerged through the body dynamics and sensorimotor integration via the spinal reflex and cerebellar learning. We clarified these adaptation mechanisms from a dynamic viewpoint by focusing on the changes in the relative positions between the center of mass and foot stance induced by reflex and learning.

Quadrupeds such as cats and mice also exhibit fast and slow changes in interlimb coordination during split-belt treadmill walking (D'Angelo et al., 2014; Darmohray et al., 2019; Frigon et al., 2013; Yanagihara and Udo, 1994). Interlimb coordination in quadrupedal locomotion is more complicated than that in human locomotion due to the increased number of legs. Rapid changes have been observed in spinal cats (Forssberg et al., 1980; Frigon et al., 2013) and slow changes and the after-effect do not appear in mice with cerebellar dysfunction (Darmohray et al., 2019), which suggest that the spinal reflex and cerebellar learning contribute to fast and slow adaptations, respectively, during split-belt treadmill walking of quadrupeds, as is the case for humans. Although previous works (Ito et al., 1998; Kodono and Kimura, 2020; Latash et al., 2020) have investigated adaptive quadrupedal locomotion on a split-belt treadmill using mathematical models and legged robots, they considered specific conditions [e.g., only one of the four legs moved at a different speed (Ito et al., 1998; Kodono and Kimura, 2020) and only the center of mass dynamics in the frontal plane were considered (Latash et al., 2020)]. The gait adaptation mechanism in quadrupedal locomotion through whole-body dynamics and sensorimotor integration for different left- and right-side speeds remains unclear.

In this study, we improve our locomotion control system for a biped robot and apply it to a quadruped robot. We demonstrate that although the basic gait pattern of our robot is different from that of general quadrupeds (due to limitations of the robot experiment), fast and slow adaptations similar to those of quadrupeds appear during split-belt treadmill walking of the quadruped robot. Furthermore, we clarify the adaptation mechanisms from a dynamic viewpoint, as done in our previous work (Fujiki et al., 2015). These results will increase the understanding of how fast and slow adaptations are generated in quadrupedal locomotion on a split-belt treadmill through body dynamics and sensorimotor integration via the spinal reflex and cerebellar learning and help the development of control strategies for adaptive locomotion of quadruped robots.

2 MATERIALS AND METHODS

2.1 Quadruped Robot

In this study, we used the quadruped robot (**Figure 1**) developed in our previous work (Aoi et al., 2013a). It consists of a body and four legs (Legs 1–4). Each leg consists of two links connected by pitch joints (Joints 1 and 2), with each joint manipulated by a motor. A touch sensor is attached to the tip of each leg.

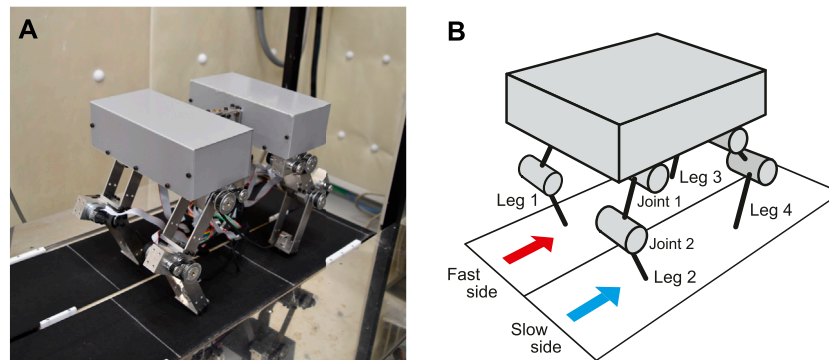


FIGURE 1 | Experimental setup. **(A)** Photograph of quadrupedal robot on split-belt treadmill. The robot body consists of two sections that are mechanically attached to each other. **(B)** Schematic model of quadrupedal robot.

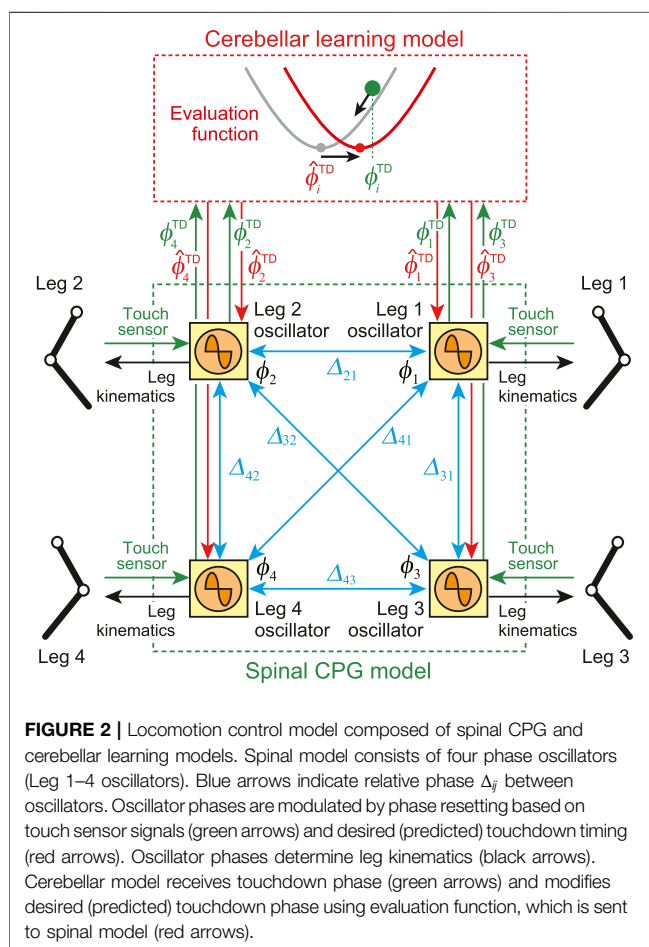


FIGURE 2 | Locomotion control model composed of spinal CPG and cerebellar learning models. Spinal model consists of four phase oscillators (Leg 1–4 oscillators). Blue arrows indicate relative phase Δ_{ij} between oscillators. Oscillator phases are modulated by phase resetting based on touch sensor signals (green arrows) and desired (predicted) touchdown timing (red arrows). Oscillator phases determine leg kinematics (black arrows). Cerebellar model receives touchdown phase (green arrows) and modifies desired (predicted) touchdown phase using evaluation function, which is sent to spinal model (red arrows).

Electric power is externally supplied and the robot is controlled by an external host computer (Intel Pentium 4 2.8 GHz, RT-Linux), which calculates the desired joint motions and solves the oscillator phase dynamics in the control system (see **Section 2.3**). The robot receives command signals at intervals of 1 ms. It is connected to the electric power

unit and the host computer by cables, which are slack and suspended during the experiment to avoid influencing the robot's locomotor behavior.

2.2 Split-Belt Treadmill

The robot walked on the split-belt treadmill (**Figure 1**) developed in our previous works (Fujiki et al., 2013, 2015). The treadmill has two parallel belts, each of which is equipped with a motor and an encoder to control the individual belt speed. The width of each belt is 15 cm and the distance between rotation axes is 64 cm.

2.3 Locomotion Control System

In our previous work (Fujiki et al., 2015), we developed a locomotion control system for a biped robot based on the spinal and cerebellum functions. In this study, we improved the control system and applied it to the quadruped robot (**Figure 2**). The control system consists of spinal and cerebellum models. The spinal model produces motor commands to manipulate the robot based on a central pattern generator (CPG) and the sensory reflex, and the cerebellum model modulates motor commands through learning.

2.3.1 Spinal CPG Model

Our spinal CPG model is based on a physiological two-layer network model composed of rhythm generator (RG) and pattern formation (PF) networks (Burke et al., 2001; Rybak et al., 2006). The RG network creates the basic rhythm. It alters the rhythm by producing phase shifts and by performing rhythm resetting in response to sensory feedback (phase resetting). The PF network shapes the rhythm into spatiotemporal motor command patterns. Based on this physiological finding, we developed the spinal CPG model using the following RG and PF models.

For the RG model, we used four simple phase oscillators (Leg 1–4 oscillators), whose phases are denoted by ϕ_i ($i = 1, \dots, 4$, $0 \leq \phi_i < 2\pi$). Because the oscillator phase determines the desired movement of the corresponding leg, as explained below, the relative phases between the oscillators $\Delta_{ij} = \phi_i - \phi_j$ ($i, j = 1, \dots, 4$, $0 \leq \Delta_{ij} < 2\pi$) determine the gait. The oscillator phases follow the dynamics

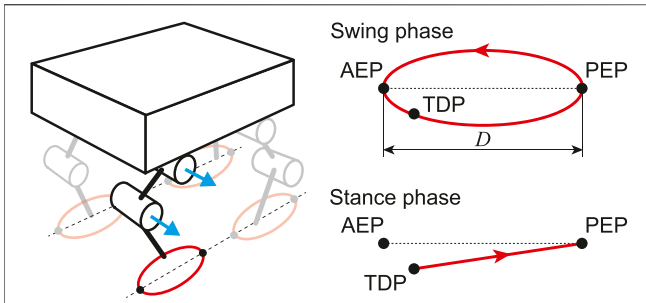


FIGURE 3 | Desired leg kinematics composed of swing and stance phases. At touchdown position (TDP), trajectory changes from swing to stance phase. When leg tip reaches posterior extreme position (PEP), trajectory moves into swing phase. Anterior extreme position (AEP) is desired position of touchdown.

$$\dot{\phi}_i = \omega - \sum_{j=1}^4 K_{ij} \sin(\Delta_{ij} - \hat{\Delta}_{ij}) + \left(\hat{\phi}_i^{\text{TD}} - \phi_i^{\text{TD}} \right) \delta(t - t_i^{\text{TD}}) \quad (1)$$

where ω is the basic oscillator frequency, K_{ij} is the gain parameter, and $\delta(\cdot)$ is the Dirac delta function. The second term on the right-hand side represents the interactions among oscillators to move the relative phase Δ_{ij} to the desired value $\hat{\Delta}_{ij}$, which is determined by the desired gait pattern. The third term on the right-hand side represents phase resetting. Taking inspiration from spinal cats walking on a treadmill, which show how touchdown information influences the locomotion phase and rhythm generated by a CPG (Duysens et al., 2000), we modulate the oscillator phase so that it responds to touch sensor signals based on phase resetting. Specifically, when the touchdown of Leg i occurs at time t_i^{TD} ($\phi_i = \phi_i^{\text{TD}}$ at t_i^{TD}), the phase of Leg i oscillator ϕ_i is reset from ϕ_i^{TD} to $\hat{\phi}_i^{\text{TD}}$ (superscript TD refers to touchdown). This $\hat{\phi}_i^{\text{TD}}$ corresponds to the desired (predicted) touchdown phase, as explained in Section 2.3.2.

For the PF model, taking inspiration from the physiological finding that spinocerebellar neurons encode the global information of limb kinematics, such as the length and orientation of the limb axis (Bosco and Poppele, 2001; Poppele et al., 2002; Poppele and Bosco, 2003), we produced the motor commands to achieve the desired leg kinematics of the robot based on the oscillator phases obtained from the RG model. We use simple leg kinematics, which consist of the swing and stance phases (Figure 3), in reference to the length and orientation of the limb axis in the pitch plane. The swing phase uses a simple closed curve for the leg tip that includes the anterior extreme position (AEP) and the posterior extreme position (PEP). It starts from the PEP and continues until touchdown. The AEP corresponds to the desired position of touchdown. The stance phase uses a straight line from the touchdown position (TDP) to the PEP. The trajectories for the swing and stance phases are given as functions of the corresponding oscillator phase, where $\phi_i = 0$ at the PEP and $\phi_i = \hat{\phi}_i^{\text{TD}}$ at the AEP. We denote the distance between the AEP and PEP as D and the gait cycle as T ($\omega = 2\pi/T$). The desired duty

factor $\hat{\beta}_i$, stride length $\hat{S}_i$, and locomotion speed $\hat{V}_i$ of Leg i are then given by

$$\hat{\beta}_i = 1 - \frac{\hat{\phi}_i^{\text{TD}}}{2\pi}, \quad \hat{S}_i = \frac{D}{\hat{\beta}_i}, \quad \hat{V}_i = \frac{D}{\hat{\beta}_i T} \quad (2)$$

To generate the desired kinematics, the desired joint trajectories are calculated based on the inverse kinematics and each joint is controlled by the joint torque based on proportional-derivative feedback control.

2.3.2 Cerebellar Learning Model

The cerebellum predicts the sensory consequences of movement based on the efference copy, and modifies motor commands to reduce errors between the predicted and actual sensory information through learning. Furthermore, it predicts the timing of sensory events (Nixon and Passingham 2001; O'Reilly et al. 2008) and contributes to achieving tasks that require accurate temporal control (Ivry et al., 2012; Ivry and Keele, 1989; Spencer et al., 2005). During walking on a surface with an unexpected hole, the absence of touchdown sensory feedback at the predicted timing triggers reflex-like reaction behavior (Hiebert et al., 1994; van der Linden et al., 2007), which suggests that the prediction of touchdown timing is important for motor learning in walking.

We focused on touchdown timing for the cerebellar model. In particular, we modulate the desired (predicted) touchdown timing $\hat{\phi}_i^{\text{TD}}$ based on the error between the predicted and actual touchdown timings. For this purpose, we define an evaluation function $E_{i,n}$ for the n th step of Leg i using the error between the predicted touchdown phase $\hat{\phi}_{i,n}^{\text{TD}}$ and the actual touchdown phase $\phi_{i,n}^{\text{TD}}$ for the n th step of Leg i , which is given by

$$E_{i,n} = \frac{1}{2} \left(\hat{\phi}_{i,n}^{\text{TD}} - \phi_{i,n}^{\text{TD}} \right)^2 \quad (3)$$

Based on this evaluation function, we predict the next touchdown timing. Specifically, from the gradient direction of the evaluation function, $\hat{\phi}_i^{\text{TD}}$ is modulated by

$$\hat{\phi}_{i,n+1}^{\text{TD}} = \hat{\phi}_{i,n}^{\text{TD}} - \alpha \frac{\partial E_{i,n}}{\partial \hat{\phi}_{i,n}^{\text{TD}}} \quad (4)$$

where α is the learning rate. Because $\hat{\phi}_i^{\text{TD}}$ is the desired timing of the corresponding leg to switch from the swing phase to the stance phase, this temporal modulation changes the desired duty factor of the corresponding leg (Eq. 2). Therefore, if the touchdown arrives earlier than predicted, the robot increases the swing leg speed in the next step ($\hat{\phi}_i^{\text{TD}}$ decreases and $\hat{\beta}_i$ increases while D remains unchanged). In addition, the TDP gravitates to alignment with the AEP (Figure 3) through this modulation.

2.4 Robot Experiment

To clarify the functional roles of the spinal and cerebellar models in gait adaptation during split-belt treadmill walking of the quadruped robot, we considered the following two cases in the robot experiment: 1) with the spinal model but without the

cerebellar model, that is, the desired (predicted) touchdown timing $\hat{\phi}_i^{\text{TD}}$ ($i = 1, \dots, 4$) was fixed, and 2) with both the spinal and cerebellar models. For both cases, we suddenly changed the treadmill speed condition during walking and investigated how the locomotor behavior changed. In particular, when we used only the spinal model, we investigated fast adaptation via the sensory reflex using various treadmill speed conditions. In contrast, when we used both the spinal and cerebellar models, we examined slow adaptation via learning as well as fast adaptation.

For the quadruped robot, we used the following control parameters: $D = 1.5$ cm, $T = 0.33$ s, and $\alpha = 0.25$. For the initial value of $\hat{\phi}_i^{\text{TD}}$, we used π , which gives $\hat{\beta}_i = 0.5$, $\hat{S}_i = 3$ cm, and $\hat{V}_i = 9.1$ cm/s. For the desired value of the relative phases, we used $\hat{\Delta}_{12} = \hat{\Delta}_{34} = \pi$ and $\hat{\Delta}_{13} = \hat{\Delta}_{24} = 0$. This means that the desired gait pattern was the pace pattern, which is different from the walk pattern ($\hat{\Delta}_{13} = \hat{\Delta}_{24} = -\pi/2$) and trot pattern ($\hat{\Delta}_{13} = \hat{\Delta}_{24} = \pi$) of general quadrupeds. This was done because the robot with the walk or trot pattern could not continue walking straight on the split-belt treadmill. Specifically, it easily changed walking direction (yaw motion was induced) due to changes in the treadmill speed condition because the fore and hind legs were in contact with different belts. Instead, we used small values for K_{ij} ($K_{12} = K_{21} = K_{34} = K_{43} = K_{13} = K_{31} = K_{24} = K_{42} = 2$, with other K_{ij} set to zero) so that the relative phases could be shifted from the desired value by phase resetting and learning through locomotion dynamics [we used 20 for K_{ij} to fix the relative phase to the desired value in our previous work (Aoi et al., 2013a)]. The same control parameters and initial conditions were used irrespective of the use of the cerebellar model and treadmill speed condition.

For the split-belt treadmill, we used the tied configuration at the beginning of the robot walk with $v_1 = v_2 = 6.5$ cm/s, where v_1 and v_2 are the speeds of the right belt (Legs 1 and 3) and left belt (Legs 2 and 4), respectively. After the robot had established a steady gait, we suddenly changed the speed condition from the tied configuration to the split-belt configuration, but did not change the control strategy and parameters. When we used only the spinal model, we used the following three speed conditions for the split-belt configuration: 3x: $v_1 = 9.8$ and $v_2 = 3.3$ cm/s ($v_1/v_2 = 3$), 4x: $v_1 = 10.8$ and $v_2 = 2.7$ cm/s ($v_1/v_2 = 4$), 5x: $v_1 = 13.5$ and $v_2 = 2.7$ cm/s ($v_1/v_2 = 5$). Therefore, we consider Legs 1 and 3 as the fast side and Legs 2 and 4 as the slow side (Figure 1B). When we incorporated the cerebellar model, we used the 5x condition for the split-belt configuration. In addition, we returned the speed condition to the tied configuration from the split-belt configuration without changing the control strategy and parameters.

We performed these robot trials five times for each speed condition and investigated the robot's behavior from the averages of the results for six steps in each configuration period. When we incorporated the cerebellar model, we separated the periods of the split-belt configuration and the second tied configuration into two halves to clarify early and late stages of adaptation in each period. We used one-way repeated-measures analysis of variance (ANOVA) to compare the differences between the periods and to clarify the significance of the locomotor behavior changes. When the ANOVA results showed a significant difference, we conducted post hoc analysis using Tukey's honestly significant

difference test, where we considered that $p < 0.05$ indicates a significant difference.

3 RESULTS

3.1 Fast Adaptation by Reflex

We first used only the spinal model for the robot experiment. At the beginning, the robot walked on the treadmill in the tied configuration with the fore and hind legs in contact with the ipsilateral belt. It continued walking after the treadmill speed condition changed to the 3x, 4x, and 5x conditions of the split-belt configuration. Note that when we did not use phase resetting in Eq. 1, the robot could not walk on the treadmill even in the tied configuration.

Figure 4A shows the relative phases Δ_{12} , Δ_{13} , Δ_{24} , and Δ_{34} for one representative trial of the 5x condition using the average value for one gait cycle obtained using $\frac{1}{T} \int_T \Delta_{ij} dt$ (see supplementary movie). Δ_{12} and Δ_{34} were almost π and Δ_{13} and Δ_{24} were almost 0 in the tied configuration. Δ_{12} and Δ_{13} decreased and Δ_{24} increased in the split-belt configuration. Figure 4B shows their averages in the tied configuration and the split-belt configuration in the 5x condition for five trials, where we used six steps for each configuration period in one trial. Δ_{13} and Δ_{24} showed significant differences between the belt speed conditions ($p < 0.01$ and $p < 0.05$, respectively) and Δ_{12} showed the most significant difference ($p < 0.001$). In contrast, Δ_{34} showed no significant difference.

Figure 5A shows the duty factors of Legs 1–4 for one representative trial of the 5x condition. The duty factors of Legs 1 and 2 were around 0.6 in the tied configuration. That of Leg 1 decreased and that of Leg 2 increased in the split-belt configuration. In contrast, those of Legs 3 and 4 slightly fluctuated around 0.6 and did not show clear trends. Figure 5B shows their averages in the tied configuration and the split-belt configuration in the 5x condition for five trials. The duty factors of Legs 1 and 2 showed significant differences between the belt speed conditions (both $p < 0.01$), whereas those of Legs 3 and 4 showed no significant difference.

Figures 6A, B show the changes in the average relative phases and duty factors, respectively, between the tied configuration and the split-belt configuration for three speed conditions (3x, 4x, and 5x). The changes in the relative phases Δ_{13} and Δ_{34} showed no clear dependence on the speed condition, whereas those in Δ_{12} and Δ_{24} increased as the speed discrepancy between the left and right belts increased. In particular, the change in Δ_{12} showed a significant difference between the 3x and 5x conditions ($p < 0.05$). The changes in the duty factors for Legs 3 and 4 showed no clear dependence on the speed condition, whereas those for Legs 1 and 2 increased as the speed discrepancy between the left and right belts increased. However, they showed no significant difference.

3.2 Slow Adaptation by Learning

We next used both the spinal and cerebellar models for the robot experiment. At the beginning, the robot walked on the treadmill in the tied configuration. It continued walking when the treadmill

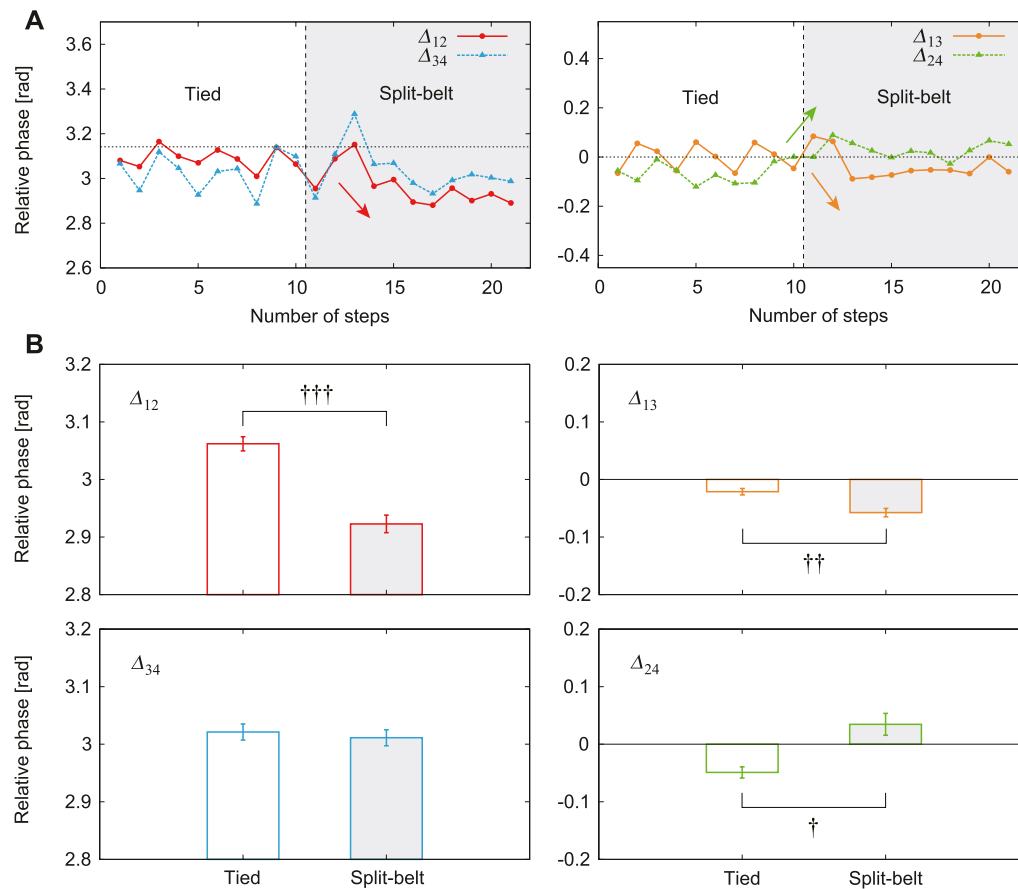


FIGURE 4 | Relative phases between leg oscillators with use of only spinal model. **(A)** Δ_{12} , Δ_{13} , Δ_{24} , and Δ_{34} for one representative trial of 5x condition. **(B)** Their averages for tied and split-belt configurations. Data points and error bars are the mean and standard error results of five experiments, respectively. † : $p < 0.05$, †† : $p < 0.01$, and ††† : $p < 0.001$.

speed condition changed to the 5x condition of the split-belt configuration. Furthermore, the robot continued walking after the treadmill speed condition returned to the tied configuration.

The relative phase Δ_{12} clearly changed depending on the treadmill speed condition, similar to previous results, whereas the other relative phases did not. **Figure 7A** shows Δ_{12} for one representative trial, where the left and right figures show the results from the first tied configuration to the split-belt configuration and from the split-belt configuration to the second tied configuration, respectively. Δ_{12} was almost π in the first tied configuration. It quickly decreased at the early stage (first half) of the split-belt configuration and slowly returned to π at the late stage (last half). In addition, it quickly decreased at the early stage of the second tied configuration, which suggests the after-effect of learning. Finally, it slowly returned to π at the late stage of the second tied configuration. **Figure 7B** shows the average in the first tied configuration and early and late stages of the split-belt and second tied configurations. Significant differences appear between the first tied configuration and early stage of the split-belt configuration ($p < 0.01$), between the early and late stages of

the split-belt configuration ($p < 0.01$), between the split-belt configuration and the early stage of the second tied configuration ($p < 0.05$), and between the early and late stages of the second tied configuration ($p < 0.05$).

In this experiment, the duty factors for Legs 1 and 2 clearly changed depending on the treadmill speed condition, whereas the other duty factors did not, similar to previous results. **Figure 8A** shows the duty factors for Legs 1 and 2 for one representative trial, where the left and right figures show the results from the first tied configuration to the split-belt configuration and from the split-belt configuration to the second tied configuration, respectively. The duty factors for Legs 1 and 2 were almost 0.6 in the first tied configuration. The duty factor for Leg 1 quickly decreased and that for Leg 2 increased at the early stage of the split-belt configuration. However, they had almost no change at the late stage, unlike the relative phases (**Figure 7**). They quickly returned to almost 0.6 at the early stage of the second tied configuration and did not change at the late stage. **Figure 8B** shows their averages for the first tied configuration and the early and late stages for the split-belt and second tied configurations. The duty factor for Leg 1 showed significant differences between the first tied configuration and early stage of

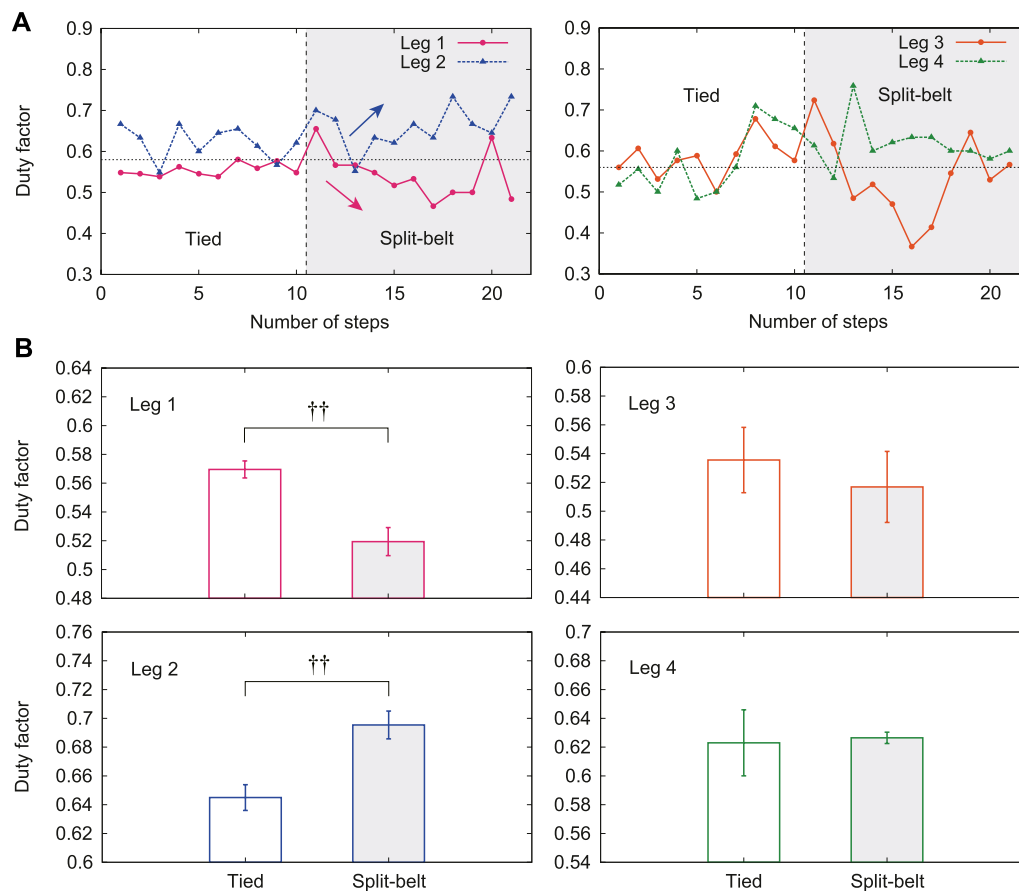


FIGURE 5 | Duty factors with use of only spinal model. **(A)** Duty factors for Legs 1–4 for one representative trial of 5x condition. **(B)** Their averages for tied and split-belt configurations. Data points and error bars are the mean and standard error results of five experiments, respectively. †† : $p < 0.01$.

the split-belt configuration ($p < 0.05$) and between the first tied configuration and late stage of the split-belt configuration ($p < 0.01$). However, it showed no significant difference between the split-belt configuration and early and late stages of the second tied configuration. The duty factor for Leg 2 also showed significant differences between the first tied configuration and early stage of the split-belt configuration ($p < 0.01$) and between the first tied configuration and late stage of the split-belt configuration ($p < 0.01$). In addition, it showed significant differences between the split-belt configuration and early stage of the second tied configuration ($p < 0.05$) and between the split-belt configuration and early stage of the second tied configuration ($p < 0.05$).

4 DISCUSSION

4.1 Fast Adaptation Mechanism Upon Change to Split-Belt Configuration

When we used only the spinal model, the relative phase Δ_{34} exhibited almost no change, whereas Δ_{12} decreased from π , Δ_{13} decreased from 0, and Δ_{24} increased from 0 due to the change in

the treadmill speed condition from the tied configuration to the split-belt configuration (Figure 4). The duty factor for Leg 1 increased, that for Leg 2 decreased, and those for Legs 3 and 4 exhibited almost no change (Figure 5). The asymmetric interlimb coordination and duty factors allow the robot to walk in the asymmetric speed condition. Furthermore, these asymmetries increased as the belt speed discrepancy increased (Figure 6). Such asymmetric locomotion parameters and increase in asymmetries induced by the speed condition have been observed in cats and mice (D'Angelo et al., 2014; Darmohray et al., 2019). Our results are consistent with these observations. Note that the fast changes in our robot were not the result of specifically designed features in our control system, but emerged through the body dynamics and sensorimotor integration via the spinal reflex. We discuss the mechanism of these gait adaptations from a dynamic viewpoint by focusing on changes in the foot contact timing because the locomotor behavior is modulated by phase resetting in Eq. 1 based on foot contact timing in the spinal model, where we assume that the forward/backward movements and pitch rotation are dominant, as assumed in our previous work on a biped robot (Fujiki et al., 2015), because the backward speed of the treadmill belts changes.

