THE PSYCHOPHYSIOLOGY OF ACTION

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THE PSYCHOPHYSIOLOGY OF ACTION

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EDITORIAL
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Editorial: The Psychophysiology of Action

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Editorial on the Research Topic

The Psychophysiology of Action

What is action? What processes are involved in initiating, guiding, and evaluating the outcomes of action? Different research disciplines have dealt with these questions, and a huge amount of empirical and theoretical work has been conducted so far. However, only a few attempts have been made to integrate the different perspectives. We think it is time to bring together the fields of psychology, neuroscience, and movement/performance science, to stimulate the in-depth exchange of ideas and advance the "psychophysiology of action" as a topic of interest, since psychophysiology and its methods provide a bridge to connect these areas. Further, we assume that to investigate actions in dynamical environments, corresponding measures are necessary that reflect the dynamics of movements; also, multivariate measures should be considered and the dynamics should be reflected in corresponding statistical parameters. Thus, the goal is to bring together theoretical and empirical research from several disciplines to foster the exchange of ideas and methods in an effort to investigate the dynamical role of movement in cognition. Therefore, we invited authors to submit research articles targeting the understanding of action across theories and disciplines.

Hoffmann et al. suggest that to study the psychophysiology of action, it is necessary to consider multiple methodological challenges. The authors describe selected theoretical accounts of how internal and external information processes interact. They suggest that research on the dynamics of action should (a) consider the dynamics of movement, (b) make use of multivariate measures, and (c) employ dynamic statistical parameters accounting. The articles presented within this research topic are diverse with respect to these three dimensions and show that each research area or research discipline touches on at least one dimension.

Indeed, if considering a multidimensional account of action, one has to think about biological motion and how this affects the perception of emotional states. Bachmann et al. show in their review that most brain regions display increased reactivity to emotional body movements in general and that some structures are related selectively to negative valence.

In addition, emotions and the perception thereof play a crucial role in the psychophysiology of action. Masaki et al. show that anxiety in sports situations where participants are evaluated is connected to feedback processing, as measured by oscillations in electroencephalograms (EEGs). They found that theta was increased for high-anxiety groups compared to low-anxiety groups, and delta was higher for a high-anxiety group, but only in an evaluation condition.

In everyday life, people find that music affects their emotions, and thus action. Kuan et al. utilized several measures (e.g., galvanic skin response and heart rate) to investigate the effect of relaxing and arousing music during imagery on dart-throwing performance. Overall, they found positive effects of relaxing music on several parameters.

The study by Cartaud et al. shows that measures of peripheral physiology might be useful for investigating social interactions: They found that interpersonal distances are relevant for effective social interactions. They utilized electrodermal activity as an indicator of emotional responses in a paradigm manipulating facial expressions (via point-light displays) and their respective peri-/extrapersonal positions. Their findings suggest that peripersonal action space and interpersonal social space are sensitive to the emotional valence of a confederate such that the personal comfort distance is affected.

Munzert and Krüger remind us of a crucial historical contribution to action research in their review: Already in the 1930s Edmund Jacobson demonstrated, as a precursor of motor imagery, that peripheral physiological effects rely on task-specific instructions. This historical perspective highlights the relevance of integrating peripheral and central mechanisms related to actions.

Performance is not modulated only by relaxation techniques or music. A recent neuroscience technique, transcutaneous vagus nerve stimulation (tVNS), might have an effect on core mechanisms of action control. This points to a close connection between peripheral and the central nervous system. Jongkees et al. investigate whether key transmitter systems related to action control—gamma-aminobutyric acid and noradrenaline—are linked to tVNS. In a serial reaction time task, they found that tVNS enhanced response selection processes.

Vidal et al. outline that the activity of motor areas seems to depend on the nature of the executed movement as well as on the cognitive context of these movements. In their review, they describe how different classes of reaction time tasks allow specifying the nature and the dynamics of motor areas' activation in different cognitive contexts. Further, the authors describe experimental results obtained from high temporal resolution methods such as EEG during voluntary action.

With respect to voluntary action, the question is how such actions are controlled. In this context, errors are of particular interest since error processing is crucial for motor learning. Joch et al. investigate how this error monitoring is involved in motor control. In a complex motor task, they show that the error negativity (N_e), a key correlate of action control, is modulated by the availability of different sensory signals in a semi-virtual throwing task. Their study suggests that in tasks where visual targets indicate motor performance, visual signals might be weighted more strongly than proprioceptive signals.

Maruo et al. demonstrate that in addition to the N_e, another correlate of action control, the error positivity (P_e), is a key correlate of error evaluation. The P_e is linked to monitoring one's own emotional state, such as anxiety. They show that these correlates differentiate between different types of sports; specifically, long-distance runners, and sprinters differed with respect to the N_e in an inverse manner: With increasing levels of competitive anxiety, the sprinters' N_e amplitude decreased, whereas the long-distance runners' N_e increased. This finding suggests that the two groups utilize their internal error-monitoring function differently.

Going back to the base of motor control, the study by Rönnquist et al. targets the questions "if" and "how" timing training might influence movement performance in athletes. They test the effect of synchronized metronome training on sensorimotor timing ability and whether that timing is related to lower limb movement planning, precision performance, and kinematics.

The study by di Fronso et al. puts endurance into the context of action control and reveals that focusing attention on core components of actions improves functional connectivity among specific brain areas and leads to enhanced performance.

The study by Betti et al. deals with a more basic question related to reach-to-grasp movements: Are corticospinal activity, kinematics, and electromyography associated with the planning and execution of prehensile actions toward either a small or a large object? By inducing motor-evoked potentials with transcranial magnetic stimulation and using several other measures, they found evidence that the index finger is involved in differential motor preparation for different types of grasps and whole-hand prehensile actions.