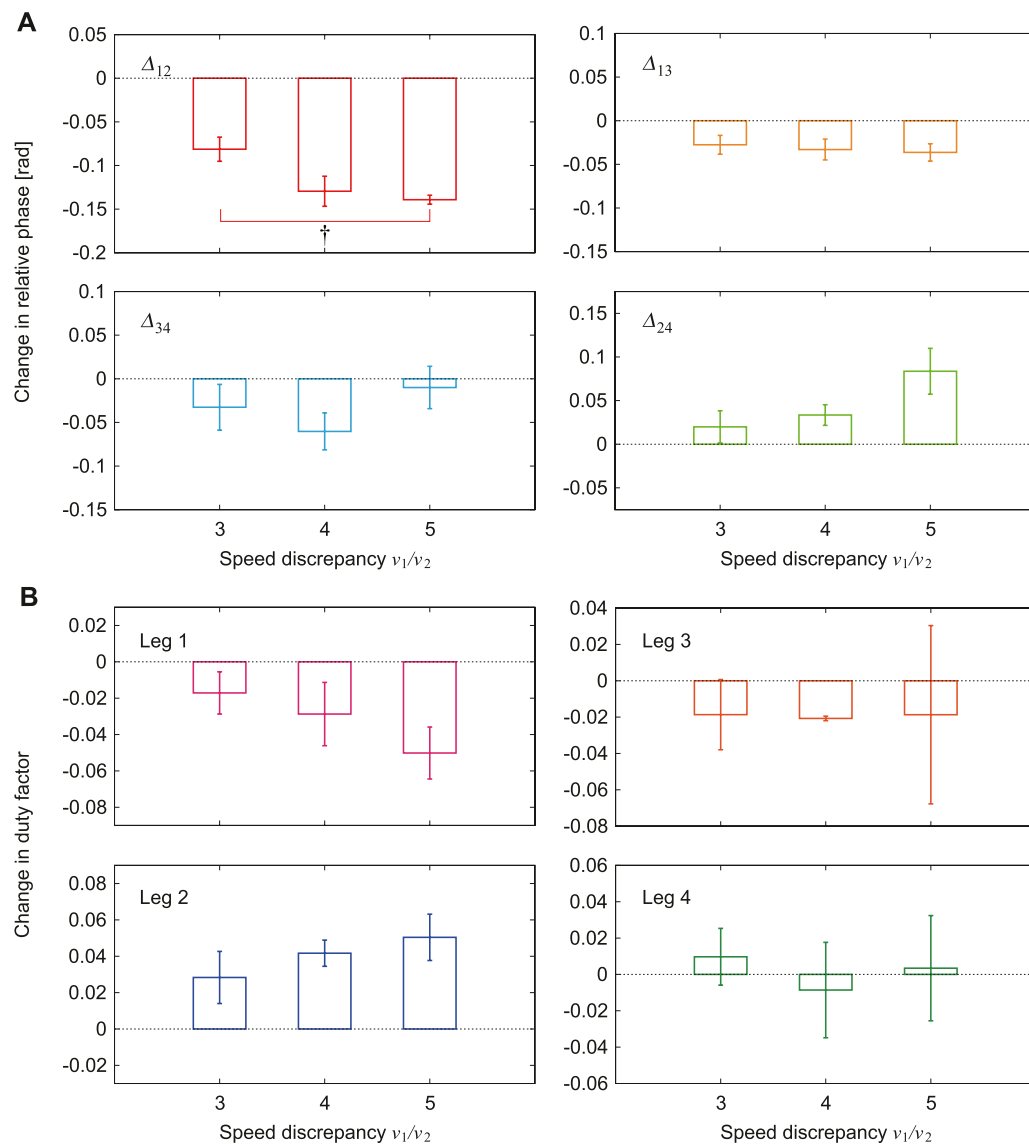


FIGURE 6 | Changes in average (A) relative phases and (B) duty factors between tied and split-belt configurations for 3x, 4x, and 5x conditions ($v_1/v_2 = 3, 4$, and 5). Data points and error bars are the mean and standard error results of five experiments, respectively. $\dagger : p < 0.05$.

In the tied configuration, the stance legs on both the fast and slow sides are pulled at the same speed. The fore and hind legs on the ipsilateral side contact the belt simultaneously (**Figure 9A**). In contrast, the stance legs on the fast side (Legs 1 and 3) are strongly pulled in the split-belt configuration, which accelerates the body and tilts it forward (**Figure 9B**). As a result, the fore leg on the slow side (Leg 2) touches the belt earlier than in the tied configuration. However, the foot contact timing of the hind leg on the slow side (Leg 4) shows almost no change because the swing leg trajectory moves upward due to the body tilt while the anterior part of the trajectory moves downward due the trajectory tilt. The stance legs on the slow side (Legs 2 and 4) are weakly pulled in the split-belt configuration, which

decelerates the body and tilts it backward. As a result, the fore leg on the fast side (Leg 1) touches the belt later than in the tied configuration. However, the foot contact timing of the hind leg on the fast side (Leg 3) shows almost no change because the swing leg trajectory moves downward due to the body tilt while the anterior part of the trajectory moves upward due the trajectory tilt. These changes in the foot contact timings change the relative phases Δ_{12} , Δ_{13} , and Δ_{24} , and the duty factors for Legs 1 and 2, without changing the relative phase Δ_{34} and the duty factors for Legs 3 and 4. As the speed discrepancy between the belts increases, changes in the body tilt and foot contact timings increase. As a result, the changes in the relative phases and duty factors increase.

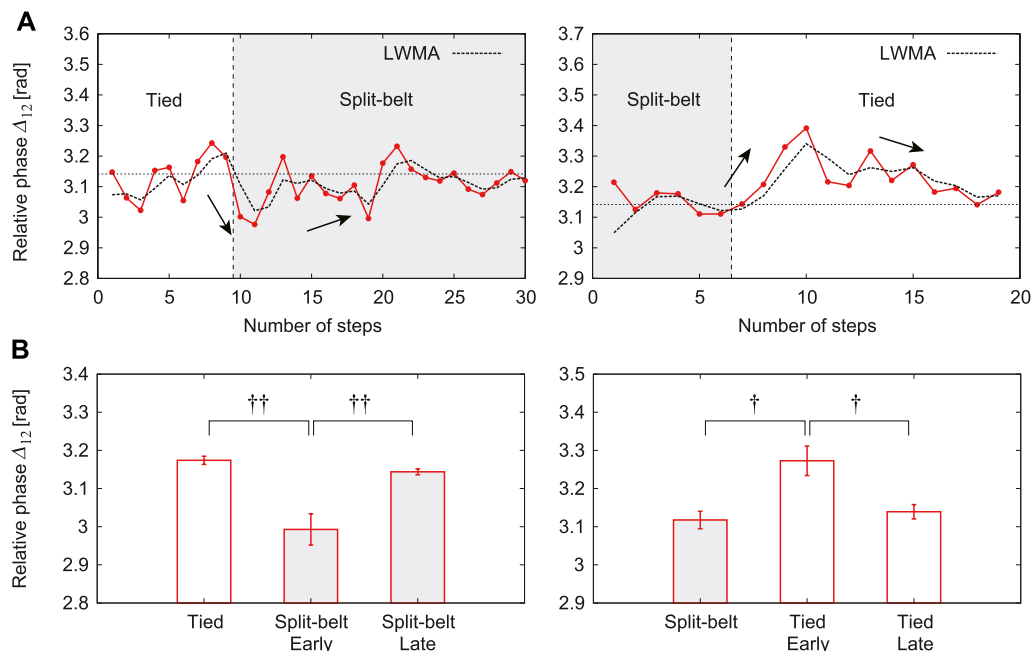


FIGURE 7 | Relative phase Δ_{12} with use of both spinal and cerebellar models. **(A)** One representative trial with moving average [five-period linear weighted moving average (LWMA)]. **(B)** Average for each period. Data points and error bars are the mean and standard error results of five experiments, respectively. † : $p < 0.05$ and †† : $p < 0.01$.

4.2 Slow Adaptation Mechanism in Split-Belt Configuration

When we incorporated the cerebellar model as well as the spinal model, adaptive changes in locomotor behaviors similar to those observed with the use of only the spinal model appeared at the early stage of the split-belt configuration. However, different adaptive behavior appeared in the late stage of the split-belt configuration due to the learning by the cerebellar model. In particular, after the relative phase Δ_{12} quickly decreased from π at the early stage, it slowly returned to π at the late stage; that is, the asymmetry in the interlimb coordination was slowly reduced (Figure 7). In contrast, although the duty factors for Legs 1 and 2 quickly decreased and increased, respectively, at the early stage, they remained almost unchanged at the late stage (Figure 8). Such a slow reduction of the asymmetry in interlimb coordination has been observed in cats and mice (Darmohray et al., 2019; Yanagihara and Udo, 1994). Our results are consistent with these observations. Note that the changes in the locomotor behavior at the late stage for our robot were not characteristics that we specifically designed into our control model, but were generated through the body dynamics and sensorimotor integration via the spinal reflex and cerebellar learning. We discuss the mechanism of these gait adaptations from a dynamic viewpoint, as done in the previous section, by focusing on changes in foot contact timings because the locomotor behavior is also modulated by the cerebellar learning model Eq. 4 based on foot contact timing through phase resetting in Eq. 1.

Because the touchdown of the fore leg on the slow side (Leg 2) is advanced at the early stage (Figure 9B), the swing leg speed

slowly increases due to learning. As a result, the stance legs on the fast side (Legs 1 and 3) are delayed relative to the slow side at the late stage, which reduces the pitching moment to tilt the body forward and induces simultaneous foot contact between the fore and hind legs on the slow side (Legs 2 and 4), as shown in Figure 9C. Similarly, because the touchdown of the fore leg on the fast side (Leg 1) is delayed at the early stage (Figure 9B), the swing leg speed slowly decreases due to learning. As a result, the stance legs on the slow side (Legs 2 and 4) are advanced relative to the fast side at the late stage, which reduces the pitching moment to tilt the body backward and induces simultaneous foot contact between the fore and hind legs on the fast side (Legs one and 3), as shown in Figure 9C. These slow changes in the foot contact timings change the relative phase Δ_{12} without changing the duty factors at the late stage. Note that although this mechanism suggests that Δ_{13} and Δ_{24} also show further changes at the late stage, we did not clearly observe such changes because they are smaller than those for Δ_{12} , as shown in Figure 9C.

4.3 After-Effect Mechanism due to Fast and Slow Adaptations Upon Return to Tied Configuration

When the treadmill speed condition was returned to the tied configuration, locomotor behaviors different from those in the first tied configuration appeared. In particular, the relative phase Δ_{12} quickly diverged from π ; that is, the asymmetry in interlimb coordination appeared again (Figure 7). Although

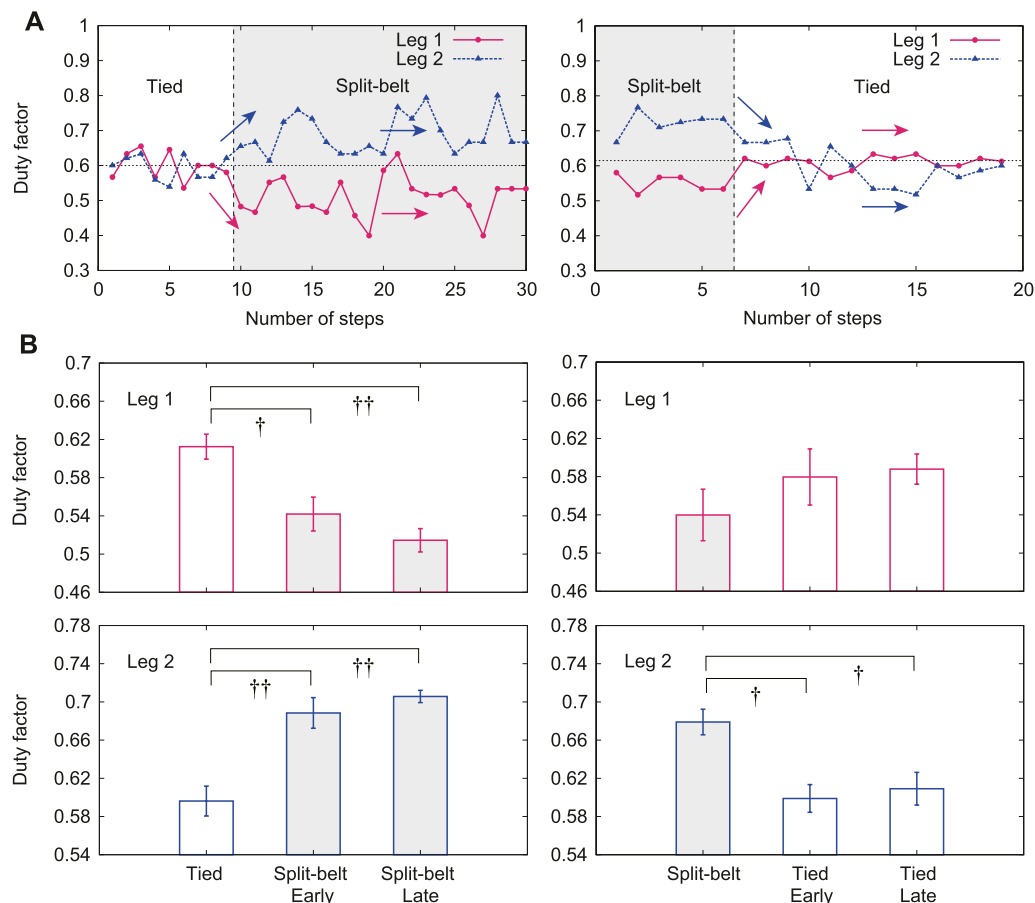


FIGURE 8 | Duty factors for Legs 1 and 2 with use of both spinal and cerebellar models. **(A)** One representative trial. **(B)** Averages for each period. Data points and error bars are the mean and standard error results of five experiments, respectively. †: $p < 0.05$ and ††: $p < 0.01$.

this quick change is due to the spinal reflex, the divergence from π is due to learning in the previous split-belt configuration. This suggests the after-effect of learning. In contrast, the duty factors for Legs 1 and 2 returned to the values in the first tied configuration (Figure 8). Such asymmetry in the interlimb coordination due to the after-effect has been observed in cats and mice (Darmohray et al., 2019; Yanagihara and Udo, 1994). Our results are consistent with these observations. Note that these changes in our robot were not the result of specifically designed features in our control system, but emerged through the body dynamics and sensorimotor integration via the spinal reflex and cerebellar learning. We discuss the mechanism of these gait adaptations from a dynamic viewpoint, as done in previous sections.

In the late stage of the split-belt configuration, the stance legs on the fast side (Legs 1 and 3) are delayed relative to the slow side due to the learning effect, which reduces the pitching moment to tilt the body forward by the strong pulling (Figure 9C). When the treadmill speed condition is returned to the tied configuration, the strong pulling also returns, which induces the pitching moment to tilt the body backward (Figure 9D). As a result, the fore leg on the slow side (Leg

2) touches the belt later than in the late stage of the split-belt configuration. The foot contact timing of the hind leg on the slow side (Leg 4) shows almost no change for the same reason as that for the foot contact timing of the hind leg on the fast side (Leg 3) in the early stage of the split-belt configuration (Figure 9B). Similarly, in the late stage of the split-belt configuration, the stance legs of the slow side (Legs 2 and 4) are advanced relative to the fast side due to the learning effect, which reduces the pitching moment to tilt the body backward by the weak pulling (Figure 9C). When the treadmill speed condition is returned to the tied configuration, the weak pulling also returns, which induces the pitching moment to tilt the body forward (Figure 9D). As a result, the fore leg on the fast side (Leg 1) touches the belt earlier than in the late stage of the split-belt configuration. The foot contact timing of the hind leg on the fast side (Leg 3) shows almost no change for the same reason as that for the foot contact timing of the hind leg on the slow side (Leg 4) in the early stage of the split-belt configuration (Figure 9B). These changes in the foot contact timings induce a different behavior of Δ_{12} from that in the first tied configuration and the same behaviors of the duty factors for Legs 1 and 2 as those in the first tied configuration.

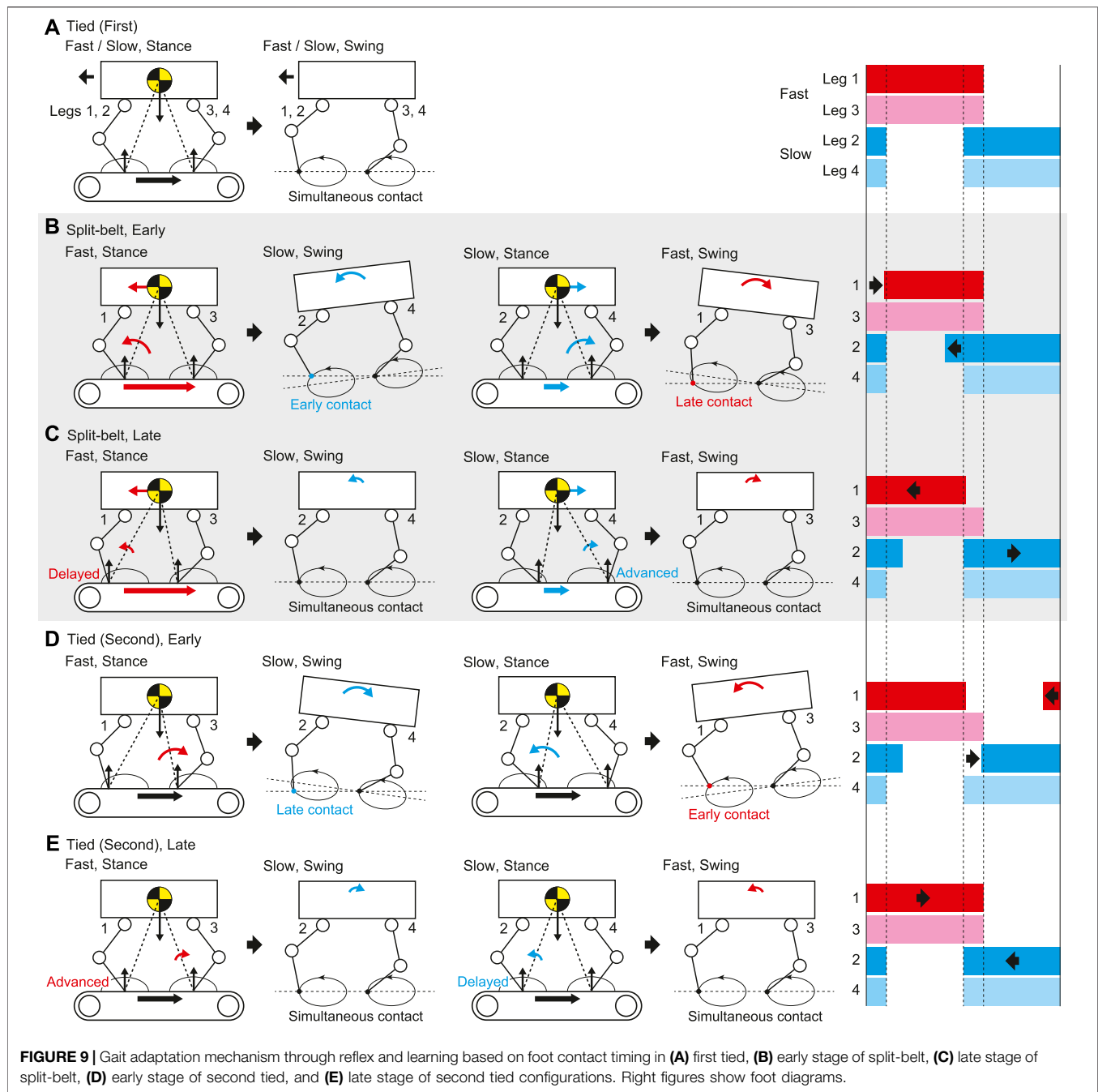


FIGURE 9 | Gait adaptation mechanism through reflex and learning based on foot contact timing in (A) first tied, (B) early stage of split-belt, (C) late stage of split-belt, (D) early stage of second tied, and (E) late stage of second tied configurations. Right figures show foot diagrams.

4.4 Slow Adaptation Mechanism After Return to Tied Configuration

Although the relative phase Δ_{12} showed behavior at the early stage of the second tied configuration different from that in the first tied configuration due to the after-effect, it slowly returned at the late stage through learning (Figure 7). That is, the asymmetry in interlimb coordination appeared at the early stage and slowly reduced at the late stage. The slow reduction of the asymmetry in interlimb coordination induced by the after-effect has been observed in cats and mice (Darmohray

et al., 2019; Yanagihara and Udo, 1994). Our results are consistent with these observations. Note that these changes in our robot were not characteristics that we specifically designed into our control model, but were generated through the body dynamics and sensorimotor integration via the spinal reflex and cerebellar learning. We discuss the mechanism of this gait adaptation from a dynamic viewpoint, as done in previous sections.

Because the touchdown of the fore leg on the slow side (Leg 2) is delayed at the early stage (Figure 9D), the swing leg speed slowly decreases due to learning. As a result, the stance legs on

the fast side (Legs 1 and 3) are advanced relative to the slow side at the late stage, which reduces the pitching moment to tilt the body backward and induces simultaneous foot contact between the fore and hind legs on the slow side (Legs 2 and 4), as shown in **Figure 9E**. Similarly, because the touchdown of the fore leg on the fast side (Leg 1) is advanced at the early stage (**Figure 9D**), the swing leg speed slowly increases due to learning. As a result, the stance legs on the slow side (Legs 2 and 4) are delayed relative to the fast side at the late stage, which reduces the pitching moment to tilt the body forward and induces simultaneous foot contact between the fore and hind legs on the fast side (Legs 1 and 3), as shown in **Figure 9E**. These slow changes in the foot contact timings change the relative phase Δ_{12} at the late stage.

4.5 Contributions of Spinal Cord and Cerebellum to Locomotor Adaptation

A split-belt treadmill imposes different speeds on the two sides of the body and highlights the functional role of interlimb coordination in adaptive locomotion. In particular, the adaptive behavior in interlimb coordination can be classified into two types, namely fast and slow adaptations. That is, the locomotion control system has two different time scales. These adaptations are primarily achieved by the contributions of different layers in the neural system, namely the spinal cord and cerebellum. The spinal cord provides motor commands through the RG and PF networks (Burke et al., 2001; Rybak et al., 2006) and modulates the commands immediately responding to sensory feedback (Grillner, 1975). This immediate modulation contributes to fast adaptation, as suggested by the fact that spinal cats walking on a split-belt treadmill show rapid adaptive behavior (Forssberg et al., 1980; Frigon et al., 2013). The cerebellum receives the efference copy from the spinal cord via the ventral spinocerebellar tract and sensory information via the dorsal spinocerebellar tract (Arshavsky et al., 1983; Fedirchuk et al., 2013). Purkinje cells provide the output from the cerebellar cortex to modulate motor commands based on error information between the sensory information predicted via the efference copy and the actual sensory information. This modification contributes to slow adaptation, as suggested from the fact that mice with Purkinje cell degeneration walking on a split-belt treadmill do not exhibit slow adaptive behavior and after-effect (Darmohray et al., 2019). The reflexive response in the spinal cord secures the ability to continue walking as the environment changes, which quickly induces asymmetric interlimb coordination. The cerebellum slowly modulates the movements under the secured condition to make walking smoother and more efficient, which slowly reduces asymmetric interlimb coordination.

Animals make predictions by evaluating various parameters to enhance their movements through learning in motor control. The cerebellum contributes to this prediction and learning. However, because it remains unclear what is predicted and how to use it in learning, modeling studies have attracted attention.

In particular, learning models of human arm movements have been proposed to minimize jerk and torque change (Flash and Hogan, 1985; Uno et al., 1989). Although learning techniques, such as deep reinforcement learning, have been used to control legged robots (Hwangbo et al., 2019; Lee et al., 2020; Lillicrap et al., 2016), cerebellar learning models for locomotion remain largely unestablished. This is partly because locomotion is a whole-body movement through leg movement and posture controls and is governed by complicated dynamics, including foot contact and lift off, which change the physical constraints. In this study, we focused on the foot contact timing for prediction and learning in the cerebellar model. This is because phase modulation in response to the stimulation of nerves in the legs (Conway et al., 1987; Duysens, 1977; Frigon et al., 2010; Fujiki et al., 2019; Schomburg et al., 1998) and reflexive reaction in the absence of foot contact sensory information (Hiebert et al., 1994; van der Linden et al., 2007) suggest that sensory information related to foot contact timing play important roles in modulating locomotor behavior. In addition, ankle stiffness is predictively modulated at foot contact in split-belt treadmill walking (Ogawa et al., 2014). Moreover, climbing fiber responses of Purkinje cells, which provide error information for motor control, increase around foot contact (Yanagihara and Udo, 1994). However, the prediction and learning of foot contact timing do not necessarily lead to the adaptations observed during split-belt treadmill walking of animals. Our previous works (Fujiki et al., 2013, 2015) showed that a biped robot with our control system exhibits the fast and slow adaptations observed in humans. Furthermore, this study showed that a quadruped robot with our control system exhibits fast and slow adaptations similar to those of quadrupeds. Our results clarify the importance of foot contact timing modification through sensorimotor integration for adaptive locomotion in animals.

4.6 Limitations of Our Study and Future Work

In this study, we used a robotic platform to investigate the gait adaptation mechanism during quadrupedal locomotion on a split-belt treadmill. The robot mechanical system is much simpler than an animal musculoskeletal system. Furthermore, the robot body is rigid and the joints are strictly controlled by motors, whereas an animal body and joints are flexible due to control by muscles. In addition, we used a much simpler locomotion control system than the neural system used by animals. These simplifications in the robot mechanical and locomotion control systems facilitated the capture of the essential aspects of adaptive locomotion. However, they caused quantitative differences in locomotor behavior. In particular, these simplifications forced our robot to use a pace pattern, unlike the walk and trot patterns of general quadrupeds. For intact cats walking on a split-belt treadmill using a walk pattern, when the left and right belt speeds are changed, the relative phases are altered on both the contralateral and ipsilateral sides to induce asymmetric interlimb coordination, where the contralateral sides for the fore and hind legs change most significantly (D'Angelo et al., 2014). These results are not necessarily the same as our results,

where the contralateral side for the fore legs showed significant changes whereas that for the hind legs showed no significant changes (**Figure 4**). Although some quadrupeds such as giraffes and camels use a pace pattern (Muybridge, 1957), there are no experimental data regarding how their interlimb coordination changes when they walk on a split-belt treadmill, which prevents us from verifying our results from a biological viewpoint and requires further biological studies. To overcome these limitations, musculoskeletal models, which can use similar walk and trot patterns to those used by general quadrupeds, would be useful (Fujiki et al., 2018; Toeda et al., 2020) in future studies.

Although this study focused on split-belt treadmill walking to investigate the contribution of interlimb coordination to adaptive quadrupedal locomotion, interlimb coordination plays an important role in numerous other locomotor tasks. For example, the gait transition between walk, trot, and gallop changes the phase relationship between the movements of four legs while creating and breaking the synchronization between the leg movements (Aoi et al., 2013a; Aoi et al., 2011; Fukui et al., 2019; Fukuoka et al., 2015; Masuda et al., 2021; Owaki et al., 2013; Owaki and Ishiguro, 2017). When crossing an obstacle during walking, the leading limb, which steps over the obstacle first, and the trailing limb, which steps over the obstacle after the leading limb, have different distances from the obstacle and these leg movements differ (Aoi et al., 2013b; Aoki et al., 2013). During walking along a curved path, the inner and outer limbs show different speeds (Gruntman et al., 2007). We would like to investigate the contributions of interlimb coordination to these locomotor tasks using our legged robots and mathematical models in the future.

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DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

SA developed the study design. TA performed the robot experiment. SA, TA, and SF analyzed the data in consultation with KS and KT. SA wrote the manuscript and all the authors reviewed and approved it.

FUNDING

This study was supported in part by JSPS KAKENHI Grant Numbers JP19KK0377 and JP20H00229, JST FOREST Program Grant Number JPMJFR2021, and Kyoto Technoscience Center, Japan.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frobt.2021.697612/full#supplementary-material>

Supplementary Movie | Quadruped robot walking on a split-belt treadmill from the tied configuration to the split-belt configuration in the 5x condition.

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Echo State Networks for Estimating Exteroceptive Conditions From Proprioceptive States in Quadruped Robots

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We propose a methodology based on reservoir computing for mapping local proprioceptive information acquired at the level of the leg joints of a simulated quadruped robot into exteroceptive and global information, including both the ground reaction forces at the level of the different legs and information about the type of terrain traversed by the robot. Both dynamic estimation and terrain classification can be achieved concurrently with the same reservoir computing structure, which serves as a soft sensor device. Simulation results are presented together with preliminary experiments on a real quadruped robot. They demonstrate the suitability of the proposed approach for various terrains and sensory system fault conditions. The strategy, which belongs to the class of data-driven models, is independent of the robotic mechanical design and can easily be generalized to different robotic structures.

OPEN ACCESS

Edited by:

Marco Mirolli,
National Research Council (CNR), Italy

Reviewed by:

Francis Wyffels,
Ghent University, Belgium
Wei Hong Chin,
Tokyo Metropolitan University, Japan

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Received: 18 January 2021

Accepted: 29 July 2021

Published: 23 August 2021

Citation:

Calandra M, Patanè L, Sun T, Arena P and Manoonpong P (2021) Echo State Networks for Estimating Exteroceptive Conditions From Proprioceptive States in Quadruped Robots. *Front. Neurobot.* 15:655330. doi: 10.3389/fnbot.2021.655330

Keywords: legged robot, echo state network, ground reaction forces, terrain classification, neural reuse

1. INTRODUCTION

Legged robots complement wheeled machines because of the potential capability of the former to explore complex unstructured terrains. However, their effective use in practical environments has not become common because of several problems that are yet to be addressed. One primary issue is locomotion. Although several efficient control strategies have already been introduced in the literature (He et al., 2019), their main drawbacks are the lack of efficient high-performance sensing devices and processing techniques for obtaining the terrain characteristics in real-time. From this perspective, haptic feedback is a primary information source for achieving reliable locomotion in legged robots, especially in uneven terrains where real-time gait adaptation and attitude control are needed. The interaction with the terrain is commonly sensed through force sensors that estimate the ground reaction forces (GRFs) acting on the individual legs. Since the first reliable applications of locomotion control strategies in legged robots (Righetti and Ijspeert, 2008), multidimensional force sensors have been installed on robot feet to sense the ground reaction forces for closing the loop with neighboring ground locations. In Montes and Armada (2016), several strategies for force control were discussed. These strategies rely on signal acquisition from force sensors integrated within the mechanical structure of the robot feet without the use of expensive and bulky commercial sensors. In Bledt et al. (2018), a combination of impedance control and model predictive control was used to perform impressive tasks such as back-flips in a quadruped robot. These control

methods require an accurate model of the terrain-leg interactions through contact force sensing or reliable estimation. In legged locomotion, ground reaction sensing at the individual foot level involves repetitive impacts with the terrain, which can easily affect and degrade the reliability of the device. Moreover, force signals detected by GRF sensors often suffer from multiple false detections, especially on uneven terrain.

For these reasons, researchers are increasingly studying reliable sensorless techniques to estimate the ground-foot contact information. In Karatsidis et al. (2016), a method to predict the GRFs in humanoid walking was presented. The method uses only kinematic information from a fully ambulatory inertial motion capture (IMC) system based on a large number of inertial motion units distributed over the body of the humanoid structure. Therefore, the enhanced accuracy of the force sensors comes at the expense of having many alternative sensor units. The force information can be obtained directly or indirectly from signals already available in the structure. The GRFs can be indirectly estimated from their inertial effects on the robotic structure, for example, from the torques or currents of the motors actuating the robot legs. In Bosworth et al. (2015), a classical approach involving the robot Jacobian matrix was used to estimate the foot force from the joint torques, which were in turn estimated from the leg actuator currents. Other approaches are based on Kalman filtering techniques or other methodologies derived from observations (Chan et al., 2013; Hu and Xiong, 2018). In Chenkun et al. (2015), a dynamic model of the leg structure was used for sensor estimation. The authors were aware that accurate parameter estimation is difficult to achieve. To match the actual robot results with the simulations, the unknown parametric uncertainties were identified through a learning process based on the actual data. In particular, radial basis function networks were used. Recently, a new method to estimate the force at the foot contacts was presented in Hu and Xiong (2018). The method is based on designing a generalized momentum observer for the robot force disturbances caused by the foot contacts on the ground. This method requires information on the joint positions and the applied control torques. The method is used to implement impedance control, in which the accuracy of the ground contact force is essential, especially soon after contact events, where the signals show large impulse-like variations. The methodology applied requires accurate knowledge of the system parameters, the most critical of which are concentrated on the robot structure and mass distribution. These parameters affect the estimation of the center of gravity motion. A deviation from the nominal parameter values can thus affect the overall performance of the method. For this reason, an additional neural network approach was used to compensate for errors due to inaccurate parametric modeling and dynamic effects. GRF estimation in legged machines has also attracted interest because of its potential applications in designing efficient prosthetic devices. In Fakoorian et al. (2016), the GRF was estimated on a leg prosthetic system using a Kalman filtering approach. Impedance control methods are often adopted to estimate the contact forces from trajectory tracking errors. In Xin et al. (2020), this strategy was applied as haptic feedback for teleoperation. The main hypothesis is

to assume that the model error is much smaller than the disturbances.

All these approaches show that legged machines are complicated structures involving the concurrent motion of multiple bodies, each of which has its own inertial effects on the overall structure. Traditional approaches based on dynamic equations are thus not completely sufficient for accurate modeling. Moreover, in general, the classical approach is dependent on the particular robot structure used. Because of the extremely large variety of different legged machines described in the literature, tailored for specific tasks and applications, extracting accurate dynamic models for sensor estimation is a time-consuming and often complex task that is further complicated by the difficulty of accurately identifying the relevant parameters. Therefore, it is useful to employ a data-driven, neural network-based learning approach that accurately estimates the GRF sensor signals independently of the particular dynamic robot structure and acts as a reliable soft sensor device that can also cope with leg malfunctions. In Hwangbo et al. (2019), a strategy to train a neural network policy in simulation and then transferring it to a legged robot is presented. Specific attention was devoted to model the robot actuators. They are modeled through a data-driven approach, mapping the joint state and position error history into the torque signals provided to the simulated robot.

In our work, we explore the application of a family of recurrent networks to estimate the GRFs using proprioceptive local information acquired at the level of the leg joints. The underlining nonlinear dynamical model is defined after a learning process by extracting the temporal dependencies between the input data. The input data are projected into a pool of interconnected neurons called reservoirs in which both space and time-relevant information can be stored in an internal memory generated through recurrent connections. This methodology, usually referred to as reservoir computing (RC), represents an interesting approach for designing data-driven models in robotic applications involving nonlinear dynamic behaviors. Among the different architectures in the RC field, we selected the echo state network (ESN), which is commonly employed in various applications ranging from handwriting recognition (Bunke and Varga, 2007) to time series forecasting (Wang et al., 2019).

The concept of reservoir computing has been further extended in literature, from a pure algorithmic solution to include the physical device in the computational effort, realizing a physical reservoir computing system (Tanaka et al., 2019; Nakajima, 2020). An interesting demonstration was provided in Nakajima et al. (2015) where a soft silicone arm was adopted for real-time computation exploiting the intrinsic characteristics of the system including nonlinearity, memory, and potentially infinitely many degrees of freedom. Similarly, in Caluwaerts et al. (2014) a Reservoir Compliant Tensegrity Robot hardware prototype was presented; it was considered as a part of the computational system used to generate a set of desired oscillatory motor signals starting from a Matsuoka oscillator. The idea to use the robot dynamics to generate an embodied control system has been applied to a quadruped robot in Degraeve et al. (2015). The main result of that

work was to demonstrate that a memoryless feedback controller can generate a stable trot by learning the desired nonlinear relation between the input and the output signals.

A key advantage of ESNs compared with other neural structures is the simplicity of the learning process. The limitation of the learning process to only the output weights, called the readout map, significantly reduces the learning time. The increase in dimensionality due to the information transfer from the input to the hidden neurons, which present recurrent connections, produces multiple combinations of dynamics that can be exploited through the readout map depending on the task to be fulfilled. Moreover, the ESN approach is particularly advantageous over the other approaches mentioned above because it is a black-box identification model that avoids the need to implement model-based strategies that, in any case, would need to be refined with data-based learning algorithms. Our approach has additional advantages when dealing with joint faults. Adapting classical methods to handle such occurrences would be extremely complicated, whereas a learning-based technique based on recurrent ESNs allows the faults to be handled efficiently and provides information on the estimated GRF even when there is serious damage in the sensory system at the level of the joint legs. Similar capabilities were demonstrated in Antonelo et al. (2007) where a reservoir network was applied to a problem of robot localization and map creation, showing good performance also in presence of limited sensory information.

The use of ESNs also contributes to building an internal memory that is particularly useful for handling time-varying signals. An additional important issue typical in reservoir computing networks results from the characteristics of the dynamics processing in the reservoir layer. The latter utilizes a sparse representation of the input signals in a high-dimension dynamical projection space, whereas the readout maps constitute only a low-dimension projection space, defined after the learning phase, that maps specific aspects of the input features. In principle, any set of information consistent with a given input signal can be extracted from a given reservoir lattice in parallel through the addition of other readout maps. This is a typical example of *neural reuse* (Anderson, 2010; Arena et al., 2013). In this work, a clear application of these characteristics is presented, and another readout neuron is added to the same neural lattice used for GRF estimation to classify the type of terrain traversed by the robot (i.e., flat, downhill, uphill).

There are different approaches in the literature related to the design of solutions for terrain classification in legged robots in particular, in relation to the material type. In Hoffmann et al. (2012), a sensory-motor classification of different terrains was presented for a quadruped robot. The role of the action context to further improves the discrimination capabilities was also demonstrated. Techniques based on extreme learning machines and reservoir computing were analyzed in Degraeve et al. (2013) to demonstrate the effectiveness of a limited combination of tactile and proprioceptive joint sensors for terrain classification. These studies can be framed within the embodied cognition framework: the idea is to find the emergence of proto-cognitive behaviors letting the robot extracting regularities in the sensory-motor space and exploit them for action generation (Hoffmann, 2014).

To analyse the flow of information in sensorimotor networks, tools from information theory were adopted in Schmidt et al. (2013). The results demonstrate the possibility to create a primitive body schema identifying structures in the sensorimotor space.

In our work we are presenting a unique network able to provide both the GRF distribution on the legs and the terrain slope with high classification accuracy. This information could be used, for example, to select the most appropriate locomotion gait for the application. Preliminary experimental results, carried out on a real quadruped robot, demonstrate the effectiveness of the proposed approach. Furthermore, although the embedded hardware implementation is not within the scope of this work, the authors identified potential solutions to develop embedded ESN structures.

A first attempt is reported in Huang et al. (2019) where a scalable RC-ESNs hardware generator for embedded computing is presented. The strategy consists of a high-level synthesis in conjunction with design automation to automatically transform an offline-trained ESN algorithm into an embedded hardware accelerator for FPGA applications. Problems related to efficiency in terms of power, performance, and occupied area were also considered and addressed. This approach is in line with another recent example that follows this hardware-oriented strategy (Huang et al., 2020): here an automatic holistic energy-aware design methodology is proposed and applied to a multilayer perceptron designed to be embedded in proactive brain-machine interface edge devices based on FPGA. Another interesting direction for hardware implementation is related to the open-source Neural Network framework called Neural Network on Microcontroller (NNOM)¹, for implementing (recurrent) neural networks on a microcontroller. It provides a user-friendly interface and supports state-of-the-art neural model structures. However, the chip market is rapidly changing and new opportunities (e.g., System-on-a-chip, tensor computers, and neuromorphic hardware) will be more and more available in the next years.

The remainder of this paper is organized as follows: The methodology employed in the paper is introduced in section 2, in which the robotic structure and the ESN structure used for the sensor signal estimation are also presented. Simulation results for both the GRF estimation and terrain classification are reported in section 3. The application of the ESN for GRF estimation to a real robot is discussed in section 4. The work is concluded and some perspectives are provided in section 5.

2. METHODOLOGY

The aim of this study is to employ reservoir computing structures to predict external signals, such as the leg ground reaction forces, using internal data such as the joint torques in a quadrupedal robot structure. All the data to be analyzed were acquired on a simulated robot moving in a dynamic simulation framework named CoppeliaSim, which has been duly extended in Rohmer et al. (2013). The framework provides an accurate dynamic

¹<https://github.com/majianjia/nnom>.

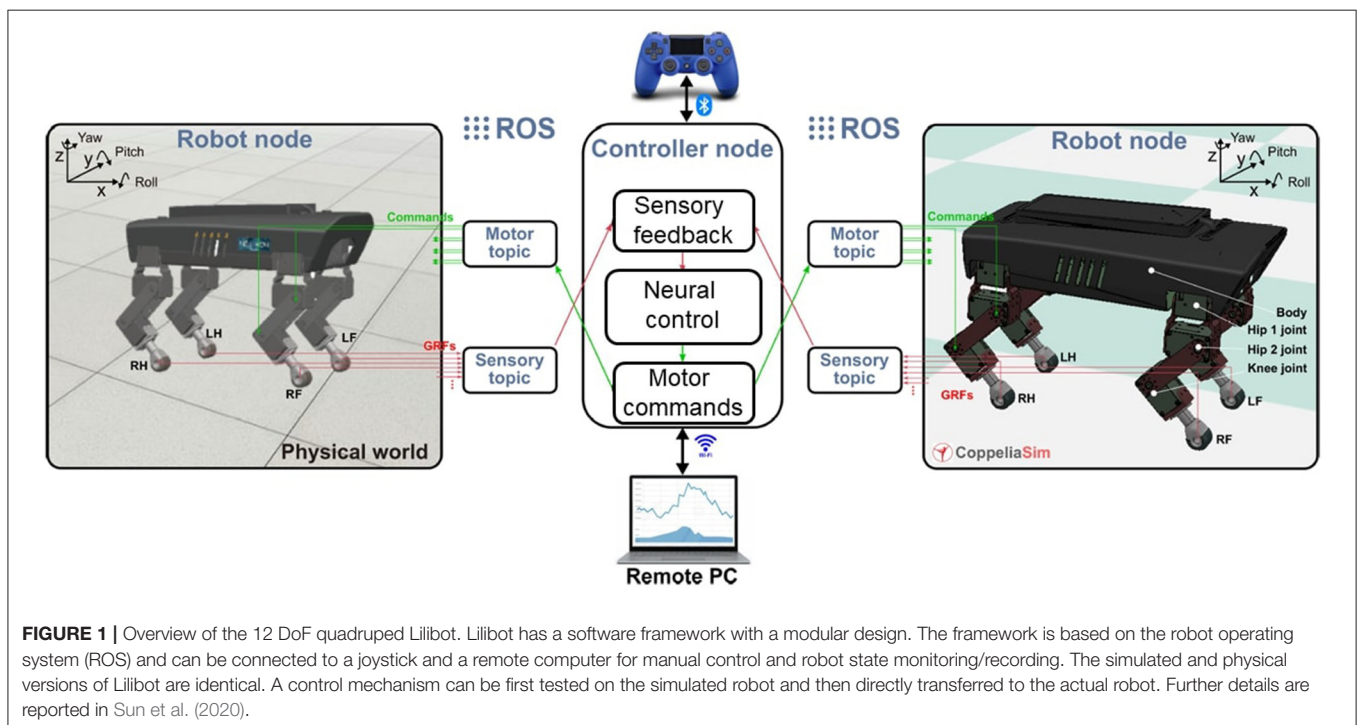
simulation environment that is particularly useful for complex robotic structures. The simulation approach becomes essential when sophisticated learning-based control techniques, which involve time-consuming runs, have to be applied to the structure before obtaining reliable results. To achieve the aim of the study, the training phase of the methodology introduced here was first performed in the dynamic simulation before implementation on the actual robot prototype. The simplified foot structures in several-legged robots do not allow the inclusion of GRF sensors, which are useful for developing adaptive locomotion control strategies. One example is the Lilibot robot, which is a small-sized robot developed for research and education purposes (Sun et al., 2020). The first attempt to solve the GRF acquisition problem adopted a simple parametric model utilizing the current through the servo motors at the knee joints as the input signal; the current was found to be positively correlated with the GRF. Our work extends this approach, which is based on a static model, by developing a dynamic structure that can utilize the time evolution of signals relevant to the joints, in particular the torque signal of a subset of joints, to estimate the GRF. The linear relationship between the joint torques and motor currents ensures that the proposed model can be applied in the robot to easily acquire information on the currents absorbed by each motor. Moreover, a significant improvement over the model in Sun et al. (2020) is the development of a unique network that utilizes the information coming from all four legs to estimate the GRF signals. This approach allows local faults within the joint sensory acquisition system to be handled and provides a good reconstruction of the GRF associated with a leg even if the corresponding joint signals are not available. The additional update is made possible by using the same reservoir lattice to

provide information about the type of terrain the robot is actually walking on.

2.1. Lilibot Robot

Lilibot is a small, lightweight, robust, open-source, and sensor-rich quadruped robot (Sun et al., 2020) (**Figure 1**). Each leg is characterized by three joints comprising two hips and a knee, as shown in **Figure 1**. The flexible configuration of the robot leg allows extensive rotation at the level of the joints and results in large workspaces due to the small dimensions of the robot. This makes the structure an ideal platform for studying adaptive locomotion strategies. An algorithm capable of estimating the GRF for each leg of the actual robot through the knee currents was also provided in the paper referenced above. In the present study, torques were used instead of currents for GRF estimation because of the lack of information on the actuator currents in the robot simulator. To demonstrate the reliability of the results obtained, different simulations were performed with varying characteristics of the ground the simulated robot walked on. Data were acquired not only for a flat surface but also for an uphill surface and a downhill surface. We focused on measuring the joint torques and the leg GRFs.

The robot operating system (ROS) was used to create a communication channel between the controller and the simulated robot. The locomotion controller is an adaptive neural controller written separately from the simulation environment. It communicates with the simulated robot through specific channels called topics which are provided by the ROS. CoppeliaSim allows some robot parameters such as the leg joint torques and the leg GRFs to be monitored. The simulation was constructed such that it almost perfectly reflected the behavior



of a real robot (Sun et al., 2020). The adopted locomotion control system is a central pattern generator (CPG) which can be adapted to generate different locomotion gaits through a series of parameters. In the following simulations, the robot walked at a fixed speed with a trot gait in which two opposite legs were in phase at each moment while the other two legs were 180° out of phase.

The CPG was devoted to low-level locomotion control, whereas the high-level ESN structure was implemented for GRF estimation and terrain classification. Therefore, the next step consisted of configuring the ESN where a different set of parameters was used to find the most reliable model that provided the best results. Different architectures were used based on the number of legs and type of joints tested during the analysis. In the following step, the robustness against faults was analyzed to train a model that can reliably react to sudden faults affecting the leg joint sensory system.

2.2. Echo State Network Overview

An echo state network proposed in the early 2000s (Jaeger, 2001) was used to predict the GRF of each leg joint torque reading. This specific neural architecture falls within the field of reservoir computing, which is a collection of methodologies useful for training recurrent neural networks. A reservoir computing system consists of a reservoir that maps input signals into a high-dimensional space and a readout map for pattern matching from the high-dimensional states in the reservoir to an output target. A simple scheme for this architecture is presented in **Figure 2**.

The advantage of reservoir computing ESNs is that, whereas the reservoir layer (which corresponds to the hidden layer in feedforward networks) has random fixed weights, only the readout is trained with simple methods consisting of, for example, the recursive least square (RLS) algorithm. Thus, the major advantage of reservoir computing compared to other recurrent neural networks is fast learning, which results in low training costs (Tanaka et al., 2019; Patanè and Xibilia, 2021). This study aims to show how powerful and lightweight an ESN can be in the development of a soft sensor for robotic applications. The reservoir can be conceived as a bucket of neurons, each of which is sparsely connected to other internal neurons. The

output neurons are all connected to individual reservoir neurons, whereas the input neurons are sparsely connected to the reservoir neurons. Each connection is described by a uniformly sampled random weight value. However, during the training phase, only the readout weights are trained to improve the model accuracy (Lukoševičius and Jaeger, 2009). This is the main characteristic that allows the ESN to be lightweight. In the absence of feedback from the output to the reservoir, the time evolution of the neuronal states in the reservoir is given by Jaeger (2001).

$$\mathbf{x}(n) = \lambda f(W^{in}\mathbf{u}(n) + W^{res}\mathbf{x}(n-1)) + (1-\lambda)\mathbf{x}(n-1) \quad (1)$$

where n denotes the discrete time, $\mathbf{x}(n)$ the state vector of the reservoir units, $\mathbf{u}(n)$ the input vector, W^{in} the weight matrix for the input-reservoir connections, and W^{res} the weight matrix for the recurrent connections in the reservoir. Function f represents the element-wise activation function of the reservoir units and $\lambda \in [0, 1]$ is the leak term, adopted when leaky integrator neurons are considered. In our case study, we chose the hyperbolic tangent as the activation function. The output is given by a linear combination of neuronal states:

$$\mathbf{y}(n) = W^{out}\mathbf{x}(n) \quad (2)$$

where $\mathbf{y}(n)$ is the output vector, and W^{out} is the weight matrix in the readout. In supervised learning, this weight matrix is trained to minimize the difference between the network output and the desired output for a certain time period (Lukoševičius and Jaeger, 2009).

An ESN is characterized by a set of parameters that are directly connected to its behavior. We tested different parameters to determine the model with the best accuracy. We provide the values of the key network parameters in **Table 1** that summarizes the relevant characteristics of the proposed architecture and the hyperparameters adopted. The selection of these hyperparameters was driven by the indications available in literature (Bengio, 2012; Dasgupta, 2015; Dasgupta et al., 2015) and by preliminary experiments. Therefore, it was performed through a trial-and-error procedure based on a

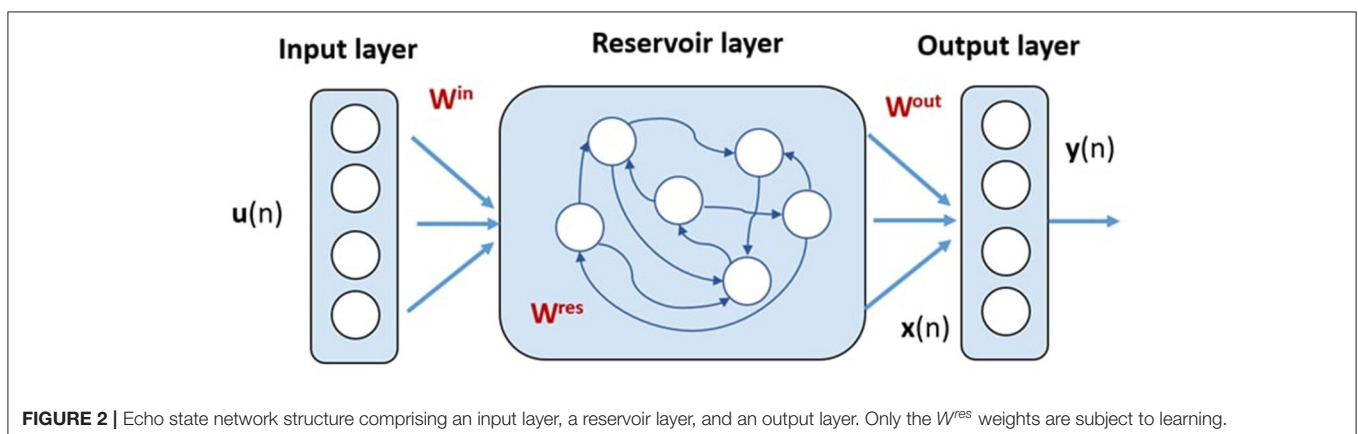


TABLE 1 | Echo State Network parameters which provided the best accuracy.

Parameter	Value
Reservoir neurons	100
Learning method	RLS
Leak	0.3
Learning rate	1.0
Input sparsity	20%
Network sparsity	50%
Spectral radius	0.95
Reservoir function	Tanh
Readout function	Linear
Washout	100
Noise bias	0.001

combination of expert knowledge to identify a searching domain, and a grid search performed on the reduced subspace of the hyperparameters to identify the best configuration in terms of prediction accuracy on the validation dataset. As a result, the reservoir neurons were set to 100 based on our previous analysis (Dasgupta et al., 2015) and grid search. The leak parameter, defining how much a single neuron in the network depends on the actual net input it receives, was analyzed in Dasgupta (2015) and Dasgupta et al. (2013) and here set to 0.3 based on the analysis. Note that a smaller value will lead to less leak of the information, i.e., larger temporal memory storage while a larger value will lead to high leak of the information, i.e., smaller temporal memory storage. The input sparsity defines the probability of connections from the input to the network which was empirically set to 20%. This provides robustness to the network and less input dependent compared to a higher sparsity value (Dasgupta, 2015). The network sparsity defines the connection probability between reservoir neurons. It is typically set to 10–50% (Dasgupta, 2015). Here it was empirically set to 50%. The spectral radius parameter (or network scaling factor) was analyzed in Dasgupta et al. (2015) and Dasgupta et al. (2013). Based on the spectral radius analysis, the parameter was set here to 0.95 such that the spontaneous network dynamics is in a stable regime and achieves the best performance of the chosen network size. The constant noise bias (i.e., 0.001) is applied to the hidden recurrent neurons of the network. The bias term is set based on Rungruangsak-Torrissen and Manoonpong (2019) and used in order to provide a small input for the hidden neurons to constantly activate them, thereby maintaining the neurodynamics. The other parameters, like learning rate and washout, were set with respect to the standard setup of the ESN learning (Bengio, 2012; Dasgupta et al., 2013, 2015).

Other hyperparameter optimization methods, based on genetic algorithms and different bio-inspired approaches, have been applied in recent works and can be considered as further searching strategies (Tian, 2020).

A particular point of interest is the choice of the learning method (here, the RLS) and the spectral radius. The spectral radius is related to the Echo State Property, an important

property that guarantees the stability of the network that is able to forget its inputs after a given time behaving as a fading memory. The spectral radius is usually kept below 1 to maintain the echo properties for zero input reservoirs. This constraint is usually enough for a large reservoir (Caluwaerts et al., 2013), although, in some application, the possibility to explore the range above 1 could be useful to improve the network generation capability of chaotic signals (Sussillo and Abbott, 2009). In presence of input-driven reservoirs, temporal and statistical properties of the driving input can be related to the spectral radius that may exceed the previous mentioned limit by continuing to hold the echo state property (Manjunath and Jaeger, 2013). As stated above, the training of an ESN is relatively faster than that of standard recurrent neural networks (Hochreiter and Schmidhuber, 1997; Mandic and Chamber, 2002).

We considered a standard ESN architecture to demonstrate the effectiveness of our strategy. However, further investigations to improve the proposed model performance could consider the introduction of the intrinsic plasticity rule to adapt the reservoir internal parameters using an unsupervised mechanism based on the maximization of the transferred information (Dasgupta et al., 2013, 2015; Dasgupta, 2015; Patané and Xibilia, 2021).

3. SIMULATIONS AND EXPERIMENTAL RESULTS

The first step consists of data acquisition. The simulation was run for several minutes on perfectly flat ground. The robot walked at a fixed speed and gait. Both joint torques and the GRF of each leg were recorded with a sampling interval of 50 ms. The same operations were performed on both downhill and uphill ground with slopes of $\pm 5^\circ$ to verify the ability of the network to generalize the GRF prediction independently of the ground shape. After collecting all the data, a pre-processing stage was implemented. The final step was to train and test the model, followed by data analysis, which led to the results reported below. Because the focus was to obtain a good estimation of the leg GRF, we analyzed what proprioceptive information should be used to achieve the most reliable results. The analysis was performed systematically by using different sets of joint torques in the input layer. Each round of analysis was performed by first training the model on 80% of samples measured on flat ground and then testing the model on the remaining 20% of the flat ground dataset together with the complete uphill and downhill datasets, which were not shown to the model during the learning phase. The size of the entire dataset was $\sim 25,000$ samples when the sampling rate was 20 Hz. The variables were normalized into the range [0, 1]. We measured the mean squared error (MSE) and its normalized version (NMSE), according to the set of joints provided to the model and the different tested surfaces. **Figure 3** depicts the ESN performance in the two cases when all 12 joint torque signals were provided in the input, and when the input layer was reduced to only 8 signals (i.e., only the Hip 2 and Knee joints). The statistical results obtained indicate that the information from the Hip 1 joint is not relevant to the analysis. This result can be explained by the leg kinematics shown in **Figure 1**. Here, the Hip 1 joint

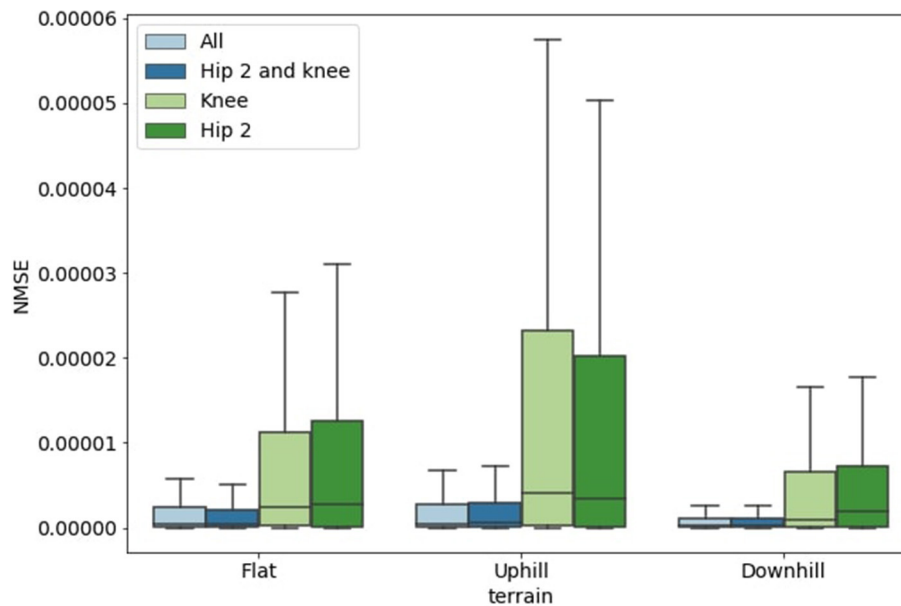


FIGURE 3 | NMSE obtained from the ESN for different terrain types. The role of the input signals was investigated considering four different cases: all (three torque signals for each leg for a total of 12 inputs), Hip 2 and Knee (8 inputs), Knee (4 inputs), and Hip 2 (4 inputs).

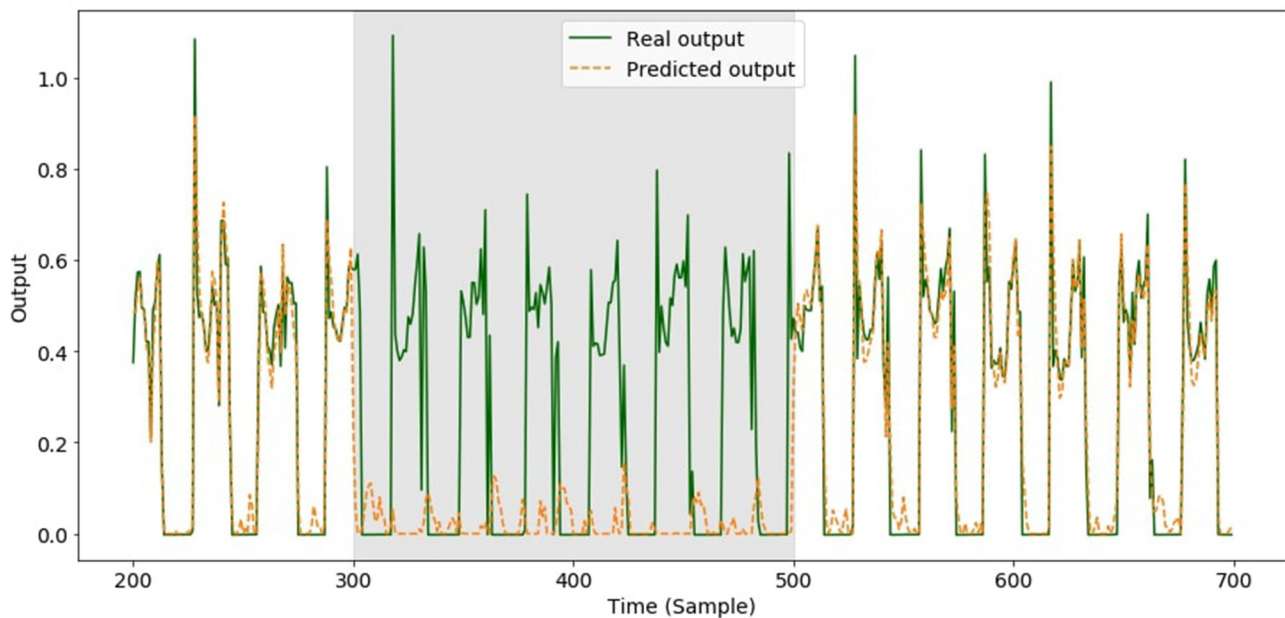


FIGURE 4 | Predicted GRFs of front right leg when the model learnt to predict all GRFs and a fault was introduced over 200 samples (gray area from 300 to 500) in both of the front right leg joints. The training set consisted of data measured using perfectly working sensors.

is required only for steering or attitude controlling maneuvers, whereas the other two joints are involved in generating the stance and the swing trajectory on the sagittal plane during forward walking. A further reduction of the input signals to only one single-joint signal for each leg produces a drastic increase in the reconstruction error. This indicates that the optimal network

configuration should include a total of 8 inputs consisting of the torque signals for the Knee and Hip 2 joints of all the legs. The outcomes of the test phase are very similar for all the terrain configurations, even when the model was trained using only data acquired on the flat surface. Thus, our model can be generalized to generate predictions for different terrain characteristics.

Another relevant characteristic of the proposed architecture that we investigated is its robustness against random faults in the torque sensors. The idea is to verify whether the model can handle the partial omission of some input signals and show a gradual performance degradation instead of an abrupt drop. The acceptability of the predicted quantities depends on the predicted error.

We first introduced faults during the test phase. The faults affected both the Knee and the Hip 2 sensors in the front right leg for 200 consecutive samples, which corresponds to ~ 6 steps. A comparison between the actual and predicted GFR for the front right leg subjected to the fault is shown in **Figure 4**.

As can be seen, the test performance in the presence of the sensor faults is very poor; therefore, our next step consisted of finding a solution to avoid or at least limit the performance degradation. We thus evaluated the behavior of our final model trained in the presence of faults to find a good strategy to improve

the accuracy of the predictions. One of the functions of the reservoir layer is to create hidden time correlations between the input joint signals, which can then be exploited by forcing the net to estimate the GRF of a leg even in the absence of torque signals from that leg. This can be achieved if the network learns the correlation between the corresponding leg joints and their involvement in the output prediction. The presence of a correlation between the joint torques of a leg and the GRFs of the other legs is reasonable because the robot is moving with a fixed gait. Therefore, we introduced artificial faults in each leg during the training phase. Each fault lasted for 100 samples and occurred in the Knee and the Hip 2 signals of each leg once every 500 samples. Situations involving faults in two or more legs at the same time were not considered.

Table 2 summarizes a statistical analysis of the prediction performance of the ESN-based model when the training and test phases were carried out with and without faults. The network can be forced to create cross relations between sensory information by introducing faults during training to significantly improve its fault-handling performance through the support of the available sensory signals coming from the other legs. This effect is obtained at the cost of a slight degradation of the prediction performance in the absence of faults.

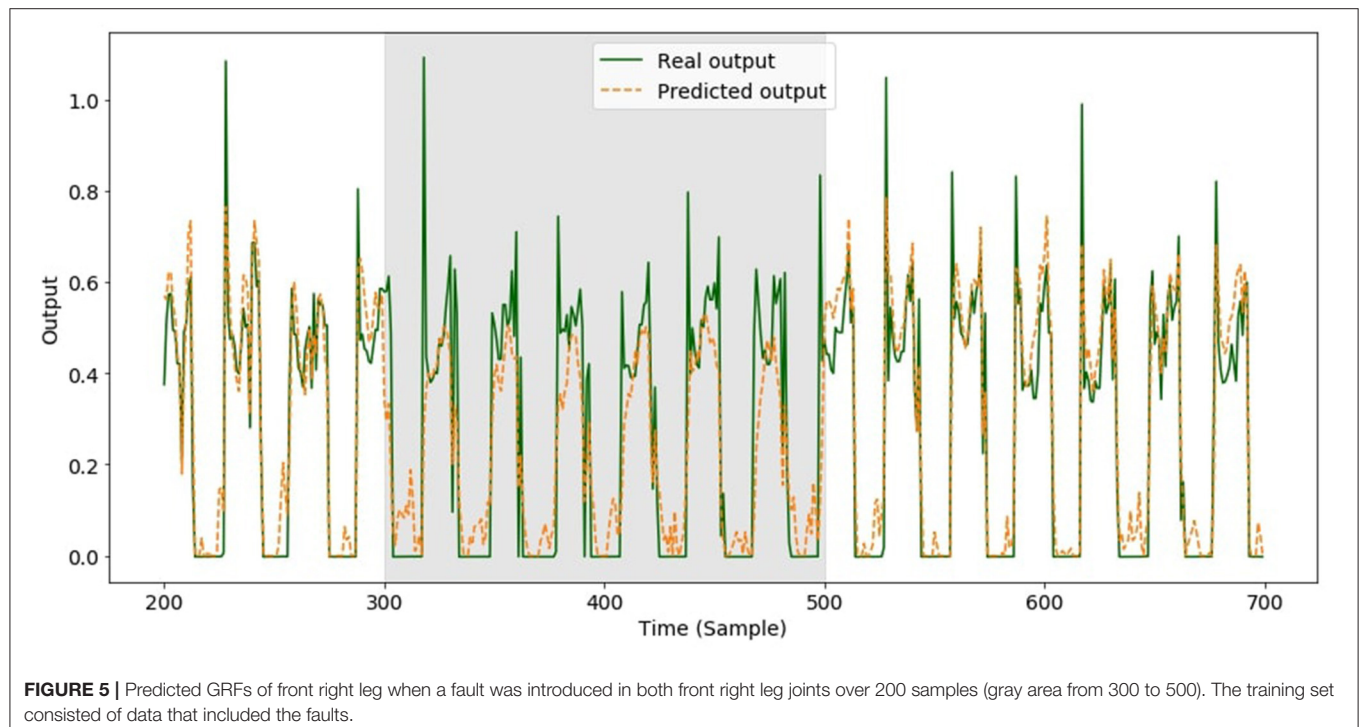
Figure 5 shows the improvement obtained for the GRF prediction of the faulty leg with the new training compared with the results previously reported in **Figure 4**.

These results can be analyzed in detail by considering the prediction error obtained for each output variable (i.e., each leg). **Figure 6A** shows the effect of a fault on both joints of the front right leg compared with the MSE obtained when all the

TABLE 2 | Mean and standard deviation of MSE in testing evaluated on all legs when the training and testing phase is performed in presence of faults as discussed in the text.

Trained with fault	Tested with fault	MSE	R
No	No	0.0036 ± 0.0015	0.98
No	Yes	0.0175 ± 0.0229	0.67
Yes	No	0.0056 ± 0.0004	0.96
Yes	Yes	0.0074 ± 0.0031	0.93

The Pearson correlation coefficient (*R*) is also reported.



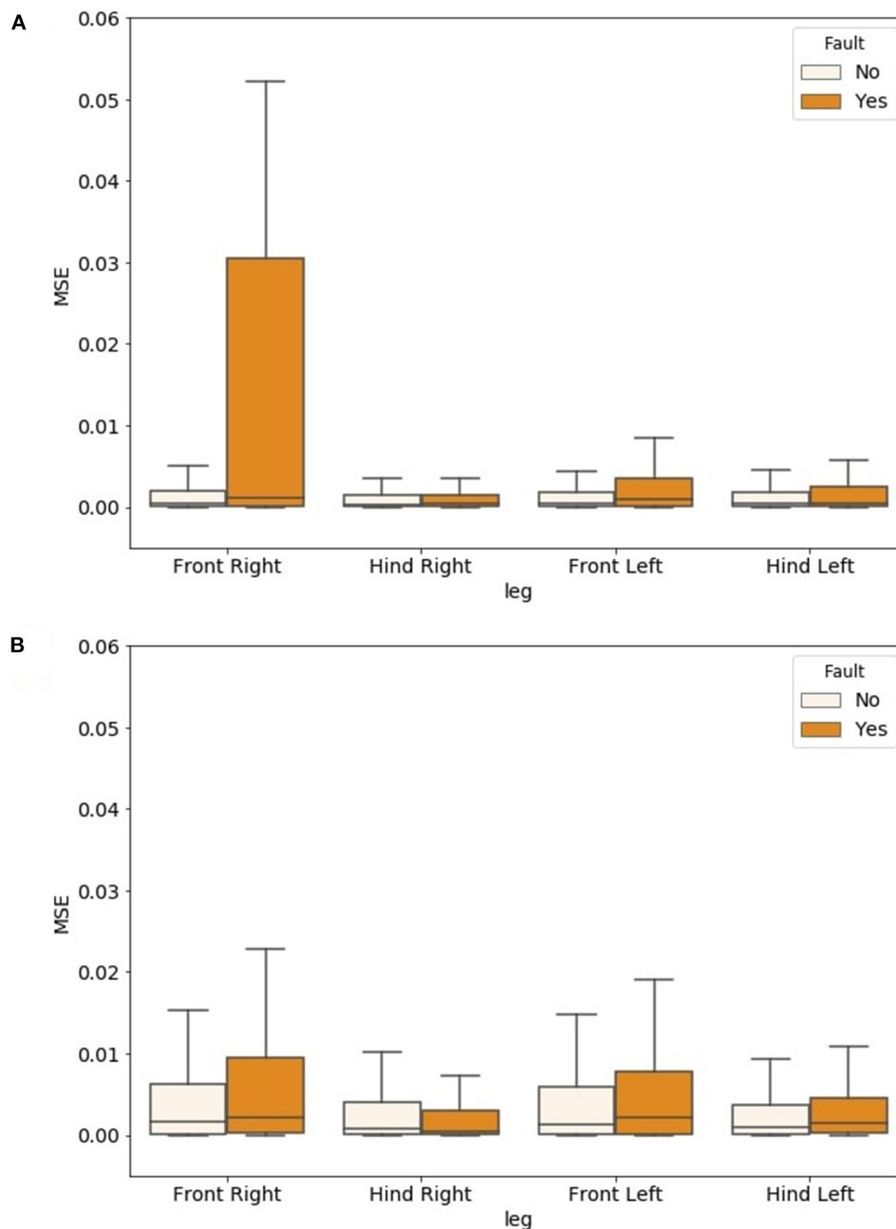


FIGURE 6 | Comparison of prediction errors between samples with and without faults for the four GRF signals predicted as output of the ESN. The model was trained using only data from normal working conditions **(A)**, and using data in which artificial faults were introduced in all the legs during the training phase **(B)**.

sensory information was provided in the input. The degradation is evident and concentrated on the corresponding leg. The effect of the same fault on the model trained with faulty signals is shown in **Figure 6B**. Here, all the legs cooperated in predicting the four outputs, improving the robustness in the presence of faults.

Similar conclusions can be drawn when a fault occurs on only one joint of a leg, given that the model was trained against faults occurring in the Hip 2 and Knee of each leg. **Figure 7** shows how the NMSE behaves differently when the faults occur on Hip 2, Knee, and on both front right leg joints

during the test over 200 consecutive samples. The error was computed as the average of all four legs. The brighter bar shows the measured error when the model was trained without artificial faults, whereas the darker one was obtained from a model trained with artificial faults. It is clear that the mean error is generally much lower if the model has learnt how to deal with faults. **Figure 8** also shows how the error behaves over time when the faults occur on a specific joint. This result, combined with the previously analyzed results, suggests that there is a weak relationship between the leg knee torque and its GRF.

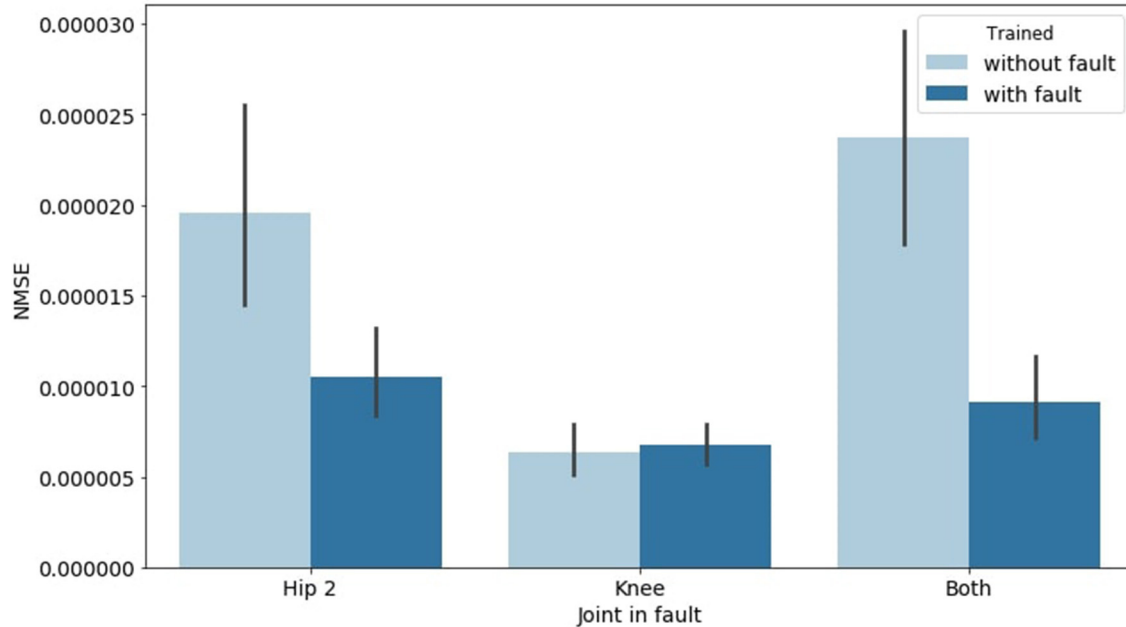


FIGURE 7 | Behavior of GRF prediction NMSE when the fault occurred on Hip 2, Knee, or both front right leg joints. The error was computed as the average of all four legs. The brighter bar shows the measured error when the model was trained without artificial faults, whereas the darker one was obtained from a model trained with artificial faults.

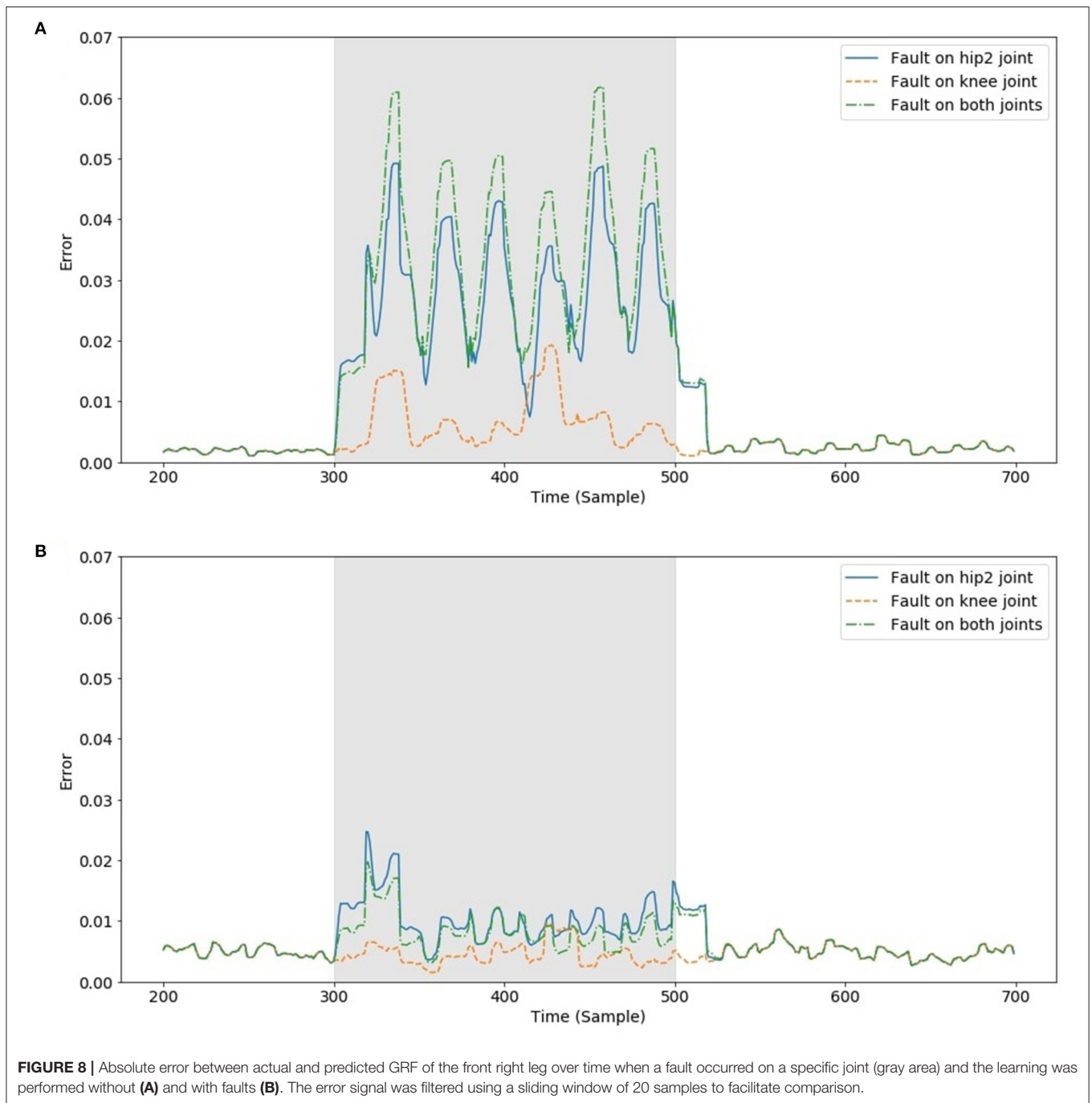
3.1. Terrain Classification

The results reported in this section show one of the most intriguing features of ESNs. As described above, the dynamics that emerge within the reservoir lattice do not depend on the target to be mapped; rather, they spontaneously arise as a result of the input signals and the random sparse arrangements of the connections and weights. Once these factors are fixed, the high-dimensional dynamics within the neuron lattice can be mapped according to an arbitrary assignment imposed by the target signals. This feature can be exploited to allow the use of a given dynamical arrangement to create many arbitrary mappings of the same input space for the realization of other readout maps. The example reported here uses the same dynamical input signals to obtain, in addition to the time-dependent GRF signals, a classification of the type of terrain traversed by the robot (i.e., flat, uphill, or downhill). This application exploits the relationship between the average slope of the climbed terrain and the interplay between the complex inertial effects caused by multibody motion and the motor torque distribution among the robot legs. Once the former ESN is trained, it is no longer necessary to run the entire network again. It is sufficient to add another readout map and exploit the output of the reservoir lattice to perform the desired mapping by training only the added map. Therefore, the terrain classification step was performed using the same network configuration and parameters used in the previous task. The new readout is extremely simple: it comprises only one output neuron that provides, as output, the three terrain types considered. This approach falls within the psychological paradigm of neural reuse (Anderson, 2010) recently adopted for

neuro-inspired structures (Arena et al., 2013): neurons, because of their interconnectivity, organize in networks that can cope with different tasks concurrently. In our case, the same ESN network can generate multiple parallel signals from a single set of input signals previously adopted for robotic applications ranging from time-dependent GRF estimation signals to static labels that account for the type of terrain currently being traversed. **Figure 9** depicts the augmented ESN structure, which includes the terrain classifier. The reservoir layer is the same layer as that for the GRF estimation, and only the additional readout map is trained.

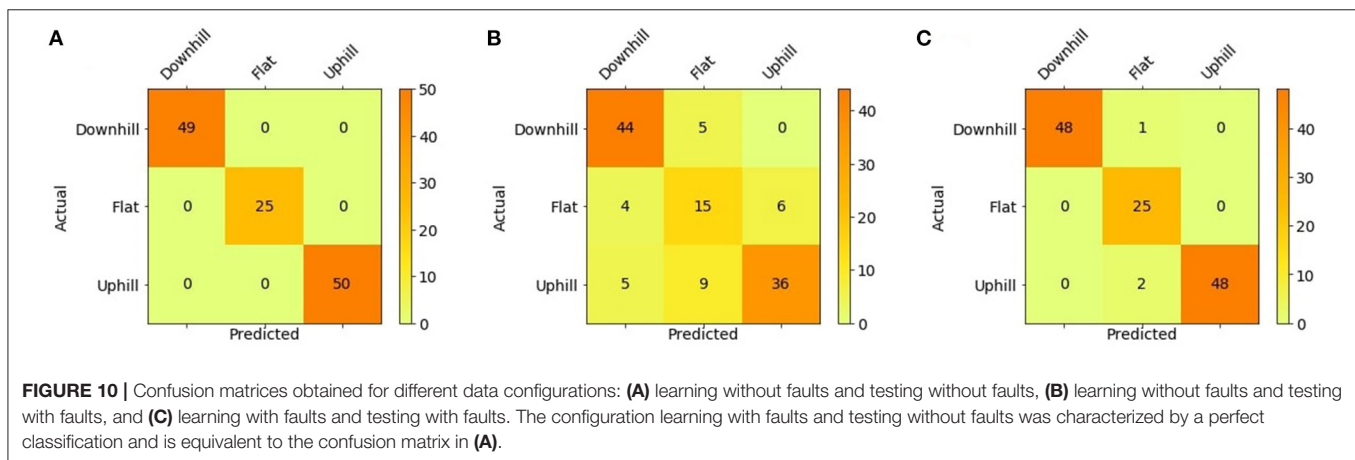
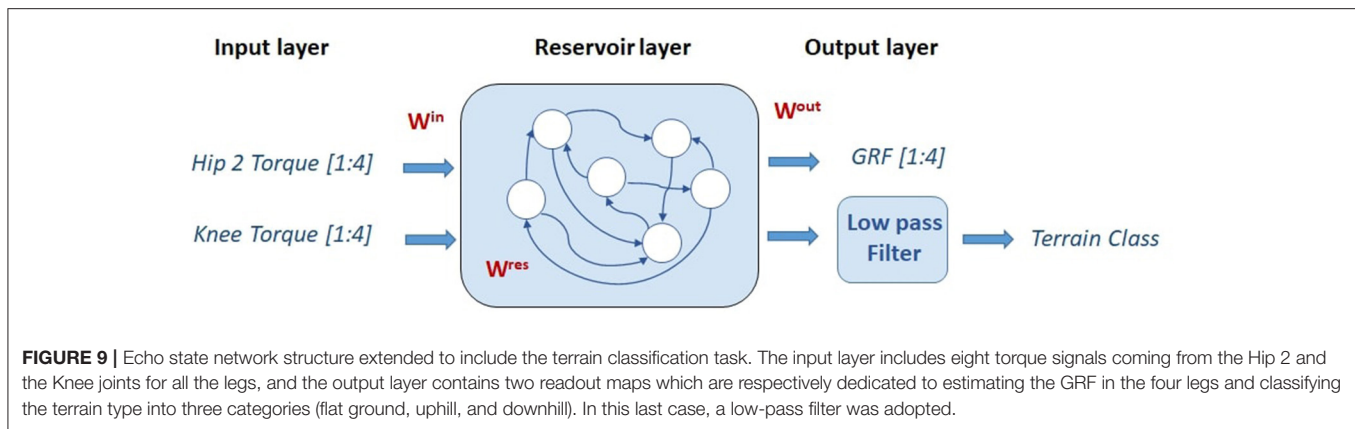
The target for each class is a constant value: 0 for downhill terrain, 0.5 for flat terrain, and 1 for uphill terrain. In the last case, a low-pass filter was adopted at the output stage to provide a smooth signal. In particular, the output of the ESN was processed using a 5th-order Butterworth filter with a cutoff frequency of 0.5 Hz. The introduction of nonlinearities in the output layer will be investigated in future works to avoid the presence of an external filter.

The classification was performed by considering the average output over a time window of 100 samples. The average error between the network output and the three target signals was computed, and the class with the smallest error was selected for the current window. As stated above, the ESN with the same topology as that in **Table 1** was considered. In addition, different datasets were considered in evaluating the capability of the network to classify the terrain when there was missing information in the input signals. When all the input information



is available the classification accuracy is 100%. However, the classification solution cannot easily handle sensory fault events. In fact, if the torque signals of one leg are missing, the performance decreases, and the accuracy is reduced to 76.6%. Similar to the GRF estimation discussed above, to improve the network prediction performance in the presence of faults, the learning dataset was modified to include faults. The resulting accuracy of the network when faults were present on both the Hip 2 and Knee joints of a single leg reached the high value of 97.6%.

The confusion matrices obtained during the testing phase for the three different cases considered here are reported in **Figure 10**. A total of 124 time windows were analyzed. The filtered output of the network is compared with the actual class in **Figure 11**. The classification accuracy is considerably reduced when the presence of faults results in multiple incorrect predictions. The addition of faulty conditions in the training dataset for the learning procedure improves the network performance and drastically reduces the number of incorrect predictions.



3.2. Real Robot Experiments

The proposed approach for GRF estimation was particularly effective on the simulated quadruped robot. To further assess the ESN-based strategy, an experimental set-up was considered to properly acquire the needed data from the Lilibot robot, as the current robot setup does not include GRF sensors (Sun et al., 2020). The experimental setup adopted consists of a custom-designed force plate platform for legged robots (see **Supplementary Material**). The Lilibot quadruped robot was monitored on the platform while moving forward using a trot gait. Data coming from the force plate platform were acquired at 20 Hz and synchronized with those ones acquired from the robot, in particular the joint motor currents, used as inputs for the network. The whole dataset acquired through a series of experimental trials on the robot is composed of 3,000 patterns properly divided between learning (80%) and test (20%). The idea to directly use the network previously trained in simulation with the newly acquired robot data was not pursued due to the differences in terms of input variables (i.e., motor currents instead of joint torques) and the actual set-up of the robot that has some differences if compared with the dynamic model from several aspects, for instance, the stepping frequency and the weight. Therefore, a new ESN was trained to design a soft sensor for GRF estimation. We considered a

reduced network with 15 neurons in the reservoir to estimate the GRF associated to the front right leg, starting from the motor currents acquired from the Knee and Hip 2 joint motors of the same leg. The other hyperparameters adopted have remained unchanged from the **Table 1**. To filter out high-frequency noise in the motor currents, a 5th-order Butterworth filter with a cutoff frequency of 1.5 Hz was adopted. **Figure 12** shows the normalized motor currents provided as input to the ESN, and the obtained GRF compared with the signals acquired from the force plate platform, applying a Z-score normalization. The GRF estimation for the first three steps is quite satisfactory, in fact, the testing performance obtained reports an MSE equal to 0.5 and a Pearson correlation coefficient (R) equal to 0.72. The behavior highlighted in the last step needs a brief explanation. The experiment here considered, as illustrated in the video of the robot walking on the sensorized platform included as **Supplementary Material**, reveals that the robot makes a slight turning to the right toward the end of the experimental trial. This change of direction affects the positioning of the legs as demonstrated in **Figure 13** where a series of snapshots extracted from the robot experiment is reported. In the last picture of the sequence, the front right leg tip is placed on the boundary of two measurement units in which the force plate could not properly identify the GRF. The effect of this event is the

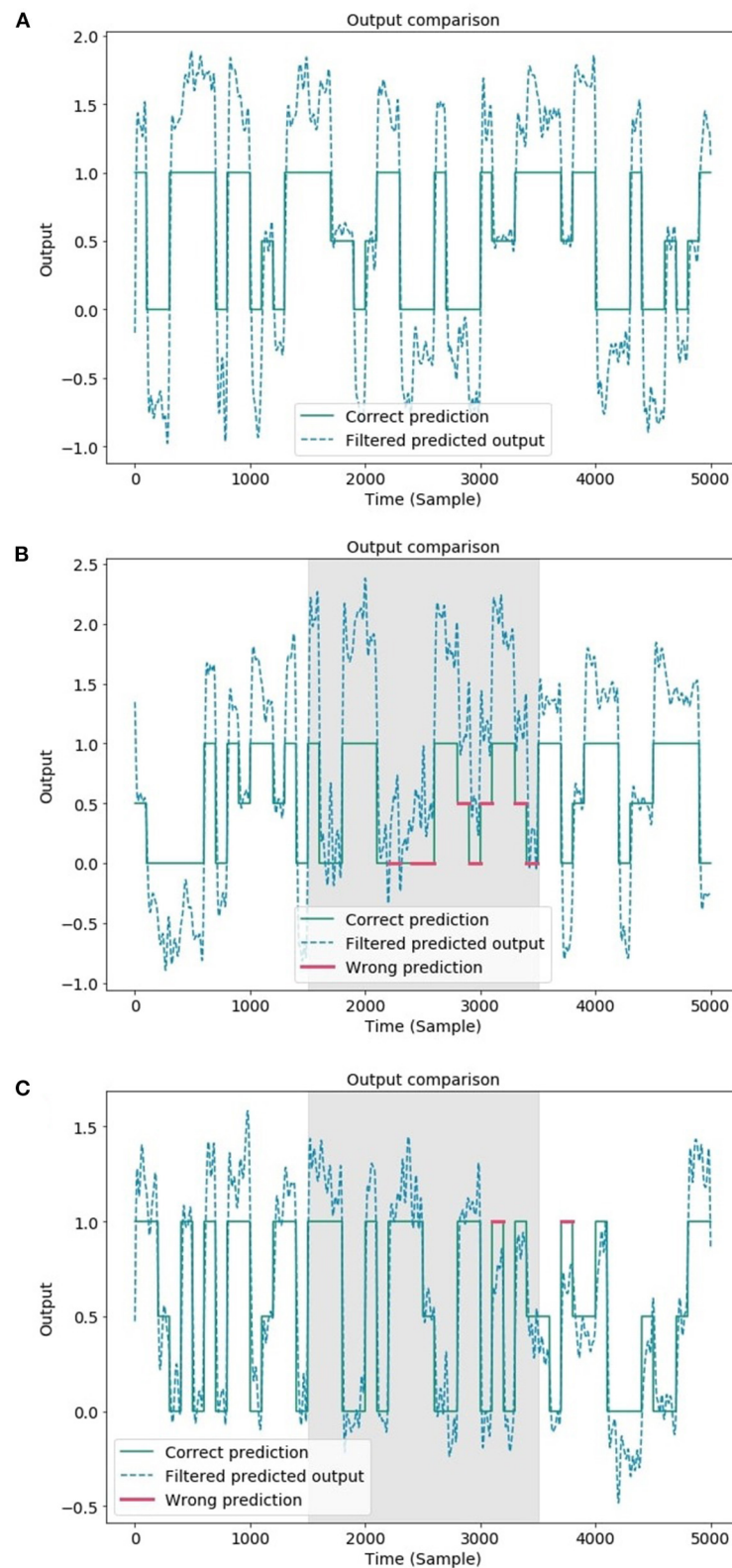


FIGURE 11 | Comparison between the filtered predicted output and the target signal obtained for different data configurations: learning without faults and testing without faults **(A)**, learning without faults and testing with faults **(B)**, and learning with faults and testing with faults **(C)**. The fault consists of the unavailability of the sensory signals coming from the front right leg (Hip2 and Knee joints) for 2,000 samples (gray area).

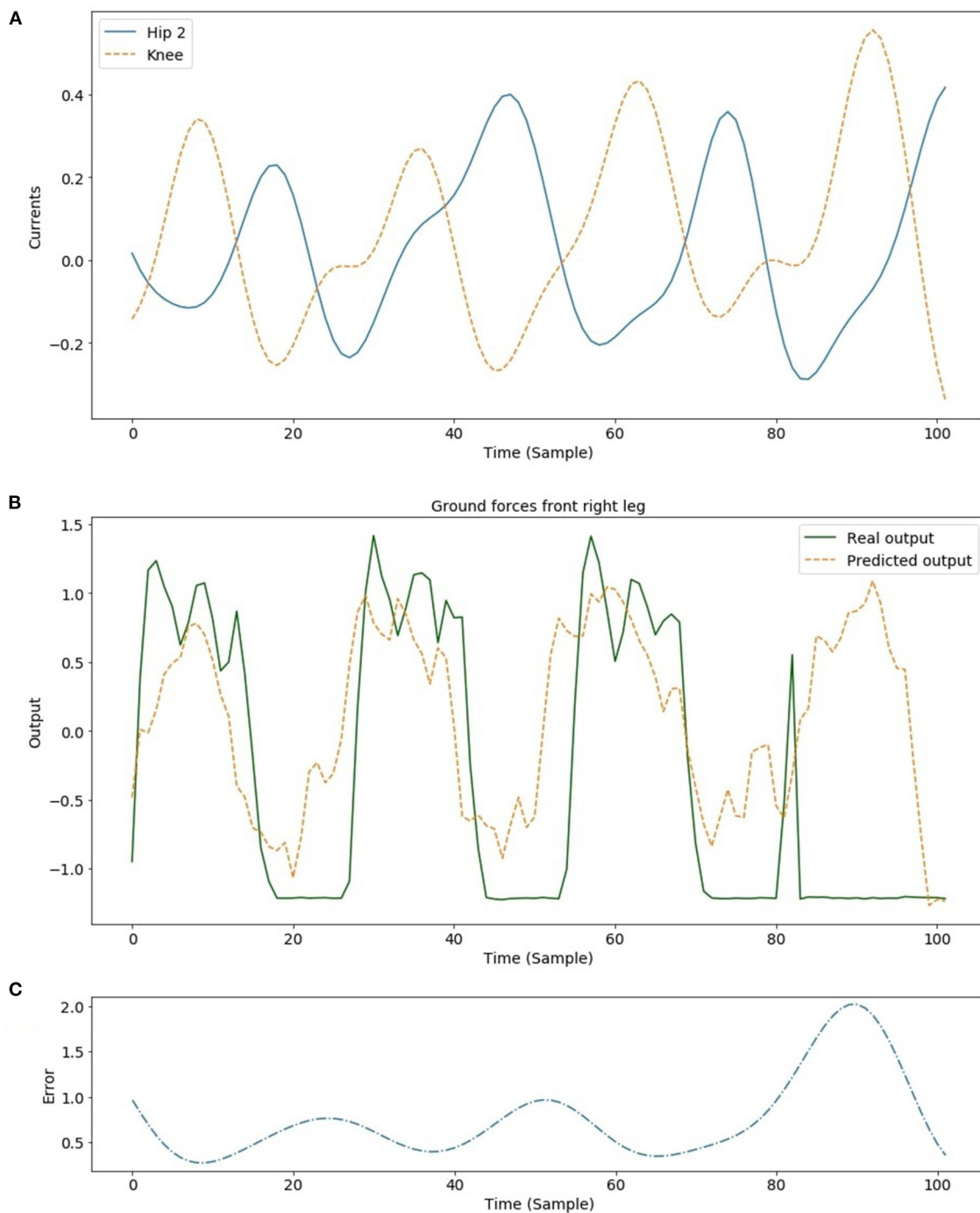


FIGURE 12 | Input and output signals for the ESN trained to predict the GRF of the front right leg of the Lilibot quadruped robot: **(A)** the trend of the filtered motor currents on the Hip 2 and Knee robot joints; **(B)** the comparison between the estimated and actual GRF acquired from the real robot during the testing phase; **(C)** the prediction error where the presence of an unexpected situation is highlighted by the increased values in the error signal.

missing of the GRF information as shown in **Figure 12** after the time sample 80. In this case, the ESN network is still able to predict the GRF and the increment of the prediction error can be used as an indicator of a possible anomaly in

either the sensing system or the robot behavior. This effect can be exploited thinking to a robot equipped with GRF sensors. The ESN model would represent an internal model capable of producing an efferent copy on which to evaluate the discrepancy



FIGURE 13 | Snapshot of the Lilibot walking on the force plate. The blue circles indicate the stance feet touching on a single measurement unit while the red circle indicate the feet (i.e., right front foot) touching on the boundary of two measurement units in which the force plate could not identify the GRF acted on the foot (i.e., right front foot).

between expectations and real conditions to identify anomalous situations.

Legged structures are good testbed to evaluate performance of neural models trying to estimate relevant information also acting as afference copy to be used to identify unforeseen situations like faults. A methodology for mapping local proprioceptive information (e.g., joint torque) into exteroceptive global information (e.g., GRFs) has been here presented. This methodology is based on reafference principle (Latash, 2021). The possibility to use recurrent neural networks (e.g., ESNs) to exploit their neurodynamics as well as embedded internal memory for robust state estimation (e.g., when missing input information) is another relevant aspect here addressed.

The obtained results demonstrate that the proposed approach is suitable to estimate the GRF in real quadruped robots walking on flat terrains. The differences between the real and simulated setups allow to conclude that the approach can be easily applied to different robot parametric configurations when input and output data can be acquired for the network training.

4. CONCLUSIONS

The methodology presented in this paper demonstrates the versatility of reservoir computing networks and exploits the ability of the reservoir to concurrently provide different analyses of the same input data and perform different static and dynamic mappings. This allows a dynamical layer constituting a high-dimensional sparse coding of the input features to be provided independently of the target output. The dynamical layer can be read out in many different ways concurrently. Moreover, the approach presented here is a clear example of a virtual sensor design. In fact, one of the functions of the ESN is to substitute actual force sensors with their estimated values using soft sensors. In addition, the structure does not use models that require analytical models of the robot, which can sometimes be complicated owing to the complexity of legged machines. In any case, the analytical representations can seldom take into account all the nonlinearities arising

from the dynamic interplay between the different bodies in motion. The data-driven approach here is easy to implement and requires only data that can be acquired easily either in simulations or in simple experimental setups with the actual robot. Preliminary experiments carried out with the Lilibot quadruped demonstrate the effectiveness of the proposed approach in estimating the GRF of a leg starting from joint motor signals.

The possibility of adding multiple readout maps to extract the required information from the reservoir with simple and effective learning strategies demonstrated by the GRF and terrain classification is of great interest. It opens the way to the implementation of the proposed networks on dedicated hardware where high-level synthesis techniques, in conjunction with design automation allow the transformation of an offline-trained ESN algorithm into an embedded hardware accelerator. The next step in the further development of the proposed approach would be to evaluate the ESN for the estimation of the actual GRF signals and terrain classification recorded on the actual Lilibot robot in more complex scenarios.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MC developed the ESN, performed the simulations, and drafted the manuscript. LP led the development of the ESN, helped with data analysis, drafted the manuscript, and supervised the entire project. TS developed the robotic system, performed the robotic simulations, and recorded the data for the robot experiments. PA drafted the manuscript and supervised the entire project. PM cooperated with PA in the general direction of the project and reviewed the manuscript. All authors contributed to the conception and design of the work, approved the final version of the

manuscript, and agreed to be accountable for all aspects of the work.

FUNDING

This research was partially funded by the NSFC-DFG Collaborative Research Program of the National Natural Science of Foundation of China under Grant 51861135306 [PM] and the MIUR project CLARA-Cloud platform for Landslide Risk Assessment grant number SNC 00451 [PA], and the NUAU Research Fund [PM].

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ACKNOWLEDGMENTS

We would like to thank Editage (www.editage.cn) for English language editing.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fnbot.2021.655330/full#supplementary-material>

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How Many Muscles? Optimal Muscles Set Search for Optimizing Myocontrol Performance

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OPEN ACCESS

Edited by:

Dai Owaki,
Tohoku University, Japan

Reviewed by:

Kazutaka Takahashi,
University of Chicago, United States
Qi An,
The University of Tokyo, Japan

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Received: 16 February 2021

Accepted: 06 September 2021

Published: 07 October 2021

Citation:

Camardella C, Junata M, Tse KC,
Frisoli A and Tong RK-Y (2021) How
Many Muscles? Optimal Muscles Set
Search for Optimizing Myocontrol
Performance.
Front. Comput. Neurosci. 15:668579.
doi: 10.3389/fncom.2021.668579

In myo-control, for computational and setup constraints, the measurement of a high number of muscles is not always possible: the choice of the muscle set to use in a myo-control strategy depends on the desired application scope and a search for a reduced muscle set, tailored to the application, has never been performed. The identification of such set would involve finding the minimum set of muscles whose difference in terms of intention detection performance is not statistically significant when compared to the original set. Also, given the intrinsic sensitivity of muscle synergies to variations of EMG signals matrix, the reduced set should not alter synergies that come from the initial input, since they provide physiological information on motor coordination. The advantages of such reduced set, in a rehabilitation context, would be the reduction of the inputs processing time, the reduction of the setup bulk and a higher sensitivity to synergy changes after training, which can eventually lead to modifications of the ongoing therapy. In this work, the existence of a minimum muscle set, called optimal set, for an upper-limb myoelectric application, that preserves performance of motor activity prediction and the physiological meaning of synergies, has been investigated. Analyzing isometric contractions during planar reaching tasks, two types of optimal muscle sets were examined: a subject-specific one and a global one. The former relies on the subject-specific movement strategy, the latter is composed by the most recurrent muscles among subjects specific optimal sets and shared by all the subjects. Results confirmed that the muscle set can be reduced to achieve comparable hand force estimation performances. Moreover, two types of muscle synergies namely “Pose-Shared” (extracted from a single multi-arm-poses dataset) and “Pose-Related” (clustering pose-specific synergies), extracted from the global optimal muscle set, have shown a significant similarity with full-set related ones meaning a high consistency of the motor primitives. Pearson correlation coefficients assessed the similarity of each synergy. The discovering of dominant muscles by means of the optimization of both muscle set size and force estimation error may reveal a clue on the link between synergistic patterns and the force task.

Keywords: myocontrol, synergies, muscles, optimization, rehabilitation, EMG, robotics, electrodes

1. INTRODUCTION

Myoelectric control or myo-control is an advanced human-machine interface technique to control robots and devices in rehabilitative and assistive applications. Myo-control decodes human motor intention in the form of analyzed electromyographic (EMG) signals into a computed control signal that drives robots or machines. The rise of myo-control was initially started by the need to drive prosthetic devices, reproducing a set of distinct muscle activity patterns after performing certain contractions of the residual limb (Lowery et al., 2003; Hargrove et al., 2007). Facing the challenge of controlling multiple degrees of freedom (DoFs), the application of pattern recognition of spatio-temporal patterns of muscle activities for prostheses control significantly increased user performance in 3D movements making it more comfortable and intuitive than direct control (Hargrove et al., 2017). As a result, the classification of movements associated to daily activities reached high performance (Sensinger et al., 2009; Young et al., 2011; Adewuyi et al., 2015). Nevertheless, the intrinsic on-off and sequential nature of this control strategy determined a gradual growing interest toward simultaneous and proportional control (SPC) or simply proportional control. In the context of myoelectrical controls, a proportional control theoretically allows for a continuous support of limb or hand movements, continuously producing a control signal to an external device (e.g., robotic device) based on user's residual muscular activity. Fougner et al. defined the proportional control as a strategy with which "the user can control at least one mechanical output variable of the prosthesis within a finite and essentially continuous interval by varying his/her control input within a corresponding continuous interval" (Fougner et al., 2012). The "essentially continuous" term refers to a digital sampling interval, small enough to not affect human perception thus being negligible. The SPC paradigm opened new possibilities to design prostheses control strategies following the way human neuromuscular system activates DoFs simultaneously and proportionally (Battye et al., 1955; Bottomley, 1965; Jiang et al., 2013). In the last decade several studies have been conducted on the proportional control of robotic devices and prostheses, using linear or non-linear regression algorithms, within isometric or dynamic setups (Cheung et al., 2012; Jiang et al., 2013; Berger and d'Avella, 2014; Roh et al., 2015; Buongiorno et al., 2018). Here, muscle activations have been used for continuously estimating either articulation torques or hand force during planar reaching tasks. Also, following the trail of bio-inspired strategy development, dimensionality-reduction algorithms have been used to extract motor primitives, aiming at explaining how the human brain produces low-dimensional perceptual representations of a high number of sensory information distributed in the whole body (Hayward, 2011; Beckerle et al., 2017). These primitives, called muscle synergies or synergies, have been theorized as a way to explain motor control and learning by the central nervous system (CNS), given the abundant number of motor units in human beings and animals (d'Avella et al., 2003; Bizzi and Cheung, 2013; d'Avella, 2016). Muscle synergies have applications in a

variety of fields, for example clinical assessments (Cheung et al., 2012; Roh et al., 2015) and control in robotics (Jiang et al., 2009; Berger and d'Avella, 2014): in the latter context, synergy-based myo-control was designed to exploit muscle activation patterns during task-related movements, reflecting the concept of CNS motor control. Synergy-based myo-controls have been tested in the hand force or articulation torques prediction, with linear-regression models, in a fixed (Berger and d'Avella, 2014) or multiple configurations of the limb (Buongiorno et al., 2017; Camardella et al., 2020a) with different synergies extraction algorithms. Most of the experiments in the literature exploited either isometric (in a virtual environment) or dynamic reaching tasks. In a work by Lunardini et al., synergy-based torque estimation algorithms revealed to be less sensitive to signal noise and no differences were found between isometric and dynamic protocols (Lunardini et al., 2015). They, thus, suggested that synergy-based estimations perform better than muscles-pair in a dynamic protocol in which signals are more likely to be corrupted by artifacts. In another work, Roh et al. found that synergy composition was conserved across isometric tasks with different bio-mechanical constraints (Roh et al., 2012). Similarly Muceli et al. found that synergies extracted from dynamic tasks were robust against electrode shifts, being suitable for an intensive clinical usage (Muceli et al., 2013). In both cases, synergies were useful to identify muscle activation patterns when extracted from reaching-movements EMG.

In both robotics and clinical assessment contexts, synergies extracted with the non-negative matrix factorization have always shown a physiological meaning, giving important insights on human motor control strategies (Dipietro et al., 2007; Cheung et al., 2009, 2012; Safavynia et al., 2011). As an example, in the cited works of Tropea et al. and Camardella et al., stroke survivors' synergies were compared to healthy subjects' ones to investigate whether the patterns similarity reflect patients' cerebrovascular injuries and consequent functional recovery (Tropea et al., 2013; Camardella et al., 2020b). In another work of Steele et al., the authors checked how the choice of muscles can influence the synergy analysis by computing the similarity of synergies among different sets (Steele et al., 2013). In all these works, physiological meaning of altered synergies was assessed through the comparison with reference ones (healthy or unaltered).

For better accuracy and sensitivity in force estimation, featuring reaching tasks with either the whole upper limb or the wrist, simultaneous and proportional myo-control studies typically include 8–14 muscles, mainly large accessible muscles for surface EMGs. In the previous studies mentioned above, the rationale behind the number of chosen muscles was mainly based on human bio-mechanics. Attaching several EMG electrodes to the subject may be feasible in an experimental setting, but not comfortable for the subject. The absence of time constraints also makes such a set-up acceptable in an experimental environment. In rehabilitation robotics applications, the use of a large muscle set is not practical both for the subject and the therapist given the limited amount of time and resources.

The hypothesis of this study is that, given a specific myo-control application, the number of muscles to record

can be reduced to a minimum set, concurrently preserving the performance of motor activity prediction and the physiological meaning of synergies. This will lead to three main achievements: (1) the reduction of inputs in a myo-control strategy and, consequently, a lower control processing time (i.e., computational cost), (2) the reduction in the number of EMG electrodes to apply on the subject, improving the comfort and ease of the setup, and (3) a higher sensitivity to changes of synergies, which could lead to a more evident motor function evolution and, if applied, to an ongoing modification of rehabilitation therapies. Nevertheless, the reduction in the muscle set size may affect the prediction capabilities of linear/non-linear models, and information on motor coordination that synergies provide. This last aspect comes from the fact that non-negative matrix factorization, used for synergies extraction, operates on the minimization of the root mean square residuals, between the input matrix and the product of output matrices, without any constraint on how muscle activities will be arranged in synergies: this means that any modification to the input matrix leads to different output patterns whose information on motor coordination may be altered. Thus, the objective of this study is to demonstrate that a minimum set of muscles, called optimal set, can be found, and that this set preserves performance of force/torque prediction and motor coordination information contained in synergies. The optimality is evaluated through the comparison between optimal and initial (namely full set) sets with two indexes: the difference in the prediction error (e.g., root mean square error, RMSE) and the correlation of synergies.

To do so, isometric contractions of nine healthy subjects, toward four directions in the horizontal plane, have been used to train a linear EMG-to-force model, for each possible combination of muscles in a total of 15, decreasing the size of the muscle set at each iteration. The authors searched for the optimal muscle set based on the RMSE of the EMG-to-force estimation in global and subject-specific conditions. These conditions depict how much a certain muscle is relevant for both all subjects (global condition) and for a specific subject (subject-specific condition), relying on a RMSE-based score. The preservation of force prediction performance has been evaluated through non-parametric statistical tools, assessing the absence of differences on the RMSE, between optimal and full set groups in both conditions. After that, the authors extracted muscle synergies from optimal and full sets and compared them through the Pearson correlation coefficient: the role of muscle synergies in this study has the aim of confirming the consistency of motor patterns generated by the optimal set. Moreover, two types of synergies have been tested for this purpose, in order to understand if the extraction process may influence the consistency of optimal set synergistic patterns.

2. MATERIALS AND METHODS

2.1. Participants

Nine healthy individuals (age 24.9 ± 1.3 years, weight 73.4 ± 14.0 kg and height 177.1 ± 5.7 cm, all males) participated in the study. All subjects were self-reported right hand dominant and

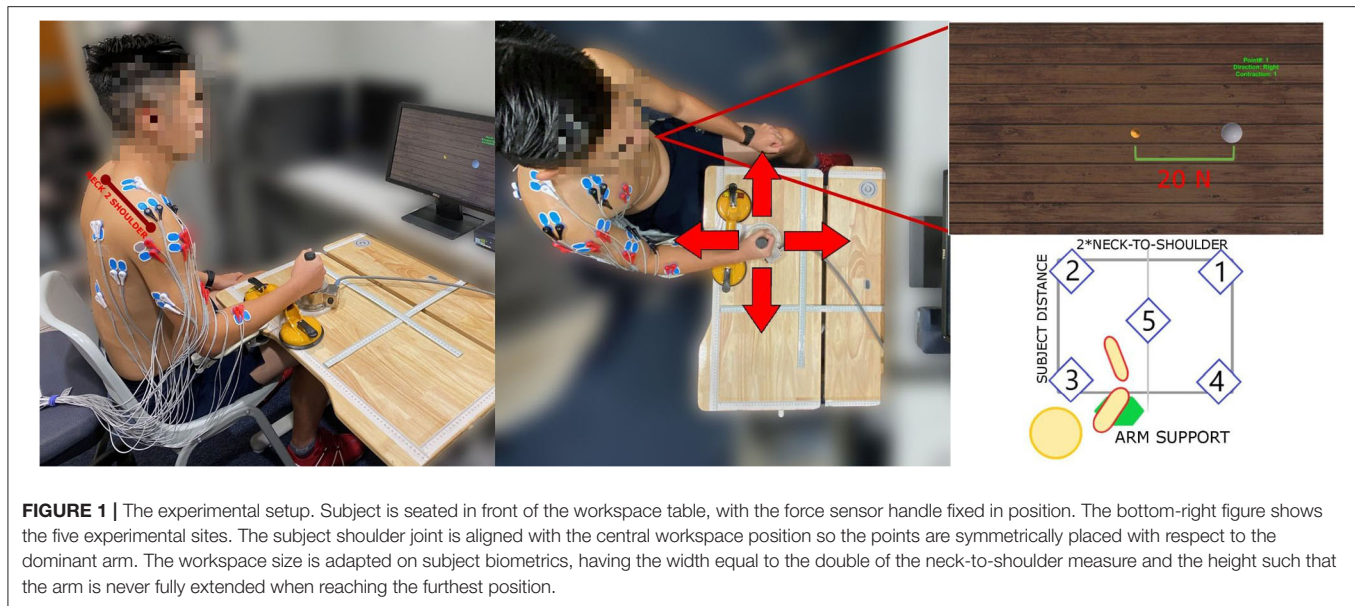
at the moment of the experiment had no neurological, muscular, and orthopedic impairments. The experiment was their first experience with a setup that included EMG recording sessions. All subjects gave an informed consent prior to the study. The study has been approved by the Joint Chinese University of Hong Kong—New Territories East Cluster Research Ethics Committee and conducted in accordance with Declaration of Helsinki.

2.2. Experimental Setup

The experimental setup was comprised of: (a) A 3D-printed cylindrical stationary joystick with ATI Gamma IP65 six-axis force/torque sensor (ATI Industrial Automation, Apex, NC, USA) with 65 N maximum load, that recorded forces generated at the hand and sampled at 125 Hz, fixed on a height-adjustable table, (b) an Ergorest elbow rest device for anti-gravity support (Ergorest Oy, Siilinjärvi, Finland) to lift tonic EMG signals resulted from sitting up with the arm raised to a table level, (c) a 16-channels surface EMG acquisition system with built-in band-pass and notch filters using two g.USBamp Biosignal Amplifiers (g.tec Medical Engineering GmbH, Austria), (d) a game environment shown on a monitor screen with a small golden ball representing the force generated cursor and a large white sphere representing the task target force (see **Figure 1**). The cylindrical stationary joystick was securely fixed in a certain position of the table. The central position (Position 5, in **Figure 1**) distance from the subject was calculated to be reachable with the subject's elbow at a 90 degree position. Surface EMG electrodes were placed after a thorough skin preparation based on the Surface Electromyography for the Non-Invasive Assessment of Muscles-European Community Project recommendations. Fifteen muscles from the dominant arm and torso were recorded for analyzing contralateral and ipsilateral contractions, as well as pushing and pulling actions, often related to reach-and-grasp movements. The full muscle set included: flexor digitorum (HAND FLEX), extensor digitorum (HAND EXT), biceps long head and short head (BI LO and BI SH), brachialis (BRACH), triceps lateral head and long head (TRI LAT and TRI LON), anterior deltoid (DELTA), medial deltoid (DELTA), posterior deltoid (DELTA), pectoralis major (PECT M), infraspinatus (INFRASP), upper trapezius (TRAP), latissimus dorsi (LAT DORSI), and teres major (TER MAJ). Ground electrodes were placed on the clavicle and the scapular acromion. Maximum voluntary contractions (MVC) for all muscles were observed at the beginning of the data collection for the EMG signals normalization. Each MVC was performed with a 1-min rest in between to avoid the effects of fatigue. EMG signals were acquired at a 1,200 Hz sampling frequency, as well as band-pass (5–500 Hz) and notch (50 Hz) filtered. The EMG acquisition PC was synchronized with the game environment and the PC that recorded the force/torque sensor using a User Datagram Protocol (UDP) connection between the two PCs.

2.3. Study Protocol

Subjects had to perform isometric contractions with the upper-limb in position, grabbing the handle in 5 sites of the horizontal workspace (see **Figure 1**). Subjects were seated on a stationary chair that was positioned to align the sternum with test positions



2 and 3, having the center of the shoulder joint approximately aligned with position 5. Subjects' neck-to-shoulder, arm and forearm measures were acquired to create a feasible workspace, symmetrical with respect to the dominant hand. Subjects grabbed the joystick, after placing their elbow on the anti-gravity support attached to an height-adjustable table. All subjects maintained their elbow at height with the help of the arm support and their distance from the workspace was computed using arm and forearm measures, in such a way that the furthest position was always reachable without the arm being in singularity. In each test position, subjects had to move the small golden ball cursor by generating force at the hand toward the target force (indicated by a large white sphere) in 4 different directions (forward, backward, right, and left). Each direction was repeated two times making a total of 8 trials. Subjects performed isometric muscle contractions to generate the force on the joystick. Target reach was deemed successful if the subjects could maintain the center of the ball cursor in the white sphere for 2 s. When subjects relaxed, meaning zero force input on the joystick, the small golden ball cursor returned to its original rest position. The start of the trial was indicated by the white sphere target appearing and the end was indicated by the white sphere disappearing. The white sphere target area is larger than the small golden ball cursor, indicating a tolerance of 5 N on the force target. A spring model $P_C = K * F_j$ has been used to compute the position of the cursor (P_C) using the measurements from isometric force exerted on the joystick (F_j) with K as the elastic constant of the virtual spring (Berger and d'Avella, 2014).

2.4. Signal Processing and Dataset Splitting

Before training and testing the model, raw EMG signals were rectified and filtered using a 4 Hz 2nd order Butterworth low-pass filter and then normalized using the MVC. Then, the processed EMG dataset was split in training and test sets. Since each subject

performed two contractions for each direction (see section 2.3), in every test of this study, one was randomly selected to be part of the training set and the other one to be part of the test set. For each subject, a datetime-dependent seed was used to determine a random sequence of numbers, as wide as the total number of combinations of muscle sets. Each value of this sequence uniquely selected a specific combination of contractions, to be used in the training set, taken as a 4-digits binary combination (one digit for each direction): if 0 the first contraction was used, otherwise the second one was included. The complementary sequence was used for building the test set. The training set was used for training the linear regressor only (see section 2.5) while the test set was used to build force estimations and extract performance indexes (see section 2.6.1): these indexes were used for the selection of optimal sets (sections 2.6.2 and 2.6.3) and the statistical analysis (section 2.6.4).

2.5. Model Building and Force Estimation

Muscle activations were always lower than the MVC value and in each workspace position the arm pose was fixed. Following this, the relation between the force exerted at the hand and the aforementioned filtered and normalized EMG signals, measured from elbow and shoulder muscles, was approximately linear (Buchanan et al., 2004; Berger and d'Avella, 2014; Buongiorno et al., 2018). The multi-variate linear regression algorithm (MVLRL), that assumes a direct relation between muscle activations and hand-force exertion, has been used as the EMG-to-force model, currently being the most used in the state of art. Thus, the evaluation of performance of each muscle set was achieved comparing the force measurements with the estimations that resulted from the linear model, trained as following:

$$H = \underset{H \in \mathbb{R}^n}{\operatorname{argmin}} \| H m_t(t) - F_t(t) \|_2 \quad (1)$$

where m_t is the training EMG data matrix ($M \times N$ where N is the number of samples) and F_t is the training forces data matrix ($2 \times N$ matrix): thus, H will be a $2 \times M$ matrix. In the case of a full muscle set M was equal to 15, otherwise it was equal to the chosen optimal muscles number. The subscript “t” in Equation (1) means that training set signals only should be used as the regressor training process relies on the training set only. Under the linear force-EMG relationship, the force estimation can be computed using the following equation:

$$F_{est}(t) = H \cdot m(t), \quad (2)$$

where $F_{est}(t)$ is the estimated 2-dimensional force, $m(t)$ is the processed test EMG signal and H is the aforementioned regression matrix. Force prediction (i.e., F_{est}) could be potentially computed for both training and test sets, for example for RMSE computation on the training set, if needed.

2.6. Data Analysis

2.6.1. Performance Indexes

Two different indexes have been used for assessing the force estimation performance of each method in each condition: Root Mean Square Error and Coefficient of Determination.

- Root Mean Square Error (RMSE)

This index is used to measure the difference between the measured and the estimated forces and it is calculated as follows:

$$RMSE = \frac{\sqrt{\frac{\sum_{i=1}^N (x_{x,i}^2 - \hat{x}_{x,i}^2)}{N}} + \sqrt{\frac{\sum_{i=1}^N (x_{y,i}^2 - \hat{x}_{y,i}^2)}{N}}}{2} \quad (3)$$

The $x_{x,i}$ and $x_{y,i}$ are the x and y components of the x_i 2D measured force sample, respectively. The $\hat{x}_{x,i}$ and $\hat{x}_{y,i}$ are the x and y components of the $\hat{x}_i$ 2D estimated force sample, respectively. N stands for the number of samples. The lower the value of the RMSE the closer the estimated force matches the measured force signal amplitude.

- The Coefficient of Determination (R^2)

The R^2 index is used to highlight a signal total variation explained by the estimates. The R^2 is computed as follows:

$$R^2 = 1 - \frac{SS_{res}}{SS_{tot}} = 1 - \frac{\sum_{i=1}^N (x_i - \hat{x}_i)^2}{\sum_{i=1}^N (x_i - \bar{x}_i)^2}, \quad (4)$$

where x_i is the original signal and $\hat{x}_i$ is the estimated output sample. N stands for the number of samples. The index ranges from minus infinite to 1 (equal to 1 in case of a perfect estimation with an error equal to zero).

2.6.2. Muscle Scores

It was necessary to evaluate the performance of all muscle set combinations given the initial full set. To do so a loop was implemented defining the muscle set size at each iteration and then cycling on all combinations of muscles: the number of muscles was iteratively decreased from 15 to a minimum set of 4. For each muscle set a linear model was trained (see section

2.5) and tested on a different set of contractions (see section 2.4). Then a force estimation was built, according to 2, using test set signals, and compared to the measured ones through the RMSE index. Each time a performance index was computed, the muscles involved got a score equal to the RMSE value (averaged on the two force components) and summed to the previous score value. At the end of this loop, muscles with the lowest score were the most significant for that subject as they were always included in the sets that achieved the lowest estimation RMSE. A “ranking” of muscles was created, following the ascending order of RMSE scores and assigning to each muscle a rank equal to the ranking position: the first muscle in the ranking got a rank equal to 1, the second one a rank equal to 2 etc. This loop was repeated for all the participants. At the end of this analysis, all the muscles scores and ranks, for all the participants, were available to be used. A step-by-step procedure is shown below in the **Algorithm 1**.

2.6.3. Selection of Optimal Sets

Once the ranks of muscles have been obtained for all the subjects, actual performance of muscle sets could be computed without considering all of their combinations. This next step is divided in two analyses: a subject-specific one and a global one. In this step, RMSE of force estimation is computed iterating on all combinations of train/test datasets and on the number of muscles from 15 (full) to 4 (minimum).

- Subject-specific: At each iteration, the muscles to be used in the set were chosen by first discarding muscles with the highest rank (i.e., highest RMSE) in the subject-specific ranking.
- Global: This analysis differed from the previous one by the muscles choice criterion. In this case, a single global ranking was created summing all subject-specific rankings. The same loop as the previous point (i.e., subject-specific) was then performed: this time, at each iteration, the muscles to be used in the set were chosen by first discarding muscles with the highest rank (i.e., the highest RMSE) in the global ranking.

Eventually, from 15 to 4 muscles, a complete picture of the force estimation performance, for all the participants in both conditions, was depicted. The minimum number of muscles that showed a comparable amount of error (in terms of mean and standard deviation of the RMSE) w.r.t the full set, was chosen to be the optimal set. This optimal set then underwent both synergies computation process and statistical analysis, to assess its usability in a myo-control application.

2.6.4. Statistics

The aim of the statistical study was to assess the expected similarity between optimal and full muscle sets force estimation performance. Thus, after choosing the optimal set to be analyzed, an ANOVA 1-way test was performed on the two populations: the acceptance of the null hypothesis would have confirmed the absence of significant differences among the two groups. Before launching the ANOVA test, Shapiro-Wilk normality test and χ^2 homogeneity of variance test were performed on the two datasets, fulfilling parametric-test requirements. The analysis was repeated for both subject-specific and global optimal sets, compared to the full set.

Algorithm 1: Set of operations for evaluating muscle scores and ranks (i.e., importance) for a given subject. A “for” loop was implemented decreasing the i -th muscle set size from 15 to a minimum set of 4 at each iteration and then cycling on all combinations of muscles of the i -th set size. First operations concern the signal processing: `envelope()` refers to the low-pass filter used to extract the signal envelope and `linreg()` refers to the linear regressor training function. `comb()` function selects the j -th combination of muscles with i elements, while `datasplit()` randomly divides the dataset into training and test set. `rmse()` computes the RMSE index from measured and estimated forces. `sort()` function extracts the sorting indexes of the input, following either the ascending or descending option: for example, with the ascending option, if the forth muscle got the lowest score, the first element of ranks was equal to 4. This algorithm is repeated for all the participants. Ranks variable refers to the subject-specific rank values.

```
% scores initialized as an array of 15 elements;
% muscles initialized as an array of 15 elements with
% indexes of amplifier channels (from 1 to 15);
for i=15:4 do
    for j-th combination of i muscles in a group of 15 do
        musclessset = comb(muscles,i,j);
        % Selecting EMG of j-th combination of muscles;
        rawEMG = rawEMG(musclessset);
        % Processing for both train/test data;
        mr = rawEMG;
        mf = bandpassfilter(mr);
        ma = rectification(mf);
        m = envelope(ma);
        [mtrain,mtest] = datasplit(m);
        % Training phase;
        H = linreg(F,mtrain);
        % Estimation phase;
        Fest = H*mtest;
        RMSE = rmse(Fmeas,Fest);
        % All muscles included in the j-th combination get a
        % score equal to RMSE;
        for k=1:15 do
            if k is in musclessset then
                scores(k)=scores(k)+mean(RMSE);
            else
                scores(k)=scores(k)+0;
            end
        end
    end
end
ranks = sort(scores,'ascending');
```

2.7. Synergies

2.7.1. Synergies Extraction

As done in previous works, muscle synergies could be extracted from electromyographical signals using the Non-Negative Matrix

Factorization (NNMF) algorithm (Lee and Seung, 1999). This has been often chosen to separate the fundamental components from the input, assuming that negative muscle activations could not be physiologically obtained. In previous works, the NNMF identified the correct muscle synergies and activation coefficients in simulated data, combined with their consistency when applied to physiological data sets. Also NNMF was able to reconstruct the original signal in a similar way with reference to other more complex algorithms (Tresch et al., 2006). As noted in the literature four synergies were enough to describe electromyographical signals total variance in planar reaching tasks (Roh et al., 2012; Steele et al., 2013; Berger and d’Avella, 2014) with both isometric and dynamic setups. Thus, always four were the synergies extracted from optimal and full sets. As specified in the introduction the only role of synergies was to assess the coherence of optimal set patterns. NNMF was launched using the alternating least squares algorithm option in MATLAB “nnmf” function, with a maximum of 100 iterations and a tolerance of 10^{-7} . According to the NNMF algorithm, muscle synergies can be computed as following:

$$m = W \cdot c + e_m, \quad (5)$$

where m is the input signal ($M \times N$ matrix, being M the number of muscles and N the number of samples), W is the synergy matrix ($M \times s$ matrix, being s the number of synergies), c is the synergy activations matrix ($s \times N$ matrix) and e_m is the muscle activation factorization residuals, dimensionally equal to the input. Having multiple upper limb poses in the experimental protocol, muscle synergies could be extracted either in each of them or merging the information of all poses in a single synergies set. The latter has shown to be the most feasible one in synergy-based myo-control contexts, and it can be obtained in many ways (Buongiorno et al., 2017, 2019, 2020). “Pose-Shared” and “Pose-Related,” have been extensively detailed in a previous work and compared in this study, since they showed different adherence to the input dataset (Camardella et al., 2019). Briefly, the “Pose-Shared” synergies (herein called W_g) are extracted running the NNMF once on a single EMG dataset using the Equation (5), in which m has been taken as the result of the union of the signals of each upper limb pose ($m = [m_1 \cup m_2 \cup m_3 \cup m_4 \cup m_5]$). Instead, the “Pose-Related” synergies resulted from clustering P (i.e., number of poses) synergies sets, using the k-means algorithm, independently extracted from each arm pose and ordered with a minimum cosine distance criterion:

$$W_c(i) = kmeans\left(\bigcup_{p=1}^P W_p(i)\right), i \in [1, s], \quad (6)$$

where the output $W_c(i)$ corresponds to the i -th element of the “Pose-Related” synergies matrix W_c , as the i -th centroid of the clustered synergy vectors. $W_p(i)$ is the i -th synergy of W_p synergies matrix extracted in the point p (i.e., an upper limb pose): P , thus, is the total number of points (i.e., 5). The “Pose-Related” synergies matrix, W_c , can be computed as the union of all the s centroids, given s the number of synergies:

$$W_c = \bigcup_{i=1}^s W_c(i). \quad (7)$$

2.7.2. Synergy-Based Model Building and Force Estimation

The synergy-based models followed the same concepts showed in section 2.5, thus, they were based on a linear relationship between the force at the hand and muscle activations, mapped in the synergy space using the synergies matrix (i.e., W). EMG signals were processed in the same way as done in section 2.5. The model was trained as following:

$$H = \underset{H \in \mathbb{R}^n}{\operatorname{argmin}} \| Hc_t(t) - F_t(t) \|_2, \quad (8)$$

$$c_t(t) = W^+ m_t(t)$$

where c_t is the training synergy activations data matrix ($s \times N$ where s is the synergies number and N is the number of samples), m_t is the training EMG data matrix ($M \times N$ with M defining the number of muscles), W^+ is the pseudo-inverse of the W matrix ($s \times M$ matrix), and F_t is the training force data matrix ($2 \times N$ matrix): thus, H is a $2 \times s$ matrix. In the case of a full muscle set, M was equal to 15, otherwise it was equal to the chosen optimal muscle number. Moreover, the synergy matrix W was chosen as W_g when using “Pose-Shared” synergies (PSS model) and W_c when using “Pose-Related” synergies (PRS model). Also in this case, the subscript “t” in Equation (8) means that training set signals only should be used as the regressor training process relies on the training set only. Finally, the force estimation could be obtained using the following formula:

$$F_{est}(t) = H \cdot c(t), \quad (9)$$

where $F_{est}(t)$ is the estimated 2-dimensional force, $c(t)$ is the synergy activation signal (built using either training or test EMG signals), and H is the aforementioned regression matrix computed using 8. Also in this case, force prediction (i.e., F_{est}) could be potentially computed for both training and test sets, for example for RMSE computation on the training set, if needed.

2.7.3. Synergy Similarities

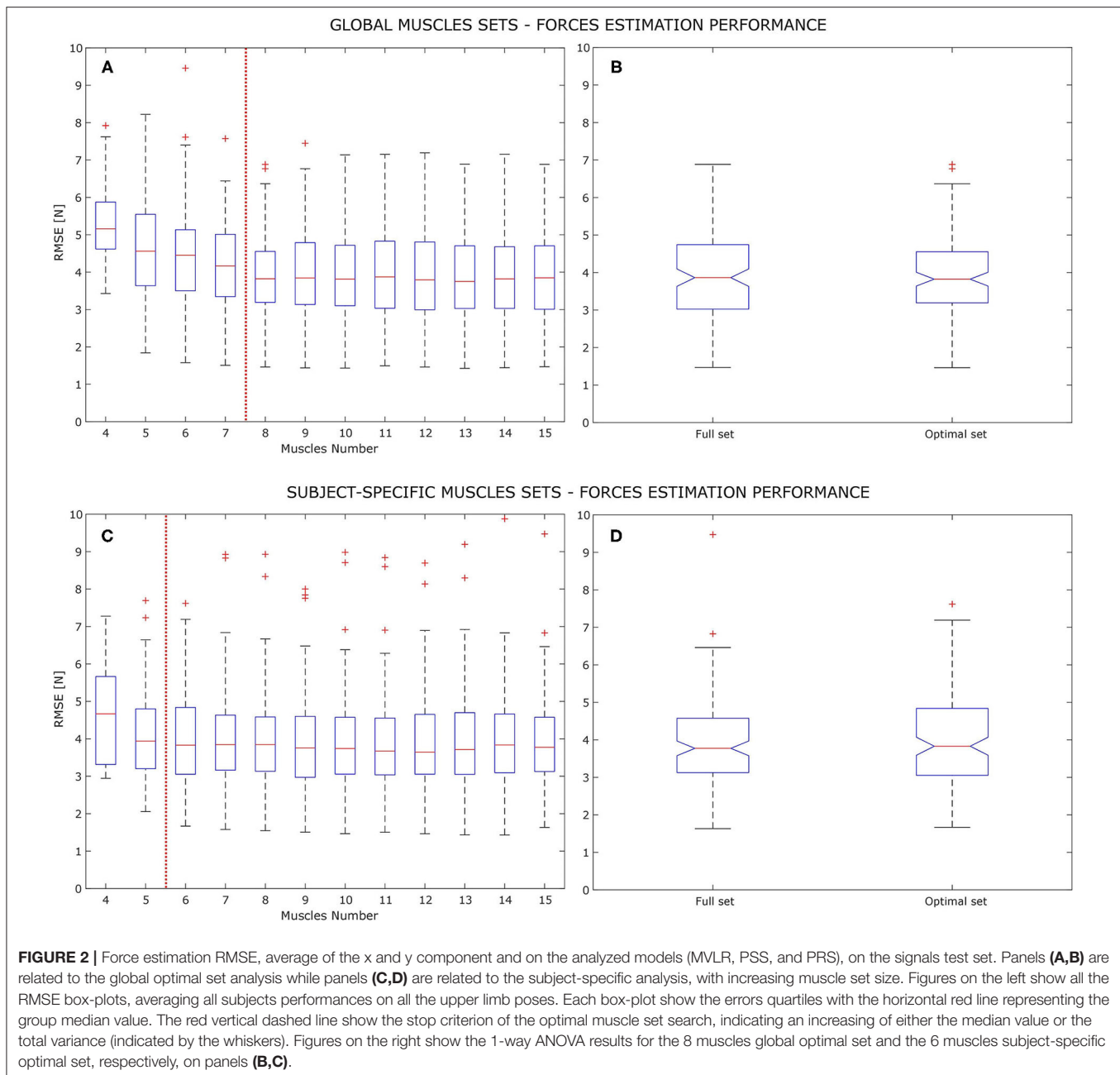
After accomplishing the analysis described in section 2.6.3, synergies extracted from the optimal and the full muscle sets have been compared for evaluating the consistency of each synergy. The Pearson correlation coefficient (r) was used for evaluating the total similarity, as the average of coefficients of each optimal-full set pair of synergies. Given two sets (from optimal and full muscle sets) with four synergies each, 16 different correlation coefficients were computed. The highest calculated coefficient identified the best match between synergy pairs. After each calculation, the previously chosen synergies from both sets were excluded to avoid double-counting. In each synergy, only the muscular contributions from the same muscles of both sets were used. As a result, 4 correlation values were obtained, indicating the best matching synergies among the extracted ones. This process was repeated for both global and subject-specific sets.

3. RESULTS

The main outcome of this study is that an optimal muscles set for the analyzed myo-control application does exist. Referring to **Figure 2**, global and subject-specific conditions are shown, regarding the RMSE performance analysis. In the global condition (**Figure 2A**), it was observed the RMSE value not to suffer from strong variations, both in variance and mean when varying the number of muscles from the full set (i.e., 15 muscles) to 8 muscles. Thus, the 8-muscles set has been taken as the global optimal muscle set, reporting 3.93 ± 1.10 N as its value. Both full and optimal set observations passed the Shapiro-Wilk normality test. The chi-squared homogeneity of variance test was performed giving $\chi^2 = 114.74$ and $p = 0.231$ as values, confirming the homogeneity of variance null hypothesis (1.40 N full set variance, 1.20 N optimal set variance). According to 1-way ANOVA results, there was not a statistical difference between optimal and full muscle set performances giving $F_{(1, 13)} = 0.02$ with $p = 0.886$ as results. **Figure 2C** instead shows the variation in force estimation performance in the subject-specific condition. In this case the RMSE does not highlight any significant variation until it reaches 6 muscles. Reducing the muscles number from 6 to 4 brings to an increase of the RMSE mean by 0.10 N at 5 muscles and by 0.73 N at 4 muscles. It has to be noted that reducing the muscle set from 6 to 5 elements increases the total variance, bringing the minimum RMSE value from 1.67 to 2.05 N. According to this, the 6-muscle set has been taken as the subject-specific optimal muscle set, reporting 3.99 ± 1.11 N as the force estimation RMSE. Also in this case full and optimal set observations passed the Shapiro-Wilk normality test and the chi-squared homogeneity of variance test with $\chi^2 = 121.34$ and $p = 0.452$ (1.40 N full set variance, 1.24 N optimal set variance). The 1-way ANOVA test did not show any statistical difference between optimal and full sets, with $F_{(1, 13)} = 0.35$ and $p = 0.561$.

Concerning synergy similarities, both global and subject-specific optimal sets were analyzed, comparing synergies extracted from these sets to the full set ones. In the former case, synergies showed a mean correlation value of $r_{(6)} = 0.74$, $p = 0.035$ for the “Pose-Shared” synergies and $r_{(6)} = 0.71$, $p = 0.048$ for the “Pose-Related.” In the latter case, a mean correlation value of $r_{(4)} = 0.78$, $p = 0.067$ with “Pose-Shared” synergies and $r_{(4)} = 0.71$, $p = 0.113$ for “Pose-Related” synergies was found. **Figure 3** depicts the comparison of synergistic patterns between full and global optimal muscle sets. All the values represent the average across subjects. R^2 values for “Pose-Shared” synergies generally advantaged the subject-specific condition in almost all cases (see **Figure 4**). Excluding the 4-muscles case, which matched the number of synergies, synergies that exploited the global sets achieved an EMG reconstruction rate ranging from a minimum of 0.878 ± 0.028 to a maximum of 0.972 ± 0.016 . In the subject-specific case the R^2 scored 0.880 ± 0.031 with 15 muscles up to 0.982 ± 0.009 with 5 muscles.

The last result regards linear regression coefficients that constitute the actual link between muscle/synergy activations and the amplitude and direction of the generated force vectors. With the aforementioned 8-muscles global optimal muscle set, the mean Pearson correlations value of regression coefficients,

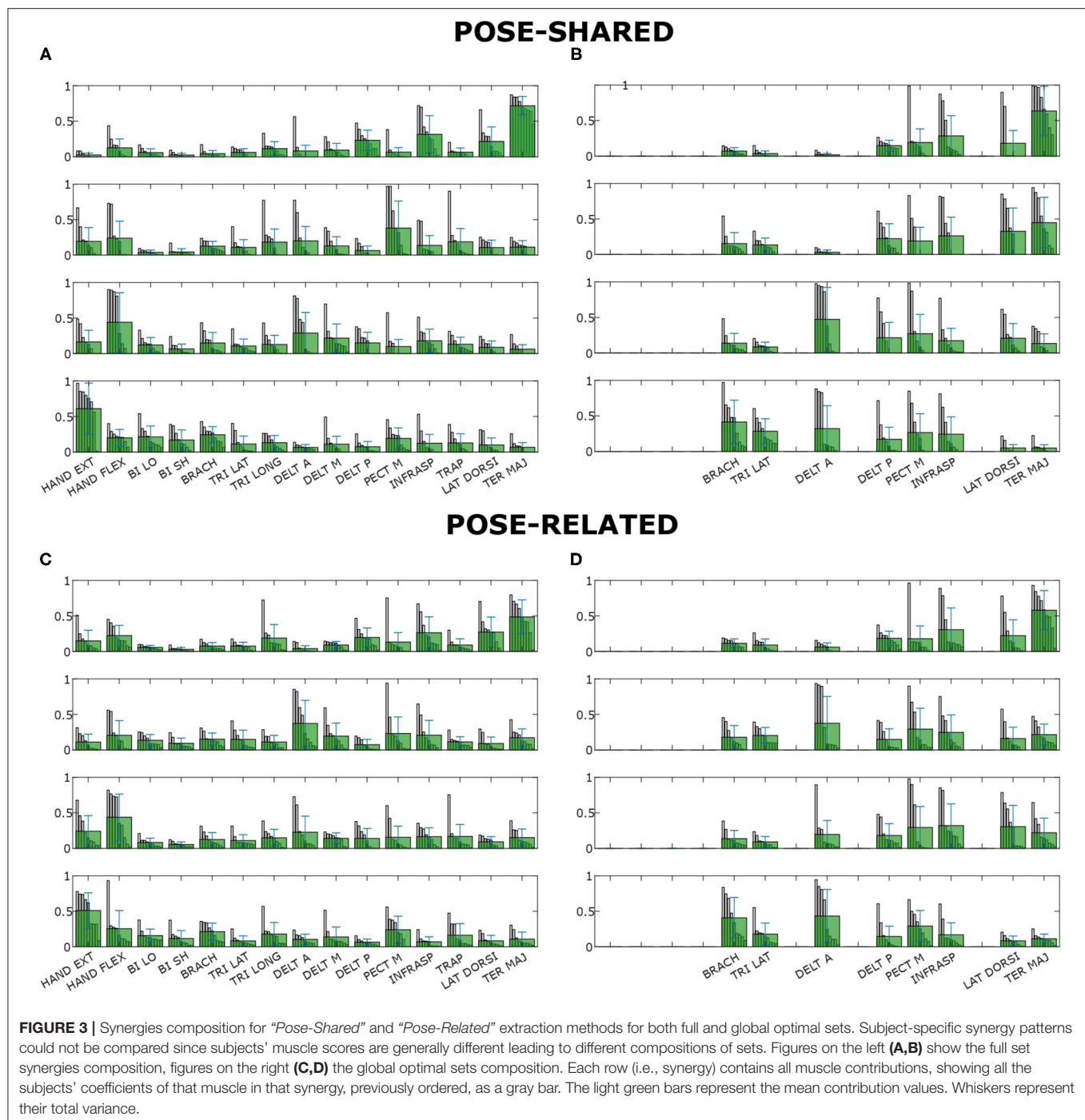


between the full muscle set and the optimal set, scored $r_{(6)} = 0.93$, $p < 0.001$ for MVLRL, $r_{(6)} = 0.88$, $p = 0.004$ for “Pose-Shared” and $r_{(6)} = 0.89$, $p = 0.003$ for “Pose-Related.” Instead, exploiting the 6-muscles subject-specific optimal muscle set, the mean correlation of regression coefficients was $r_{(4)} = 0.87$, $p = 0.024$ for MVLRL, $r_{(4)} = 0.85$, $p = 0.032$ for “Pose-Shared” and $r_{(4)} = 0.89$, $p = 0.021$ for “Pose-Related.”

4. DISCUSSIONS

The search for an optimal muscle set, in the planar myo-control application, gave a positive answer. The analysis on a

pool of 9 healthy subjects led to two different optimal muscle sets, depending on the selected muscles choice criteria. If a subject-specific optimal muscle set was chosen, muscles could be reduced up to a minimum of 6, resulting in a loss of correlation significance with full set synergies while keeping similar estimation performance, and significant muscles-to-force and synergies-to-force coefficients coherence. This comes from the statistical analysis results from which no statistical significance was found between 6-muscles and 15-muscles groups ($p = 0.350$), regarding force estimation RMSE, while force fields showed a statistically significant correlation ($p = 0.024$ for MVLRL, $p = 0.032$ for Pose-Shared, and $p = 0.021$ for



Pose-Related). The global optimal muscle set, i.e., 8 muscles shared across all the subjects, revealed to be a reliable subset on all analyzed indexes. This means having a similar force estimation error (no statistically significant differences between groups with $p = 0.886$) and significant synergy similarities with respect to the full set ones (Pearson correlation between synergies scoring $p = 0.035$ for “Pose-Shared” and $p = 0.048$ for “Pose-Related”). Also a statistical significance on the muscle-to-force and synergy-to-force mapping coefficients was found, enforcing the coherence

of the optimal set composition. The global set, thus, counted two more muscles with respect to the subject-specific one but synergy similarities were comparable, reaching a statistical significance. Nevertheless, the force estimation performance given by the two optimal sets were comparable both in mean and standard deviation. This result suggests that although a subject-specific optimal set is functional in estimating the force in a certain application, synergies change their composition (i.e., the contribution of each muscle) when lowering the number of

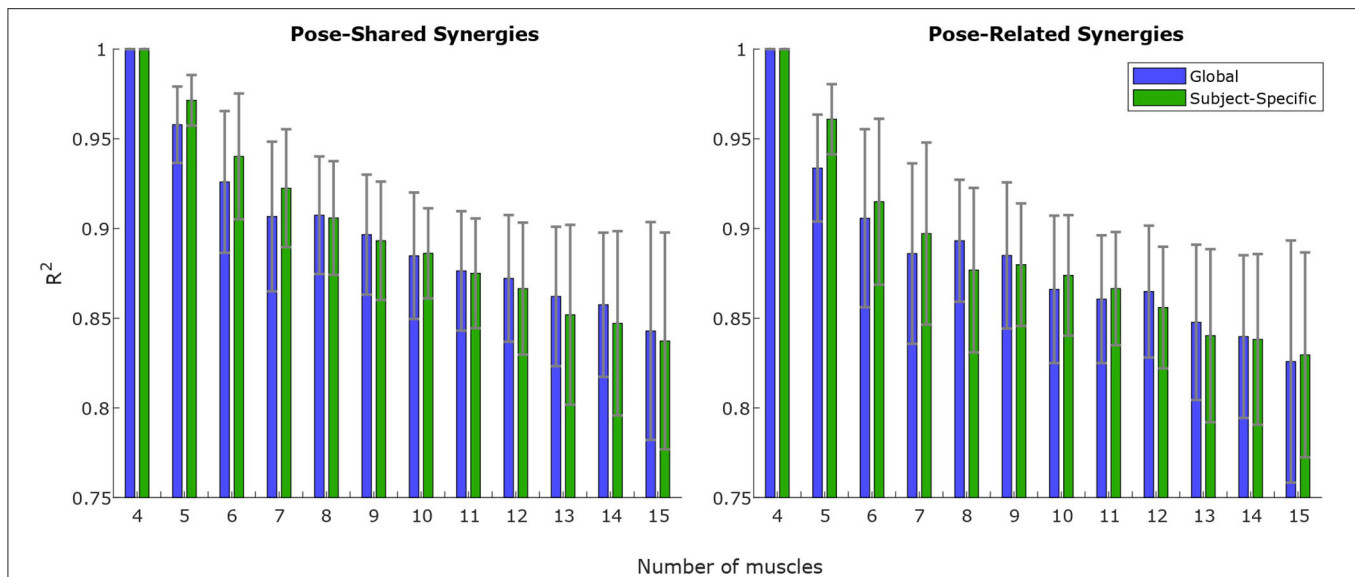


FIGURE 4 | R^2 ongoing mean and standard deviation values for increasing muscle set size, on “Pose-Shared” and “Pose-Related” synergies. Each value is computed by reconstructing training EMG signals using NMF outputs (see Equation 5) without residuals. The R^2 -value is computed on EMG signals merged from all the experimental workspace sites. The smaller the muscle size is, the higher the difference is in the EMG variance explained between Global and Subject-Specific conditions: for a lower number of muscles the choice of the muscle set, for each subject, that achieves the lowest estimation error, determines a higher reconstruction rate in terms of R^2 . This behavior is more evident when the number of muscles is lower than 8.

muscles under a certain threshold. In any case the global optimal set does not seem an obstacle to a fully working myo-control application, rather reducing the computational cost of the overall force estimation process when synergies are not used.

In the R^2 graph shown in **Figure 4**, global and subject-specific optimal set synergies generally explain the original signal total variance in a comparable way, for both “Pose-Shared” and “Pose-Related,” until the 8-muscles set is reached. Below this threshold, as expected, synergies in the subject-specific set achieve a higher R^2 value, since every subject could exploit a slightly different movement strategy that led to optimal sets that are different from the most shared one. This aspect leads to important implications in the rehabilitation context if synergies are used as an assessment tool. Without exploiting an optimal set, synergies already have shown to be important markers for detecting cortical damages or new skills acquisitions (Safavynia et al., 2011; Cheung et al., 2012; Tropea et al., 2013). The optimal muscle set, specifically selected for a stroke individual, could better highlight abrupt variations in synergy correlation with respect to initial patterns, after rehabilitation, meaning a change in movement strategy. As explained before, this is given by the computation of a similarity index of synergies that involves sub-computations on each muscle. Moreover, this specific set could better reflect how motor units in muscles are recruited for that specific subject, differently from the global set that may depict a generalized behavior. These suggestions will be deeply investigated in future studies, involving rehabilitation training in the analysis. Moreover, no strong differences have been found between “Pose-Shared” and “Pose-Related” synergies, with Shared synergies slightly outperforming the Related ones. In a previous work, with a larger workspace and a similar setup,

the ability of “Pose-Related” synergies to reconstruct the initial EMG dataset was higher than “Pose-Shared” ones (Camardella et al., 2020a). This discrepancy in results may confirm the ability of “Pose-Related” synergies to better explain datasets that include limb poses that are very different, since synergies are extracted independently on each pose and clustered together.

The subject discomfort deriving from bulky setups and long-lasting preparations with a high number of electrodes could be alleviated thanks to reduced sets. Although subjects benefit from a subject-specific set, this would inevitably require at least one training session with a full set, to find his/her specific movement strategy and, thus, his/her optimal set. In the case of altered motor patterns, subjects would require multiple training sessions each time an abrupt drop in correlation with the initial patterns is detected. Moreover a global optimal set could be of difficult usage in this context, since stroke generally induces unpredictable alterations and a priori muscle set does not seem suitable (Dipietro et al., 2007; Roh et al., 2013, 2015; Camardella et al., 2020b). Nevertheless, a representative healthy global optimal set could be helpful as a comparison with physiological patterns.

Regarding differences between “Pose-Shared” and “Pose-Related” synergies, the former achieved a higher correlation on both subject-specific and global optimal sets. “Pose-Related” synergies keep a comparable correlation value between subject-specific and global optimal set. This suggests that “Pose-Shared” may suffer the changing of muscles in the set, instead of the “Pose-Related” ones that seemed more robust to those variations. In a previous work by Camardella et al. (2019), synergy-based myo-control strategies, with “Pose-Shared” and “Pose-Related” synergies, were compared on the test set on both RMSE of force estimation and EMG reconstruction performance.

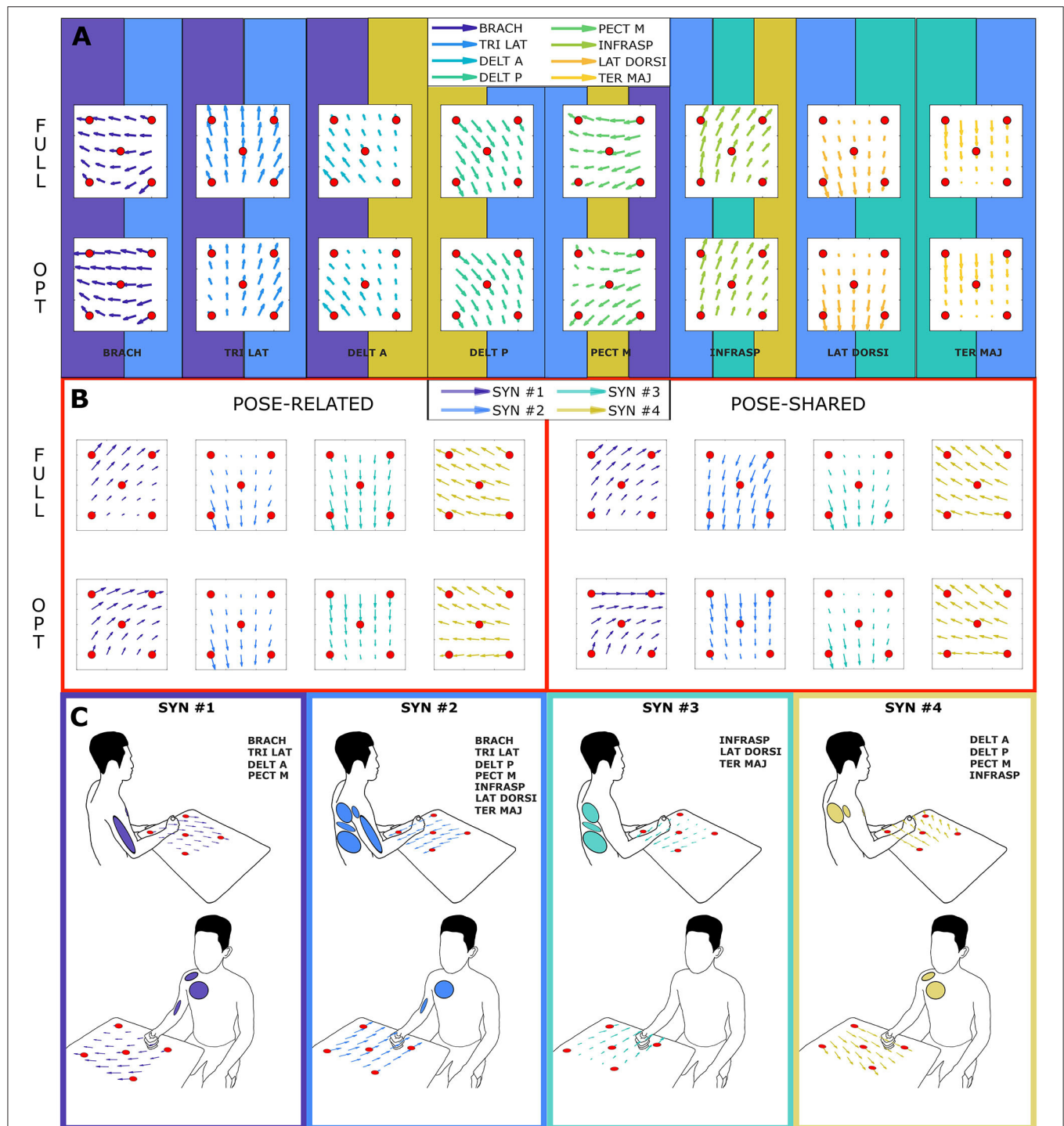


FIGURE 5 | Amplitude and direction of pulling vectors of recorded muscles and extracted synergies (force fields), in the global optimal muscle set. Each force field interpolates the information of the columns of the H matrix (see sections 2.5, 2.7.1). Each red sphere represents the action of a muscle/synergy in one experimental point. Arrows are then interpolated in a 6 by 6 grid. The section (A) shows the force field of each muscle in the full and optimal set: muscle force fields are taken from columns of H matrix trained with Equation (1). The background tile of each muscle explains the synergy of influence: multiple tiles refer to as many synergies of the same color in the section (B,C). The section (B) shows the force field of each synergy in the full and optimal set: synergy force fields are taken from columns of H matrix trained with Equation (9). The right panel illustrates the “Pose-Related” synergies force fields while the left one the “Pose-Shared” ones. The section (C) summarizes force fields and involved muscles, depicting the frame color and the muscle ellipses as the synergy color of the section (B).

In this instance “*Pose-Related*” seemed to better trace upper limb features on different workspace sites, when using a full muscle set, as well as to better estimate the force at the hand. In another work (Camardella et al., 2020a), “*Pose-Related*” synergies were used in a synergy-based myo-control during an online virtual session, suggesting the feasibility of such method in estimating the hand force in real-time. In this study, the coherence of “*Pose-Shared*” and “*Pose-Related*” synergies have been investigated in the case of a reduced muscle set, under similar protocol and signal processing conditions. “*Pose-Shared*” synergies revealed to be more similar to the full set ones, with correlation values always higher than “*Pose-Related*” ones. Also, referring to **Figure 4**, they better reconstruct the original EMG signals, mostly having higher values of R^2 with smaller muscle set size. This outcome may suggest that “*Pose-Related*” could be preferable in the case of a large muscle set, when directly involved in a synergy-based myo-control application trying to exploit the modular organization of the musculoskeletal system and projecting it onto the force task, rather than using it as an assessment tool.

As proposed by Steele et al. (2013), it is possible to label as dominant those muscles that have the highest contribution in a specific synergy. Looking at the **Figure 3**, synergies do not show a big difference in the correspondence of dominant muscles between full and optimal sets, at a glance. In particular, as showed in **Figure 5**, it is important to associate muscle pulling vectors to synergies that group them and, eventually, to have a quick overview of how a specific synergy act in task-oriented movements such as reaching motions. When dominant muscles are included, a good variance accounted for can be achieved even with a low number of muscles, better than choosing them randomly. Although the task, from which the EMGs were recorded, was different, the optimal sets that have been found include most of the muscles showed to be important in the work of Steele et al. (2013) (TER MAJ, LAT DORSI, TRI LAT, and BRACH). Moreover the number of muscles found to be the most representative in the muscle set, corresponds to the minimal one found, which includes 5/6 muscles. According to this outcome, force estimation performance revealed to be a good muscles choice criterion, highlighting the link between synergies and force task. The global optimal set information showed in **Figure 5** reveal the field of action of each muscle and synergy in the experimental workspace. Both the composition of synergies and their field of influence, in the global optimal set, trace common features already stated in the state-of-art. In a previous work by Cheung et al. (2009), synergies extracted from more than 12 muscles, during dynamic tasks, on a pool of seven out of eight total stroke subjects, revealed a strong similarity between affected arm and unaffected arm patterns. Among those patterns, there were synergies including co-activations of the brachialis and the triceps lateral head, the pectoralis major and the deltoid anterior, and the infraspinatus with the deltoid posterior and the teres major, as stated previously. Another work by Berger and d’Avella (2014), showed similar synergy compositions coming from eight healthy subjects, extracted from 13 muscles during isometric contractions, keeping a fixed pose of the upper limb. In all the cases, it is interesting to

notice how some muscles (e.g., the pectoralis major or the infraspinatus) are not fully included in a single synergy but participate in multiple synergies (for example acting as rotator or stabilizer of the shoulder joint) with different contributions. Moreover, muscle and synergy force fields did not show strong differences between full and optimal sets, confirming that the global optimal set owned the most important features of the full set, concurrently bringing the aforementioned advantages. Also “*Pose-Shared*” and “*Pose-Related*” synergy differences did not seem remarkable, suggesting that both extraction methods may present consistent outcomes and be used wisely judging the right application field.

5. CONCLUSIONS

In this work, the existence and feasibility of an optimal muscle set to be used in a myo-control application has been investigated. An 8-muscles global optimal set, the best trade-off in terms of myo-control performance and the muscle set size, shared among the analyzed pool of subjects, has been found. The optimal set has shown no statistical differences in terms of force estimation performance and a high correlation with the initial (full muscle set) synergistic patterns. Also muscle and synergy force fields in the optimal set resulted to be coherent with the full counterpart. Tailoring the muscle choice to the specific subject, the optimal set could get to include up to 6 muscles, nevertheless losing statistical similarity on synergies but retaining the ability to explain a higher variance of EMG signals, with respect to the global one, with the same number of muscles and synergies. A link between synergies and force task was identified, thus, dominant muscles that cover an important role in the chosen protocol can be found through the minimization of the force estimation error. Future studies will involve an actual usage of optimal sets in either a real-time myo-control application or an assessment tool for rehabilitation.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Joint Chinese University of Hong Kong—New Territories East Cluster Research Ethics Committee. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

CC, AF, and RT: conceptualization. CC, MJ, and RT: methodology. CC, MJ, and KT: software, validation, and visualization. CC: formal analysis. CC and MJ: investigation and

writing—original draft preparation. MJ and KT: data curation. AF and RT: supervision. RT: project administration. AF: funding acquisition. All authors contributed to writing—review and editing and have read and agreed to the published version of the manuscript.

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ACKNOWLEDGMENTS

This work has been partially funded by the RoboGYM project, in collaboration with IIT—Italian Institute of Technology Foundation—with PR19-RR-P2 grant number.

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Adaptive Interlimb Coordination Mechanism for Hexapod Locomotion Based on Active Load Sensing

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Insects can flexibly coordinate their limbs to adapt to various locomotor conditions, e.g., complex environments, changes in locomotion speed, and leg amputation. An interesting aspect of insect locomotion is that the gait patterns are not necessarily stereotypical but are often highly variable, e.g., searching behavior to obtain stable footholds in complex environments. Several previous studies have focused on the mechanism for the emergence of variable limb coordination patterns. However, the proposed mechanisms are complicated and the essential mechanism underlying insect locomotion remains elusive. To address this issue, we proposed a simple mathematical model for the mechanism of variable interlimb coordination in insect locomotion. The key idea of the proposed model is “decentralized active load sensing,” wherein each limb actively moves and detects the reaction force from the ground to judge whether it plays a pivotal role in maintaining the steady support polygon. Based on active load sensing, each limb stays in the stance phase when the limb is necessary for body support. To evaluate the proposed model, we conducted simulation experiments using a hexapod robot. The results showed that the proposed simple mechanism allows the hexapod robot to exhibit typical gait patterns in response to the locomotion speed. Furthermore, the proposed mechanism improves the adaptability of the hexapod robot for leg amputations and lack of footholds by changing each limb’s walking and searching behavior in a decentralized manner based on the physical interaction between the body and the environment.

Keywords: hexapod locomotion, inter-limb coordination, decentralized control algorithm, active load sensing, chains of reflex

OPEN ACCESS

Edited by:

Poramate Manoonpong,
University of Southern Denmark,
Denmark

Reviewed by:

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Tel Aviv University, Israel
Yaguang Zhu,
Chang'an University, China

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Received: 23 December 2020

Accepted: 05 January 2022

Published: 08 February 2022

Citation:

Fukuhara A, Suda W, Kano T,
Kobayashi R and Ishiguro A (2022)
Adaptive Interlimb Coordination
Mechanism for Hexapod Locomotion
Based on Active Load Sensing.
Front. Neurobot. 16:645683.
doi: 10.3389/fnbot.2022.645683

1. INTRODUCTION

Insects exhibit versatile interlimb coordination patterns to move around adaptively. For example, some insects possess various gait patterns (e.g., wave gait, tetrapod gait, and tripod gait) that change in response to changes in locomotion speed and loads applied to the body (Wilson, 1966; Dean, 1991; Zollikofer, 1994; Wosnitza et al., 2013). Furthermore, they can generate feasible locomotor patterns in response to leg amputation (Hughes, 1957; Delcomyn, 1991; Grabowska et al., 2012). In addition to steady walking, they flexibly change limb motion between walking and searching steps when they walk on uneven terrain with some gaps in the foothold (Pearson and Franklin, 1984; Theunissen and Dürr, 2013; Theunissen et al., 2014, 2015). While insects exhibit long stride steps during steady walking (i.e., walking) on uneven terrain, they exhibit short searching steps

where the limb repeats a retracting and protracting motion in a short stride distance to obtain secure footholds. Understanding these flexible interlimb coordination mechanisms underlying insect adaptive walking sheds new light on developing adaptive legged robots that can move around stably through rough environments (e.g., disaster sites).

Biological and modeling studies have investigated decentralized control mechanisms underlying adaptive insect locomotion through comparative studies focusing on distinct insect species, e.g., stick insects and cockroaches (Ayali et al., 2015a). Stick insects (e.g., *Phasmida*) can climb unpredictable environments, and their relatively slow locomotor patterns allow researchers to address underlying sensory-motor mechanisms. Biological studies have elucidated that thoracic neural circuits generate rhythmic locomotor patterns neither sensory input from the leg nor the descending command from the brain (Mantziaris et al., 2020). Furthermore, sensory input in the limbs contributes to modifying intra- and interlimb coordination for adaptive stick insect locomotion. In contrast to stick insects, cockroaches (e.g., *Blattaria*) exhibit fast and stable locomotion and are ideal insects to address the interaction between neural control and body dynamics. While their conservative tripod gait patterns are generated by CPG, their flexible body can negotiate uneven terrains (Full et al., 1998; Watson et al., 2002; Weihmann et al., 2017). Furthermore, recent studies elucidate the sensory feedback mechanism underlying cockroach's locomotion in which signals from mechanoreceptors modulate muscle contractions to establish interlimb coordination (Ayali et al., 2015b; Weihmann et al., 2017). Although the mathematical models for insect's interlimb coordination have been developed differently depending on the focusing insect animals (e.g., stick insects and cockroaches), the common distributed control mechanisms in distinct insect animals have induced to unify them into common limb coordination model (Koditschek et al., 2004; Büschges et al., 2008; Daun-Gruhn, 2011; Toth et al., 2013). However, these unified models are too complex to analyze and apply to legged robots in simple manners.

In contrast to complex models describing the insect's sensory-motor system with large numbers of differential equations, redacted models significantly help us test hypotheses and interpret the substantial interlimb coordination mechanism underlying insect locomotion (Kimura et al., 1993; Dürr et al., 2004; Kukillaya et al., 2009; Owaki et al., 2017). The simple models reduced dimensions by using simple elementary processes, e.g., phase oscillators and reflexes, to generate interlimb coordination. For example, Cruse et al. proposed a series of reflex rules based on the behaviors of stick insects (Dürr et al., 2004). They predicted the pathway of sensory-motor modulation for interlimb coordination in the insect animal's thoracic nervous system. For another example, Owaki et al. proposed a simple CPG model where one phase oscillator controls each limb's stride motion and demonstrated that phase modulations depending on loads of limbs contribute to generating various gaits locomotion speed and leg amputation (Owaki et al., 2017). Regarding adaption to uneven environments, however, previous models still require recruiting a large number of neural components for modulating

interlimb coordination depending on situations (Durr, 2001; Bläsing, 2006; Schilling et al., 2013a,b; Ngamkajornwiwat et al., 2020). This is because the limb without a stable foothold should adaptively change its foot trajectory and frequency comparing other limbs to search steady footholds. Therefore, the development of a simple interlimb coordination mechanism involving searching behavior will contribute to deeply understanding the essential mechanism underlying flexible insect locomotion.

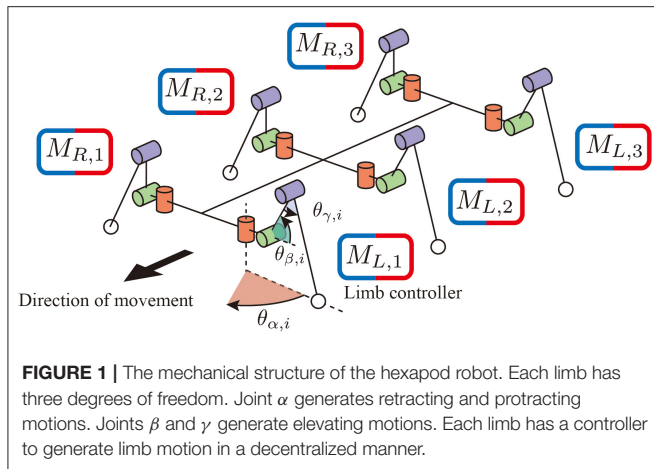
To this end, this study develops a simple interlimb coordination model to extract substantial mechanisms underlying adaptive hexapod locomotion, including searching behavior on uneven terrain. We hypothesize that a simple local sensory feedback mechanism, "active load sensing," plays an essential role in generating flexible hexapod interlimb coordination patterns in flat and uneven environments. In this scheme, each limb actively moves and detects the reaction force from the ground to judge whether it plays a pivotal role in maintaining the steady support polygon. As a result of the simulation experiments, a hexapod robot that could generate flexible gait patterns in response to locomotor speed and leg amputation was developed. Furthermore, the robot flexibly changed its limb behaviors between the walking step in steady walking and the searching step depending on the lack of the foothold. During particular limb searching, other limbs flexibly modulate their interlimb coordination through the same mechanism in walking in flat terrain. These results suggest that a simple decentralized control mechanism exploiting physical interaction between body and environment (e.g., the proposed active load sensing) allows insects to generate flexible interlimb coordination for flat terrain and unpredictable environments.

The remainder of this paper is organized as follows: Section 2 exploits the proposed simple interlimb coordination mechanism; Section 3 presents the results of the 3D simulation; Sections 4 and 5 present the discussion and conclusion.

2. MODEL

According to insect behaviors, the insects adaptively generate long limb strides for walking and short limb strides for searching. Besides, the periods of one limb stride locally and drastically change during a pass through uneven terrains. Therefore, modeling based on phase oscillators is required to discontinuously modulate the phase (e.g., phase reset) and also modulate limb trajectories, resulting in a complex interlimb coordination mechanism. To develop a simple model, this study employs two feedforward limb control modes and four fundamental transition rules that induce a hexapod robot to generate walking and searching behaviors. In the following modeling section, we first explain a robot model in the simulation environments. Then, we illustrated two basic limb control modes "swing mode" and "stance mode" and fundamental transition rules.

Regarding the mechanical structure, a robot consists of six identical limb units and a rigid trunk unit, as shown in **Figure 1**. Each limb has three degrees of freedom: joint α connects the



trunk unit and limb unit and generates the protraction and retraction motion by changing the angle of the joint θ_{ij}^α ($i = R, L$ and $j = 1, 2, 3$). The other two joints β and γ generate flexing/extending and elevating motions by changing the angles of the joints θ_{ij}^β and θ_{ij}^γ .

Regarding the basic components of a limb controller, each limb has a controller with two control modes, that is, *stance modes* and *swing mode* to generate limb stride motions, as shown in **Figure 2A**. The controller state is described with the symbol M_{ij} . When $M_{ij} = \text{Swing mode}$, the limb controller is in the swing mode, and the limb generates protracting motion. Furthermore, the proposed model has two stance modes: early stance mode and late stance mode. In both stance modes, the limb generates retracting motion for kicking the ground.

In the proposed robot mode, we simplify the coordination between the joints (i.e., intralimb coordination) to realize a specific foot trajectory. In all control modes, the joint α is controlled to achieve the target joint angular velocity $\bar{\theta}_{ij}^\alpha$. In the swing mode ($M_{ij} = \text{Swing mode}$), $\bar{\theta}_{ij}^\alpha$ is set to a positive constant value ω_{sw} to generate the protracting motion, whereas in the stance modes ($M_{ij} = \text{Early stance mode}, \text{Late stance mode}$), $\bar{\theta}_{ij}^\alpha$ is a negative constant value ω_{st} to generate the retracting motion. The joints β and γ are controlled to achieve a joint target angle $\bar{\theta}_{ij}^\beta$ and $\bar{\theta}_{ij}^\gamma$, respectively, so that the foot moves along a specific trajectory, as shown in **Figure 2B**. Details of the foot trajectory design are described in **Appendix A**. Note that there is no additional control mode to stand stably (not walk) in the proposed mode. To realize a transition between walking and standing, the target angular velocity of *alpha* joint $\bar{\theta}_{ij}^\alpha$ will change between negative for walking and zero for standing. However, in the present study, we focus on flexible changes walking and searching and set the parameter $\bar{\theta}_{ij}^\alpha$ constant value for limb stride motion.

To generate adaptive interlimb coordination patterns, each controller should switch the control modes depending on the situation. The present study proposes four simple transition rules between the swing and stance modes, as shown in the overview

control scheme (**Figure 2C**). Note that most rules conduct in a decentralized manner by exploiting physical interactions between the whole body and the environment. The details of the four simple rules are explained in the following sections.

Rule (i): Stretch Reflex

In the first rule, the limb changes its control modes between the swing and stance mode at the anterior extreme position (AEP) and posterior extreme position (PEP) of the foot to generate periodic limb stride motion (**Figure 3**). If the angle of joint α in the swing mode reaches a positive threshold angle θ_{AEP} ($\theta_{ij}^\alpha \geq \theta_{AEP}$), then the limb controller changes its mode from swing mode to early stance mode. In contrast, if the joint angle α in the stance mode reaches a negative threshold angle θ_{PEP} ($\theta_{ij}^\alpha \leq \theta_{PEP}$), then the limb controller changes its mode from stance to swing. The above transitions are described as follows:

$$\begin{cases} \text{if } \theta_{ij}^\alpha \geq \theta_{AEP} \text{ then } M_{ij} = \text{Swing mode} \rightarrow \text{Early stance mode}, \\ \text{if } \theta_{ij}^\alpha \leq \theta_{PEP} \text{ then } M_{ij} = \text{Late stance mode} \rightarrow \text{Swing mode}. \end{cases} \quad (1)$$

Note that after mode transition from the swing to stance at the AEP point, the limb first becomes the early stance mode ($M_{ij} = \text{Early stance mode}$), not the late stance mode ($M_{ij} = \text{Late stance mode}$).

Rule (ii): Searching Reflex

The second rule realizes adaptive switching between stepping and searching behavior depending on the lack of footholds. Although insects usually exhibit long retracting and protracting motions to generate stride lengths, the insect repeats short retracting and protracting motions to search for the next foothold in response to the foothold gaps (Pearson and Franklin, 1984; Theunissen and Dürr, 2013; Theunissen et al., 2014).

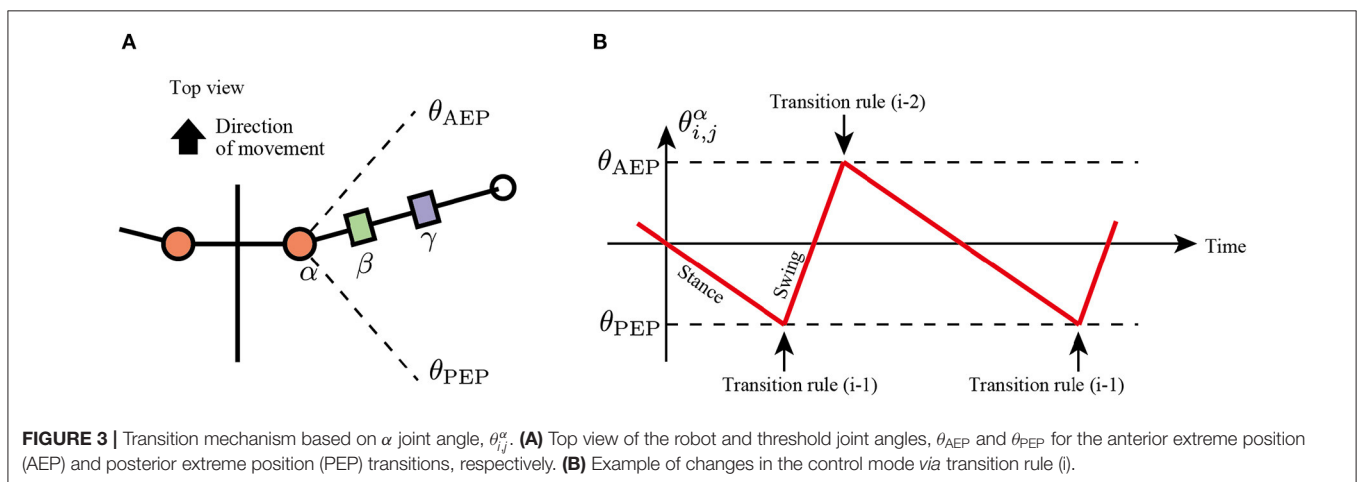
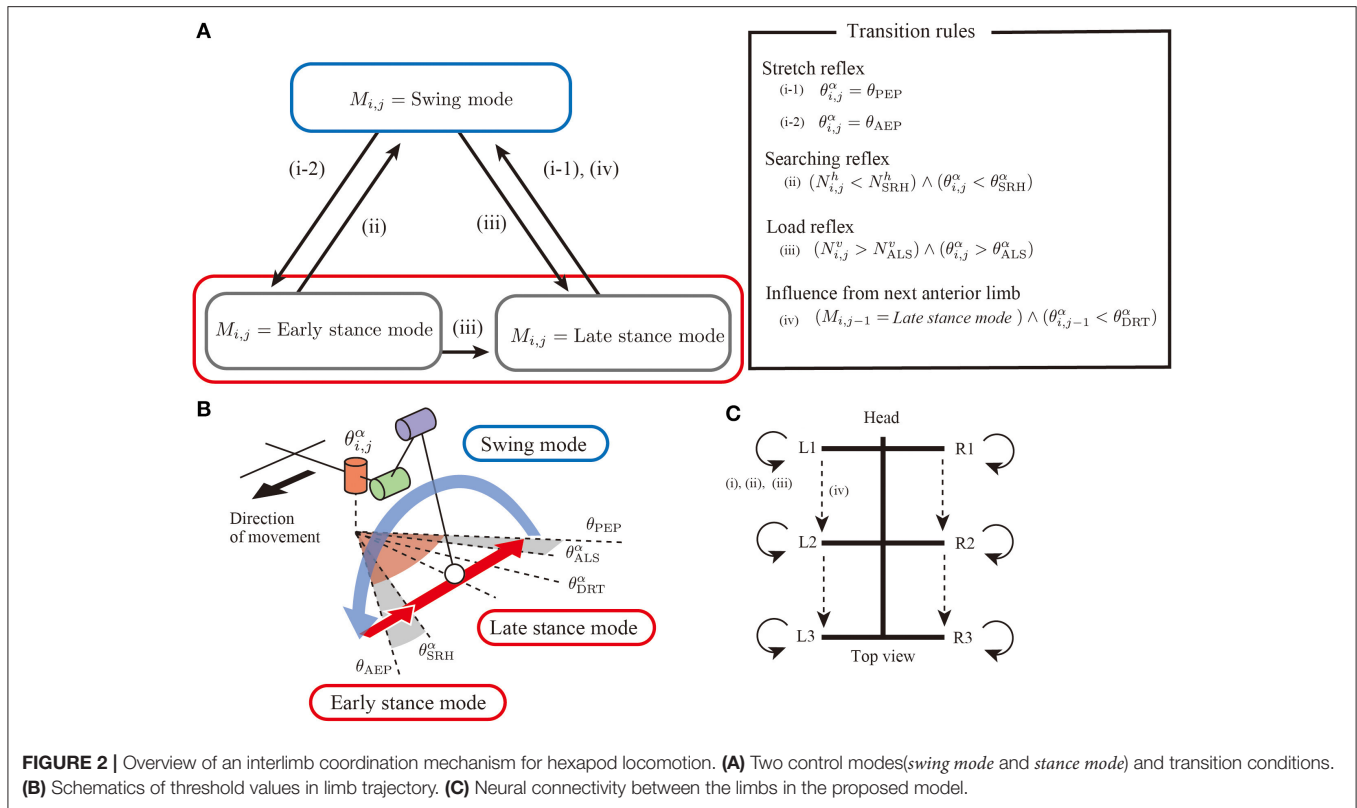
To implement the flexible changes between the stepping and searching behaviors, the present study assumes a simple transition rule for the transition from the stance mode to the swing mode as follows:

$$\begin{aligned} &\text{if } (N_{ij}^h < N_{SRH}^h) \wedge (\theta_{ij}^\alpha < \theta_{SRH}^\alpha) \text{ then } M_{ij} \\ &= \text{Early stance mode} \rightarrow \text{Swing mode}, \end{aligned} \quad (2)$$

where N_{ij}^h is a horizontal component of ground reaction force (GRF) applied at the i, j limb (driving force is positive), N_{SRH}^h is a threshold value for detecting where the limb obtains the foothold, and θ_{SRH}^α is a constant value describing a range of joints α for the searching behavior. According to rule (i), the protracted limb changes the control mode from swing to stance and starts to retract. If the limb has no propulsive force after the retraction motion, then the limb changes to the swing mode immediately, resulting in the protracting motion (**Figure 4**).

Rule (iii): Active Load Sensing at the Beginning of the Swing Phase

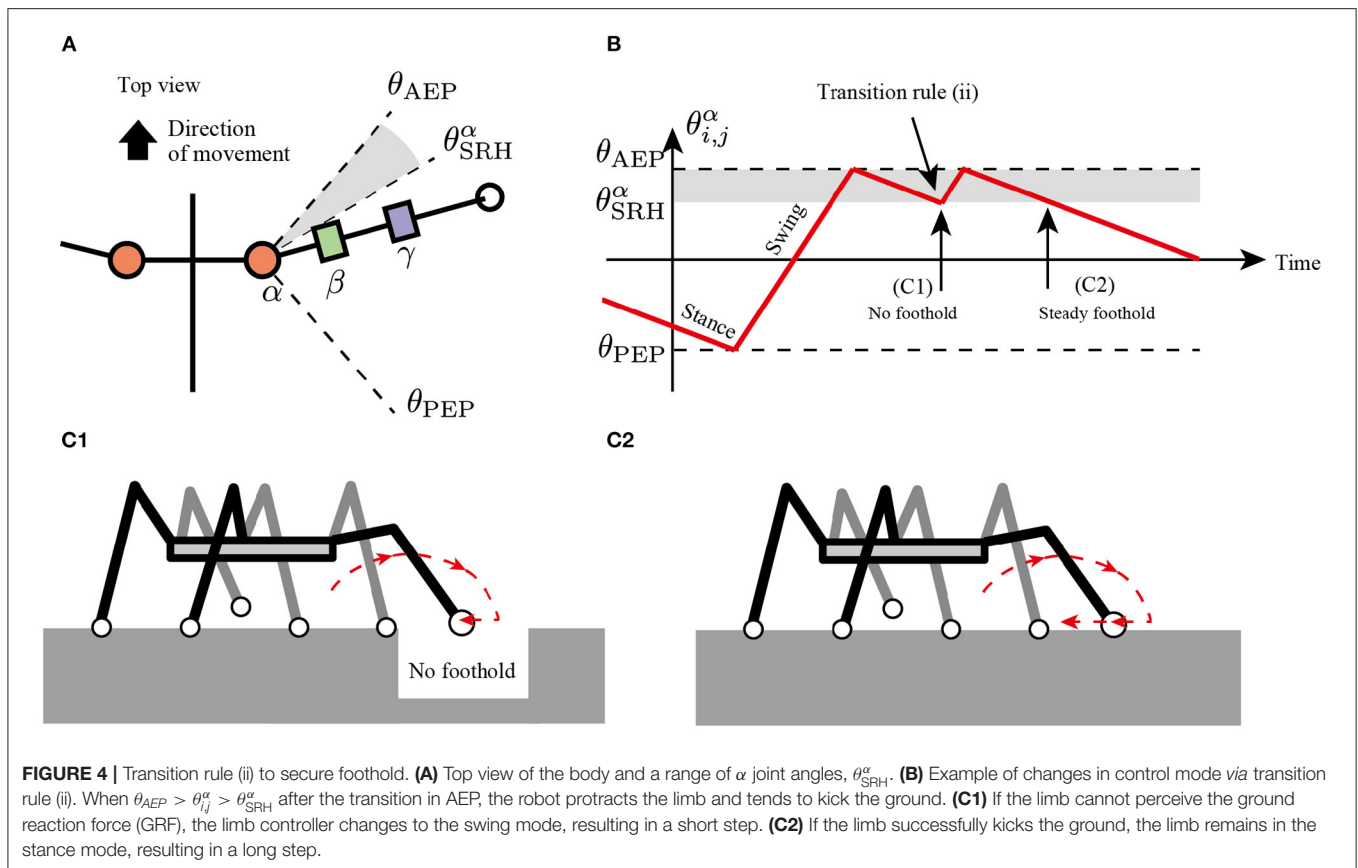
The third rule is attempted to secure a support polygon at the beginning of the swing phase in a decentralized manner. The support polygon is a convex horizontal region whose vertices



correspond to the support limbs. For example, in **Figure 5A**, the support polygon comprises the contact points R1, R2, L2, and L3. When the center of mass (COM) lies in the support polygon, static stability is achieved during locomotion.

To achieve static stability during locomotion through a decentralized control manner, this study classifies the stance limbs into two types: “free limb” and “responsible limb.” The free limb is a stance limb in which the robot maintains static stability when the concerned limb lifts off the ground. For example, consider the support polygon shown in **Figure 5A**, where the R1, R2, L2, and L3 limbs are in the stance phase. When the R2

limb lifts off, the new support polygons with R1, L2, and L3 still contain the COM of the insect, maintaining static stability. Therefore, the R2 limb can be classified as a free limb. In contrast to the free limb, the responsible limb is a stance limb in which the robot cannot keep the static polygon when the concerned limb lifts off the ground. For example, in **Figure 5B**, when the L2 limb lifts off, the COM of the insect is located outside the new support polygon with R1, R2, and L3, resulting in a lack of static stability. Consequently, the L2 limb in **Figure 5B** can be classified as a responsible limb. For stable and adaptive locomotion, the challenge is to instantly detect the free and



responsible limbs and accordingly modulate the limb movements to maintain static stability.

The proposed study distinguishes between free and responsible limbs and modulates the limb control mode adaptively in a simple, decentralized manner. For detection of the limb state, the stance limb close to the PEP first attempts to lift off the ground. If the concerned limb perceives no GRF, then it can be interpreted as a free limb, and it changes the stance mode to swing mode. In contrast, if the concerned limb still perceives GRF, then it can be interpreted as a responsible limb and should be maintained in the stance mode. We describe these sequences of action and detection as “active load sensing.”

In the proposed model, we implement active load sensing around the PEP as follows. The lifting action is realized by other transition rules. Then, the sensory feedback mechanism based on active load sensing is described as follows:

$$\begin{aligned} &\text{if } (N_{ij}^v \geq N_{\text{ALS}}^v) \wedge (\theta_{ij}^{\alpha} > \theta_{\text{ALS}}^{\alpha}) \\ &\text{then } M_{ij} \rightarrow \text{Late stance mode.} \end{aligned} \quad (3)$$

where N_{ij}^v is a vertical component of GRF applied at the i, j limb, N_{ALS}^v is a positive constant value for a threshold whether the limb is loaded or unloaded, and $\theta_{\text{ALS}}^{\alpha}$ is a constant value to describe a blind-sector angle for active load sensing (Figure 5C). When $\theta_{\text{ALS}}^{\alpha} > \theta_{ij}^{\alpha} > \theta_{\text{PEP}}$ during the swing mode, the limb maintains the protracting motion for lifting. After the lifting motion, if

the protracting limb perceives GRF, it changes the control mode from swing to stance immediately like Figure 5D to achieve static stability.

Rule (iv): Sensory Feedback From Next Anterior Limb

In slow insect walking gaits (e.g., tetrapod gait and wave gait), the limbs of the ipsilateral side exhibit a metachronal wave from the tail to the head (i.e., wave gait; Wilson, 1966). Based on the insect walking trend, we assume the fourth transition rule in which each limb tends to switch its control mode from the stance mode to the swing mode when the anterior next limb reaches the PEP (Figure 6). More specifically, the enforcing early protraction refers to whether the angle of the next anterior joint α , θ_{ij-1}^{α} , achieves a threshold angle $\theta_{\text{DRT}}^{\alpha}$ using the following equation:

$$\begin{aligned} &\text{if } \theta_{ij-1}^{\alpha} \leq \theta_{\text{DRT}}^{\alpha} \\ &\text{then } M_{ij} = \text{Late stance mode} \rightarrow \text{Swing mode (for } j \neq 1). \end{aligned} \quad (4)$$

where $\theta_{\text{DRT}}^{\alpha}$ is the threshold angle in the joint α that detects the limb closer to the PEP. Note that rule (iv) is the only transition rule that assumes the neural coupling between limbs in the proposed model.

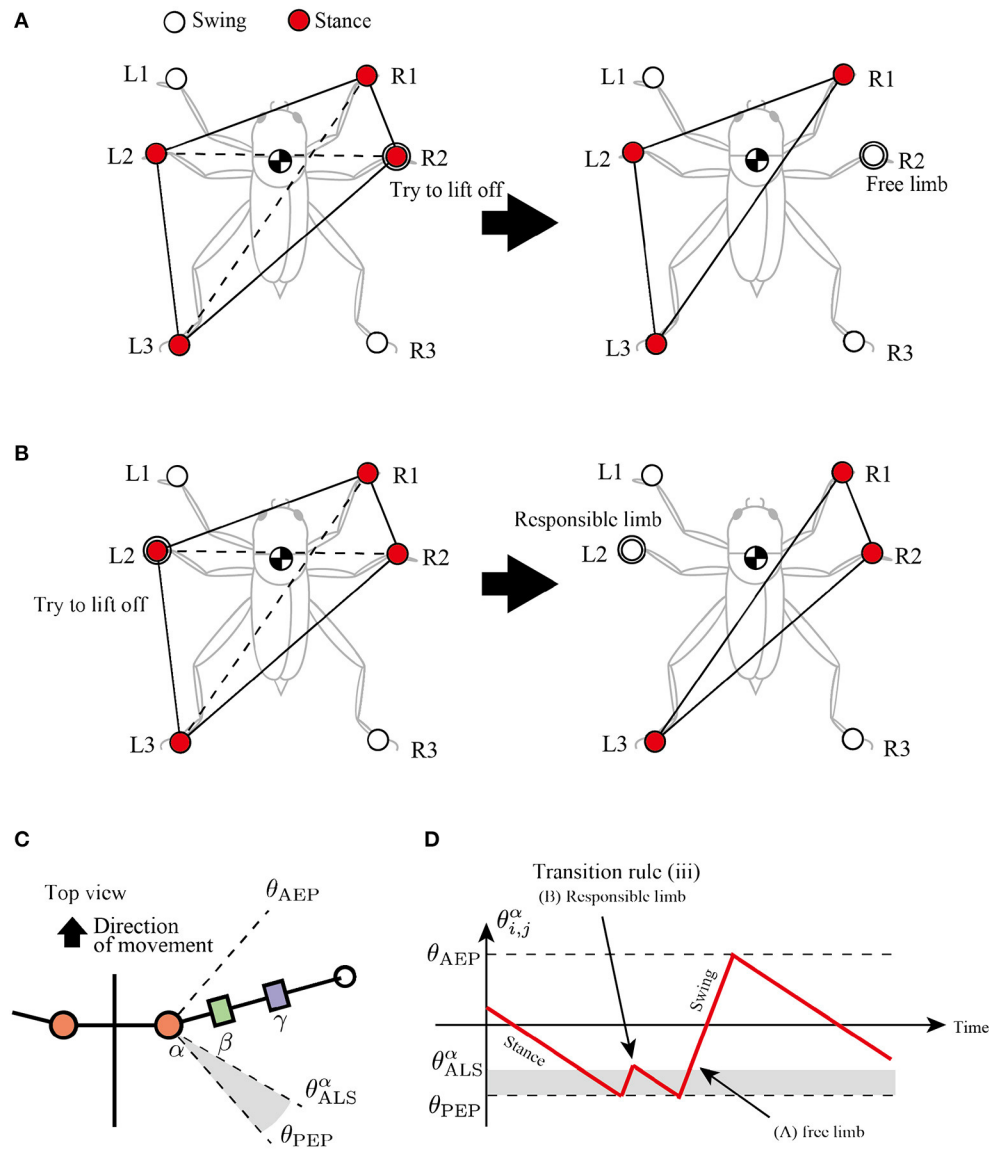


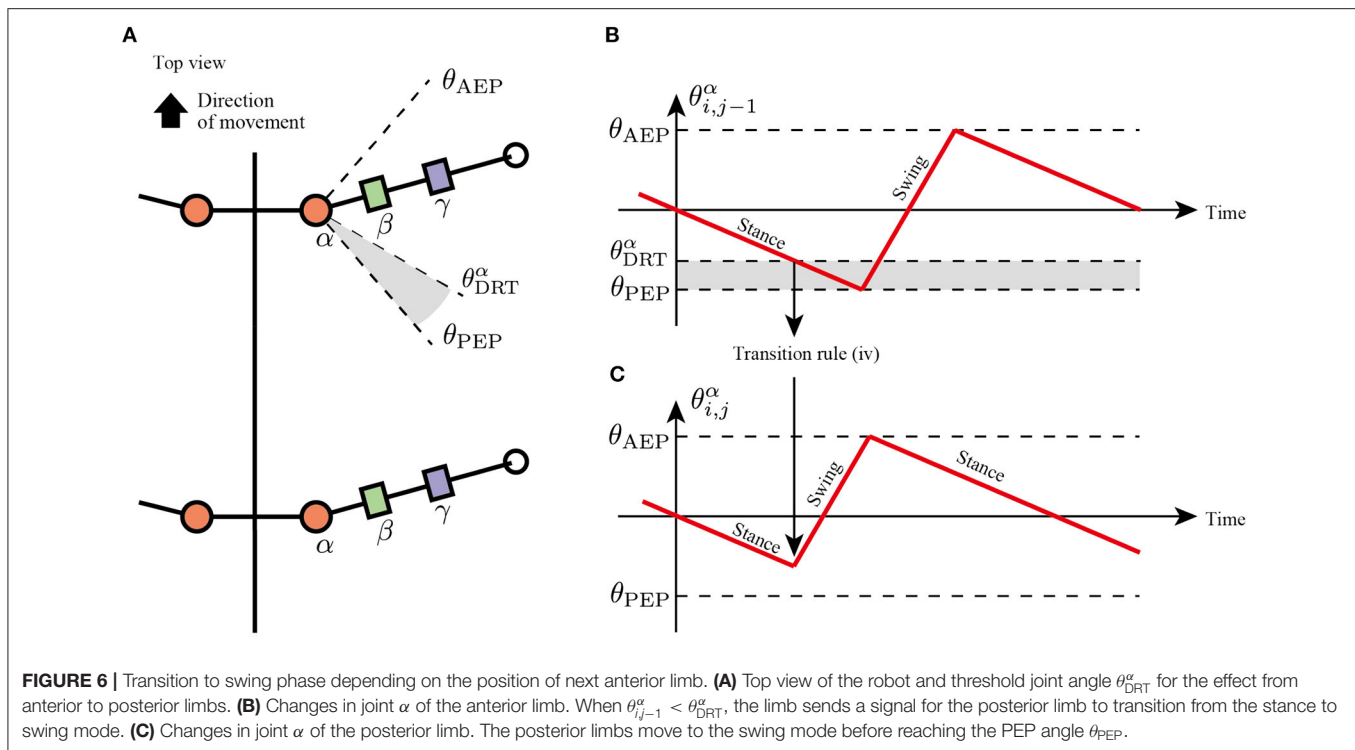
FIGURE 5 | Active load sensing scheme for detecting free and responsible limbs in hexapod locomotion. **(A)** Free limb situation. After the R2 limb lifts, the center of mass (COM) is still in the supporting polygon. **(B)** Responsible limb situation. After the L2 limb lifts, the COM moves outside the support polygon. By exploiting the physical interaction between the body and the environment, each limb can simply modulate its control mode for the steady support polygon. **(C)** Top view of the body and a range of α joint angles, θ_{ALS}^α . **(D)** Example of changes in control mode via transition rule (iii).

3. RESULTS

To evaluate the proposed interlimb coordination mechanism, the present study conducts three kinds of simulation experiments: the emergence of typical hexapod locomotion, adaptation to leg amputation, and adaptation to gap environment. We use an open dynamics engine (ODE) to calculate the hexapod robot's three-dimensional physical dynamics in all experiments. The parameters in the simulation are heuristically determined as shown in **Table 1** so that the robot can generate a typical tripod gait when the target angular velocities in the stance mode ω_{st} are the same as that in the swing mode ω_{sw} .

3.1. Emergence of Typical Hexapod Gait Patterns

The first simulation experiment aims to evaluate how the proposed rules affect the locomotion patterns of the robot in response to various locomotion speeds. Regarding the experimental setup, the robot with an intact body (i.e., no leg amputation) walks on flat terrain. To address the flexibility of the locomotor patterns in response to locomotor speed, we conducted walking experiments with various swing-stance ratios. More specifically, we set constant values of ω_{sw} and ω_{st} , as shown in **Table 1** for various locomotion frequencies. This setup

**TABLE 1 |** Parameters in simulation experiments.

Body			Control		
Parameters	Unit	Values	Parameters	Unit	Values
total mass	[kg]	0.92	W	[m]	0.12
width	[m]	0.24	H	[m]	0.07
length	[m]	0.18	θ_{AEP}	[rad]	$\pi/6$
height	[m]	0.1	θ_{PEP}	[rad]	$\pi/6$
L_{UPR}	[m]	0.12	θ_{DRT}^{α}	[rad]	$\pi/8$
L_{BTM}	[m]	0.12	θ_{ALS}^{α}	[rad]	$7\pi/60$
			θ_{SPH}^{α}	[rad]	$13\pi/80$
			N_{ALS}^{α}	[N]	0.3
			N_{SPH}^{α}	[N]	0.01
			ω_{sw}	[rad/s]	$\pi/3$
			ω_{st}	[rad/s]	$\pi/3, \pi/6, \pi/15$

is according that various insects likely maintain duration in the swing phase while they change the various durations in the stance phase (Wosnitza et al., 2013; Reinhardt and Blickhan, 2014; Weihmann et al., 2017; Dürr et al., 2018). As the phase oscillator based CPG models set the intrinsic frequency of periodic limb motion (Owaki et al., 2017), this study simply set limb swing speed of joint α to generate protract and retract motions in the swing and stance modes.

The results of the simulation experiments showed that the robot exhibited various gait patterns depending on the locomotor speed. When $(\omega_{sw}, \omega_{st}) = (\pi/3, \pi/3)$, the robot exhibited

synchronous coordination in two groups: L1 and R2 are L3 moves in phase, and R1 and L2 are R3 moves in phase as shown in **Figure 7A**. The interlimb coordination patterns correspond to the tripod gait. The locomotion speed is 10.7 [cm/s]. Additionally, when the target angular velocity in the stance mode ω_{st} decreases to $\pi/6$, the robot exhibits different coordination patterns: L1 and R3 synchronize, L2 and R1 synchronize, and L3 and R2 synchronize. These coordination patterns correspond to the typical tetrapod gait, where the two limbs are in the swing phase and the other four limbs support the body weight. The locomotion speed is 8.8 [cm/s]. Furthermore, the parameter ω_{st} decreases to $\pi/15$, and the robot exhibits a typical wave gait, as shown in **Figure 7C** where the ipsilateral anterior limbs move to the swing phase after the next posterior limb. These speed-dependent gait patterns of the robot correspond to the trends of insect locomotor patterns (Wilson, 1966). The locomotion speed is 2.4 [cm/s].

For each locomotor condition, the proposed reflex rules modulate the interlimb coordination patterns as shown in **Figures 7D,E**. At the beginning of walk, the limb motions are frequently modulated by the reflex rules, for example, active load sensing (rule iii) in **Figure 7D**. As each interlimb coordination pattern converges, the reflex rules rarely modulate the limb's motion. This is because the locomotor patterns that emerge establish support polygons. With low stance speed (e.g., $\omega_{st} = \pi/15$), the searching reflex (rule ii) and active load sensing (rule iii) rarely occurs, as shown in **Figure 7F**, because the long stance period contributes to maintaining the support polygons.

Although the robot exhibits speed dependent interlimb coordination patterns, several limbs show vague takeoff and

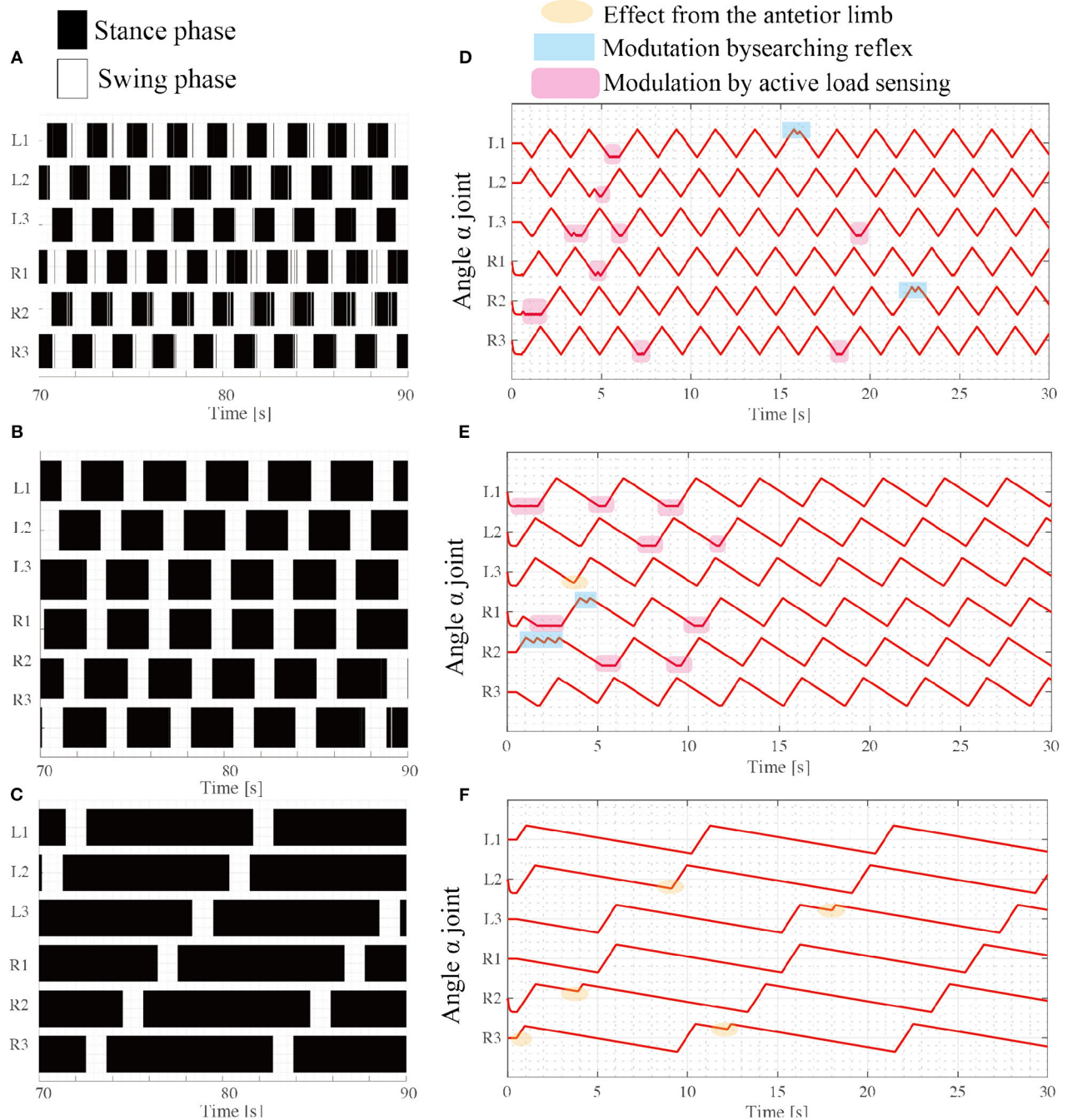


FIGURE 7 | Various insect-like walking patterns depend on the speed ratio during the swing phase. Emerging gait patterns: **(A)** Tripod gait at $(\omega_{sw}, \omega_{st}) = (\pi/3, \pi/3)$, **(B)** Tetrapod gait at $(\omega_{sw}, \omega_{st}) = (\pi/3, \pi/6)$, and **(C)** Wave gait at $(\omega_{sw}, \omega_{st}) = (\pi/3, \pi/15)$. The colored region represents the stance phase where the limb contacts the ground, while the white region represents the swing phase, where the limb has no ground contact. **(D–F)** show changes in the joint angle α from the beginning of the tripod, tetrapod, and wave gaits simulations, respectively.

touchdown, resulting in chattering in the gait diagram in the border between the swing phase and stance phase. This chattering is more conspicuous in a fast walking pattern like tripod gait (Figure 7A) than slow walking gait like metachronal wave gait (Figure 7B). This is because the low

duty ratio in fast walking induces difficulty for limbs to translate next supporting polygon. In contrast, the large support polygon in the high duty ratio like Figure 7C facilitates the free limb to translate from the stance mode to the swing mode.

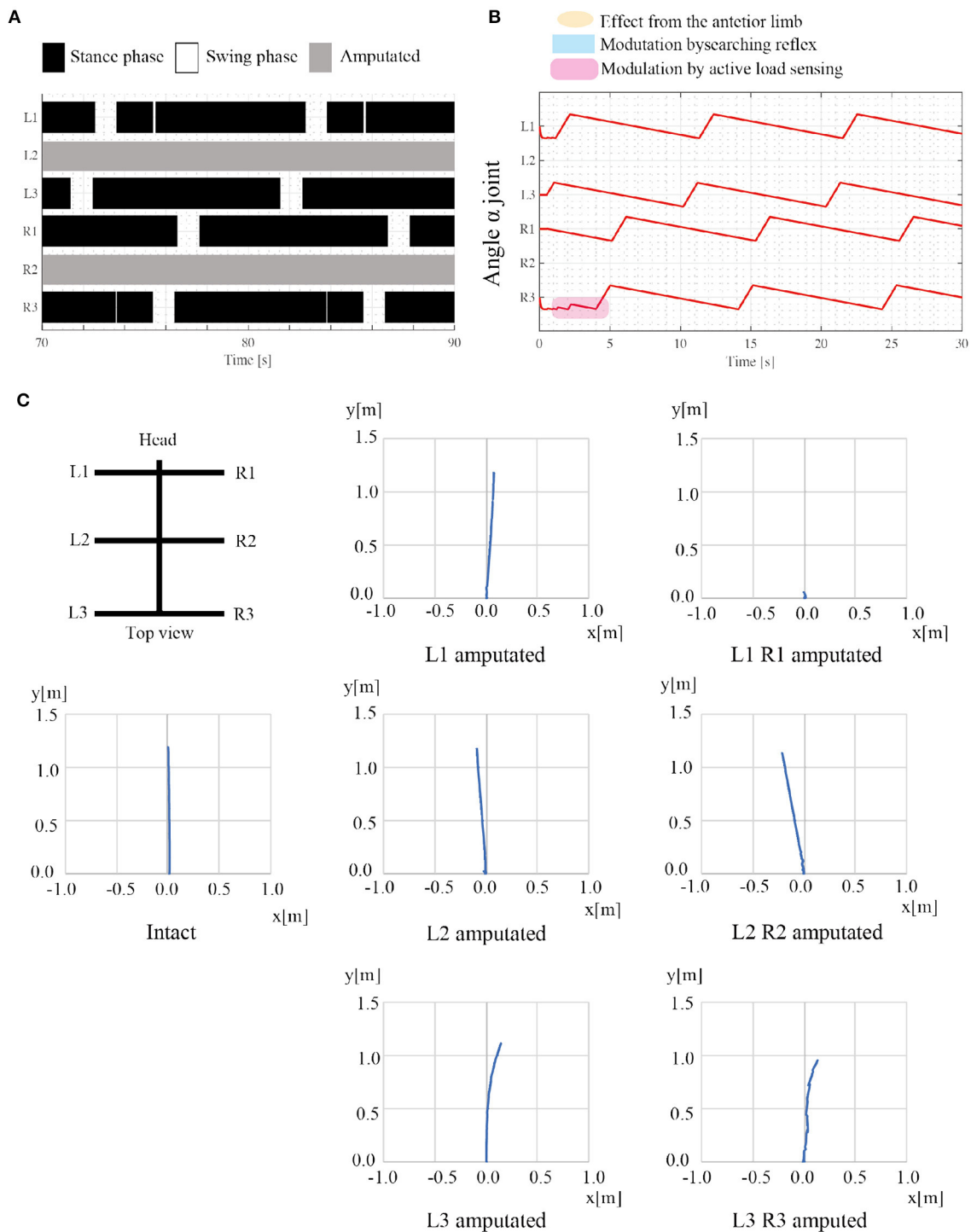


FIGURE 8 | Results of adaptation to leg amputations. **(A)** Gait diagram of the walking robot with amputated L2 and R2 limbs. Regarding the target angular velocity, $(\omega_{SW}, \omega_{ST}) = (\pi/3, \pi/15)$. The robot exhibited a lateral sequence gait. **(B)** The history of each joint angle α from the beginning of walking with the leg amputation. **(C)** Robot trajectories with various combinations of leg amputation. The robot can move despite the leg amputations, whereas the robot stacks when the L1 and R1 limbs are amputated. Note that there is no direction control mechanism and the direction of robot movement changes depending on the physical interaction between the robot and the environment.

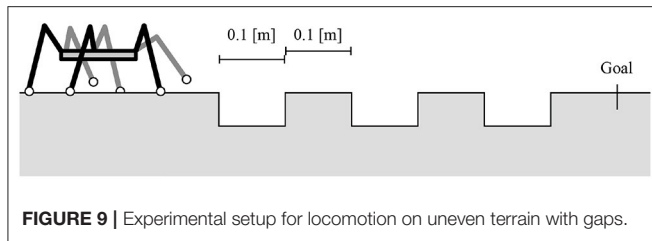


FIGURE 9 | Experimental setup for locomotion on uneven terrain with gaps.

3.2. Adaptation to Leg Amputation

The second simulation experiment aims to evaluate the adaptability of the proposed model to leg amputation. In this simulation, we removed the middle limbs (L2 and R2), and the robot walked on leveled ground. We assume that the amputated limb does not induce the next posterior limb to change early from the stance to swing mode, and consequently, rule (iv) is invalidated. Additionally, the control parameters are the same as in the first simulation experiment, as shown in **Table 1**. Regarding angular velocities, we set $(\omega_{sw}, \omega_{st}) = (\pi/3, \pi/15)$, referring to the low locomotion speed.

Figure 8 shows the results of the amputation. When L2 and R2 limbs are amputated, the robot generates feasible locomotor patterns that differ from the locomotor patterns by the intact robot. As shown in **Figure 8A**, the posterior limb on the ipsilateral side (e.g., L3 limb) moves before the anterior limb (e.g., L1 limb) despite no neural communication by the transition rule (iv). **Figure 8B** shows that the active load sensing (rule (iii)) modulates the responsible limb motions so as to generate feasible interlimb coordination at the beginning of walking. The emerging interlimb coordination well reproduces the actual amputated insect (Hughes, 1957; Graham, 1977; Dean, 1991; Grabowska et al., 2012). Furthermore, **Figure 8C** shows the trajectory of the walking robot with various combinations of leg amputation at specific periods. The robot can adapt to various combinations of leg amputations (e.g., middle limbs and hind limbs). However, when the L1 and R1 limbs are amputated, the robot falls forward, and it cannot generate feasible locomotor patterns. In the falling case, the COM moves the outside of the support polygon during the stance phase of the middle limbs. Although the proposed model still has room for improvement, it well reproduces parts of the insects' adaptive behavior (e.g., lateral sequence gait with L2R2 amputation) as well as the previous model (Owaki et al., 2017).

3.3. Adaptation to Gap Environment

The third experiment addresses the flexible transition between the stepping and searching behaviors in response to the lack of footholds. In this experiment, the robot walked on the ground with gaps and footholds of a specific width, as shown in **Figure 9**. To evaluate the effect of transition rule (ii), we compare the robot with and without transition rule (ii) and measure the success ratio over 30 trials for the two control conditions. In each trial, the initial joint α angles θ_{ij}^α are randomly set. When the transition rule (ii) is eliminated, the transition rule (i) at the AEP

in Equation (1) is modulated as follows:

$$\text{if } \theta_{ij}^\alpha \geq \theta_{AEP} \text{ then } M_{ij} = \text{Swing mode} \rightarrow \text{Late stance mode. (5)}$$

Because of this modulation, the controller has two states: $M_{ij} = 0$ for the swing mode and $M_{ij} = 1$ for the stance mode.

During gap crossing, the proposed model modulates the interlimb coordination and resulting in adaptive changes between walking and searching behaviors. At the beginning of the walk with the random, the active load sensing (reflex rule iii) and the effect from the posterior limb (reflex rule iv) modulates the interlimb coordination from the random initial condition to tetrapod gaits as shown in **Figure 10**. During the gap crossing, several limbs generate searching behaviors depending on the lack of foothold. Note that other limbs adaptively keep their control modes of *stance mode* by using to secure the support polygon by the feedback from the active load sensing. Then, after the gap crossing, all limbs modulate their interlimb coordination for stable locomotor patterns by the fundamental reflex rules. The robot with the searching reflex achieves 60% success ratio, while the robot without the searching reflex achieves a success ratio of under 30% (**Figure 10B**).

Figure 10C shows snapshots of the successful trial in the gap crossing by the robot with reflex rule (ii). The L1 limb retracts over the gap and does not obtain the foothold. Then, the L1 controller switches the control mode from the stance mode to the swing mode *via* the searching reflex. During the L1 limb's protraction, the robot body moves forward by other limbs' retractions, and consequently, L1 overcomes the gap and obtains a new foothold.

The robot with the searching reflex, however, fails to cross the gap due to stacking behaviors as shown in the snapshots of the failed trial (**Figure 10D**). In these snapshots, when the L1 and R1 limbs lift, the robot maintains the static support polygon with the L2, L3, R2, and R3 limbs. However, as the supporting limbs retract, the COM moves outside the support polygon, and consequently, the robot loses body balance during searching. Although the proposed model sometimes fails the crossing gap because of no sensory modulation during the stance phase, these results show that the proposed simple interlimb coordination mechanism play a pivotal role for the robot to change its limb behavior between walking step and searching step in response to the lack of footholds around AEP.

4. DISCUSSION

The significance of the present study is to demonstrate that insect-like adaptive locomotor patterns (e.g., adaptation to locomotion speed, leg amputation, and gap crossing) can emerge *via* a simple chain of reflex mechanisms. Owing to the simplicity of the proposed model, the series of transition rules can be interpreted as a simple control strategy: each limb tries to create a static support polygon in a decentralized manner. This simple control strategy seems to be reasonable in insect locomotion because the insect's morphology (e.g., low COM due to the sprawled posture and a redundant number of limbs) has great advantages in securing support polygons. While complex neural

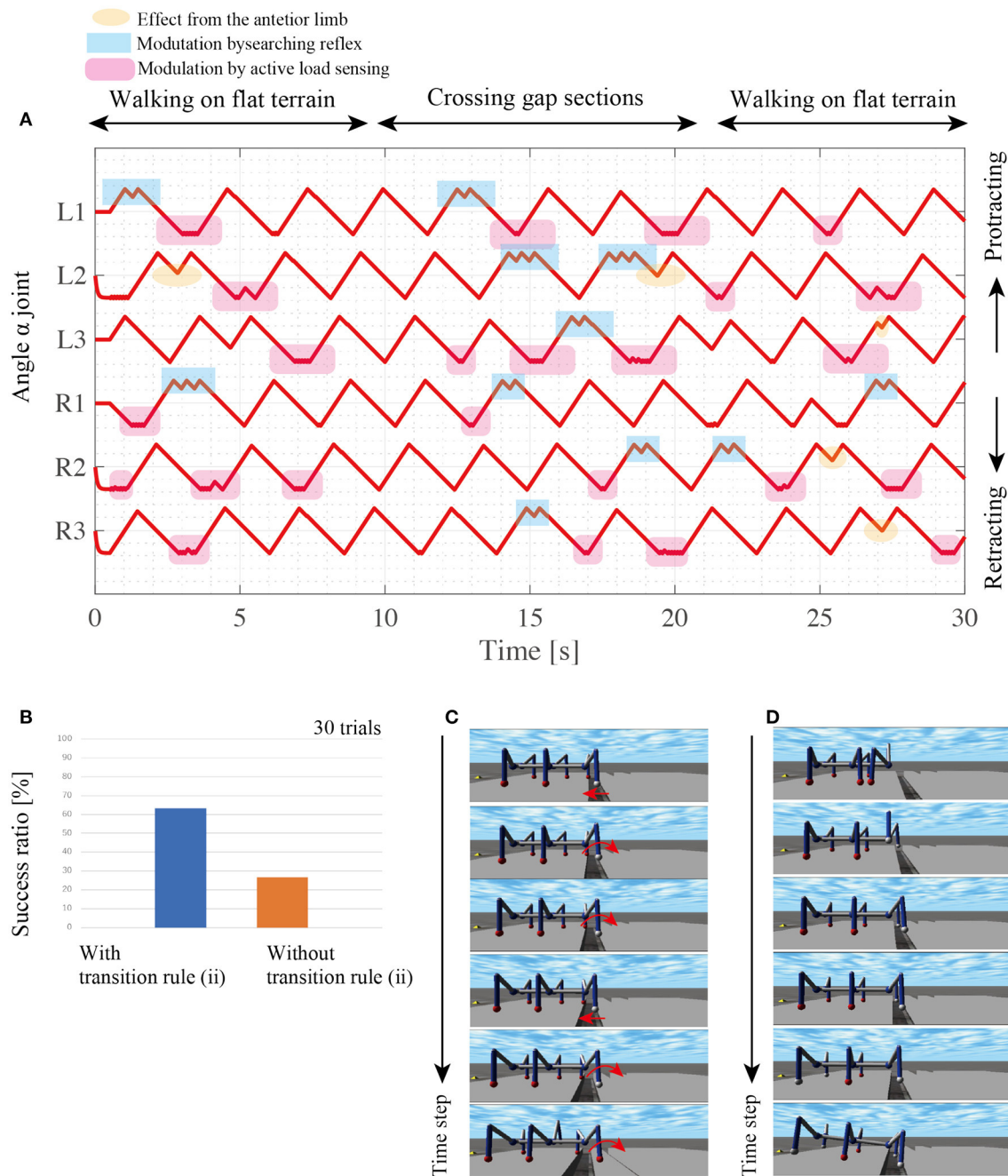


FIGURE 10 | Results of walking experiments on uneven terrain. **(A)** Each history of α joint's angle during crossing gap sections. **(B)** Comparison of success ratios with and without the transition rule (ii). For each control condition, we conducted 30 trials with random initial angles for each limb's α joint. **(C)** Snapshots of successful gap crossing in the trial with transition rule (ii). **(D)** Snapshots of gap crossing failure during walking with transition rule (ii).

network models help us to clarify the correspondence between the neural networks in the insect and the structure of neural modules in the modeling studies, the simple model allows us to understand the essences of the underlying control mechanism as well as introduce them to adaptive robot control.

While our model is abstracted, each reflex mechanism is similar to the biological findings. Rule (i) follows the reflex

mechanism based on joint angles (Akay et al., 2004; Ekeberg et al., 2004). Rule (ii) and rule (iii) satisfy the physiological findings that sensory input signaling ground contact takes over the effects of command neurons for searching behaviors (Berg et al., 2015). Rule (iv) is similar to the effects from the posterior to the anterior limbs (Borgmann et al., 2009). Although our proposed model does not describe the details of the above sensory

feedback mechanisms with interactions among sensor organs (e.g., mechanoreceptors), motor- and intern-neurons, the simple model integrates substantial sensory feedback mechanisms for adaptive interlimb coordination in response to locomotor frequency, leg amputation, and a gap of foothold.

Furthermore, the structure of the proposed model could shed new light on the control mechanism underlying insect adaptive searching behaviors. According to biological experiments, two control schemes, the “two motor patterns hypothesis” and “two control modes hypothesis,” have been proposed (Dürr et al., 2018). In the two motor patterns hypothesis, the control system has two distinct motor patterns for the long step of the walking limb and the short step of the searching limb. Walking and searching behaviors are realized by switching these motor patterns depending on the sensory information. In contrast, the two control modes hypothesis assumes a control mechanism for each swing phase and stance phase, and adaptive walking and searching steps emerge from reasonable switching between the control mechanisms. In this sense, our proposed model agrees with the two control modes hypothesis. Note that our simple model shows the significance of physical interaction in the two control modes hypothesis. Although each limb locally implements two control modes (namely, swing mode and stance mode) and simple reflex rules, the physical interaction with the environment globally affects among limbs and makes each limb free or responsible to support body weight. These interactions should be important for each limb to flexibly generate walking and searching steps as well as secure support polygon when an other limb is searching the foothold.

The failure case in the simulation experiments suggests that flexible coordination between the joints of one limb (e.g., intralimb coordination) is required to improve the adaptability of the proposed model. In the amputated experiments, the robot with amputated L1, R1 limbs cannot secure the support polygon by other limbs, and it tumbles. The simulated robot body model has COM at the middle of the trunk, the PEP limb position of the middle limbs induces the projected COM on the ground to go outside of the support polygon. These failure cases suggest that limbs should change the AEP and PEP position for a stable support polygon. According to insect behaviors, the actual insects modulate the AEP and PEP positions depending on the limb amputation and carrying loads (Delcomyn, 1991; Zollikofer, 1994).

Besides, in the gap crossing experiments, the COM also goes outside of the support polygon during the responsible limb's stance phase, whereas the anterior limbs searching footholds. This is because the target angular velocities of the α joints are set as constant values ω_{sw} and ω_{st} , and the supporting limb keeps retracting regardless of the projected COM going outside the support polygon, as shown in **Figure 10C**. In contrast, actual insect animals modulate their joint angular velocity depending on the situation (Watson et al., 2002). Furthermore, the searching behavior of each limb in simulation moves around the predesigned AEP in the sagittal plane whereas the insects (e.g., stick insect) spread the AEP of the forelimb forward and lateral (Theunissen and Dürr, 2013). These gaps in limb behaviors between the simulation and insect animals suggest that

intra-limb coordination should be considered to generate flexible limb motion in both swing and stance modes.

Although we simplified the robot structure, a more insect-like limb structure may induce the robot to exploit physical interaction with the environment. The proposed model exhibits various insect-like gait patterns as shown in **Figure 7**; however, each limb shows a chattering step at the PEP position. This is because active load sensing is conducted by the limb lifting off the ground. Therefore, if the limb is responsible for the static supporting polygon, once the limb lifts off the ground, the responsible limb touches the ground again, resulting in chattering behaviors. Introducing a flexible foot segment like an insect's tarsus makes it possible to detect the limb's responsibility by sensing the strain of the flexible tip of the foot segment before the limb lifts off completely.

5. CONCLUSION

To elucidate the essential interlimb coordination mechanism underlying adaptive insect's walking and searching behaviors, we developed the simple model that consists of two control models (i.e., swing and stance modes) and four substantial reflex rules. Although the results of the simulation experiments suggest the requirement of additional control mechanisms for flexible intralimb coordination, the robot with the proposed simple interlimb coordination mechanism exhibits various speed-dependent gait patterns, adaptation to leg amputation, and flexible switching between the walking step and searching step during the gap crossing. These results show that simple decentralized control mechanism, e.g., active load sensing, and physical interaction with the environment generate the flexible changes between walking and searching limb behaviors with interlimb coordination for secure support polygons.

For further study, we will develop a physical robot considering the flexibility of the foot segment and evaluate the proposed model in a real-world environment. Furthermore, the intralimb coordination mechanism will be introduced in the proposed model so that each limb can adaptively change its stride speed and foot trajectory depending on the robot morphology and locomotor environments.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

AF, TK, RK, and AI conceived the research. AF and WS conducted the experiments and analyzed the results. All authors developed the mathematical modeling and reviewed the manuscript.

FUNDING

This work was supported by JSPS KAKENHI [Grant-in-Aid for Scientific Research(S)] grant no. JP17H06150.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fnbot.2022.645683/full#supplementary-material>

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Supplementary Movie 1 | Tripod gait in Section 3.1.

Supplementary Movie 2 | Tetrapod gait in Section 3.1.

Supplementary Movie 3 | Wave gait in Section 3.1.

Supplementary Movie 4 | The behavior of the robot with amputated L2 R2 limbs in Section 3.2.

Supplementary Movie 5 | Gap crossing experiment in Section 3.3.

Supplementary Movie 6 | The searching behavior of the robot with reflex rule (ii) in the successful trials in Section 3.3.

Supplementary Movie 7 | The stacking behavior of the robot with reflex rule (ii) in the failed trial in Section 3.3.

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APPENDIX A: FOOT TRAJECTORY

In the stance mode, the limb generates retracting motion to kick the ground with a target angular velocity in the α joint, $\bar{\theta}_{ij}^\alpha$. More specifically, the target values for each joint are described to generate a specific state foot trajectory as follows:

$$\bar{\theta}_{ij}^\alpha = \omega_{st}, \quad (6)$$

$$\bar{\theta}_{ij}^\beta = \frac{\pi - \bar{\theta}_{ij}^\gamma}{2} + \tan^{-1} \left(\frac{H \cos \theta_{ij}^\alpha}{W} \right) - \frac{\pi}{2}, \quad (7)$$

$$\bar{\theta}_{ij}^\gamma = \cos^{-1} \left(\frac{L_{UPR}^2 + L_{BTM}^2 - L_{st}^2}{2L_{UPR}L_{BTM}} \right), \quad (8)$$

where L_{UPR} and L_{BTM} are the lengths of the upper and bottom links of the limb, respectively, and L_{st} is a parameter that reflects the target foot trajectory. The parameter L_{st} is calculated as follows:

$$L_{st} = H^2 + (W / \cos \theta_{ij}^\alpha)^2. \quad (9)$$

where H and W are the target height of the body unit and width of the target foot trajectory, respectively.

In the swing mode, the limb generates a protracting motion along a round trajectory for ground clearance. As in the stance

mode, the joint α is controlled to achieve the target angular velocity, where the joints β and γ are controlled to achieve target angles. The target values are described as follows:

$$\bar{\theta}_{ij}^\alpha = \omega_{sw}, \quad (10)$$

$$\bar{\theta}_{ij}^\beta = \frac{\pi - \bar{\theta}_{ij}^\gamma}{2} - \frac{\pi}{2}, \quad (11)$$

$$\bar{\theta}_{ij}^\gamma = \cos^{-1} \left(\frac{L_{UPR}^2 + L_{BTM}^2 - L_{sw}^2}{2L_{UPR}L_{BTM}} \right), \quad (12)$$

where L_{sw} is a parameter that reflects the target foot trajectory. The parameter L_{sw} is calculated as follows:

$$L_{sw} = (H - h(\theta_{ij}^\alpha))^2 + (W / \cos \theta_{ij}^\alpha)^2, \quad (13)$$

$$h(\theta_{ij}^\alpha) = H \cos \left(\frac{\pi}{\theta_{AEP} - \theta_{PEP}} (\theta_{ij}^\alpha - \frac{\theta_{AEP} + \theta_{PEP}}{2}) \right). \quad (14)$$

where $h(\theta_{ij}^\alpha)$ is a function of θ_{ij}^α for the calculation of the target height of the foot. θ_{AEP} and θ_{PEP} are positive and negative constant values for the angular limitation of joint α at the AEP and PEP, respectively. By switching between the two control modes, the limb generates stride motion along the semicircular trajectory.

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