Fritz et al. contribute an interesting study on endurance. They show that combined musical agency experience and physical exercise can reduce pain perception, hypothetically via some endogenous opioid mechanism. This suggests that the combination of musical agency experience and physical exercise could be utilized in rehabilitation therapies where sometimes the physical treatment may be painful.

The research presented here reflects the diversity of disciplines involved in the psychophysiology of action, as well as their theories and empirical findings. Yet this impressive collection is but a stepping stone on the path to a full understanding of the topic. We hope that this multidisciplinary approach will motivate interested readers to go beyond their own discipline, that is, to go beyond their own theoretical and methodological borders: Together, we may arrive at a "psychophysiology of action."

AUTHOR CONTRIBUTIONS

SH wrote the manuscript. CB and MR co-authored and edited the manuscript.

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PERSPECTIVE
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The Psychophysiology of Action: A Multidisciplinary Endeavor for Integrating Action and Cognition

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There is a vast amount of literature concerning the integration of action and cognition. Although this broad research area is of great interest for many disciplines like sports, psychology and cognitive neuroscience, only a few attempts tried to bring together different perspectives so far. Our goal is to provide a perspective to spark a debate across theoretical borders and integration of different disciplines via psychophysiology. In order to boost advances in this research field it is not only necessary to become aware of the different areas that are relevant but also to consider methodological aspects and challenges. We briefly describe the most relevant theoretical accounts to the question of how internal and external information processes or factors interact and, based on this, argue that research programs should consider the three dimensions: (a) dynamics of movements; (b) multivariate measures and; (c) dynamic statistical parameters. Only with an extended perspective on theoretical and methodological accounts, one would be able to integrate the dynamics of actions into theoretical advances.

Keywords: psychophysiology, cognition, action, decision making, performance monitoring, embodiment

A BRIEF DEFINITION OF ACTION

Imagine Wladimir Klitschko, one of the most successful heavyweight boxing champions of all times, aiming at winning his next boxing match. To win the fight he has to plan and execute different actions that are embedded in a continuous stream of ongoing behavior. A precise definition of action is difficult given its manifold manifestations. Some actions can be characterized as ephemeral, like a hook during the fight. Other actions are more complex and enduring, like "winning the match," and could be seen as a sum of sequential actions. The question of how to separate single actions is often solved by determining their underlying goals (Herwig et al., 2013; Künzell et al., 2017). In this vein, goals can either be within the perceptual range (e.g., hitting the opponent's rib cage with the fist) or in anticipated future states that cannot yet be perceived in the environment (e.g., winning this match to become the leader of one's weight division). According to Prinz (2013), goals can be "hot" and require active intervention to achieve them (e.g., sidestep to a counter strike) or they can be "cold" and temporally uncritical (e.g., increasing one's stamina). Herwig et al. (2013) stated that "an action starts with the first behavioral activity directed toward a particular goal and ends with the achievement of the goal" (p. 106). To achieve a goal, external and internal factors must be geared toward the prospective goal state. For our Klitschko example, this would mean that actions might be influenced by internal factors like fitness level, accuracy, and speed of punches or by external factors such as the opponent being southpaw or noise and lighting conditions in the arena. In extension to the definition of Herwig et al. (2013), we propose that the dynamics of movements and behavioral activity, defined as one element of action besides goals, need to be further specified and partitioned. We suggest that a psychophysiological perspective on actions extends the existing definition by offering an explanation of how internal and external factors interact. Thus, a perspective on integrating action and cognition has to ask the questions: Which are the relevant mechanisms that initiate, guide, and evaluate action? And which methodological challenges arise when the aim is to integrate mind and motion? Answering these questions requires a consideration of different theoretical accounts, but also of new technical developments and methodological advances.

CORE THEORETICAL ACCOUNTS RELATED TO THE INTERPLAY OF ACTION AND COGNITION

Multi-Sensory Integration

Most action is embedded in a rich perceptual environment and perceptual inputs coming from different input modalities have to be integrated to allow proper action selection. Multi-sensory integration is a crucial physiological theory that has, for instance, explained psycho-physiological phenomena such as the rubber hand illusion (Botvinick and Cohen, 1998) or the McGurk effect (McGurk and MacDonald, 1976). Multi-sensory integration addresses the perceptual binding problem (Milner, 1974; Mioche and Singer, 1989), which considers the question of how neural inputs from different modalities (e.g., vision, audition, olfaction) are integrated into one coherent, valid, and robust perceptual experience (Spence, 2011). The neurobiological bases of multi-sensory integration are bi- or multimodal neurons that are excited by more than one input modality existing in a large number of brain areas, such as the somatosensory cortex (Stein et al., 2009). Various complementing principles have been formulated for multi-sensory integration. The principle of visual dominance postulates that vision has a greater influence on the other senses than vice versa (Witten and Knudsen, 2005) the principle of modality appropriateness claims that cross-modal influences depend on the modality's appropriateness for a given task (Welch and Warren, 1980). Finally, the principle of Bayesian integration postulates that the brain uses a form of Bayesian inference to integrate multimodal information into a coherent perception of the world (Deneve and Pouget, 2004).

Embodied Cognition

The concept of embodied cognition assumes strong interactions between cognition, perception, and movement (Shapiro, 2010; Fischer and Coello, 2015), implying they cannot be studied independently of each other. In recent years, more and more evidence pointed to a considerable plasticity of the brain with respect to the integration of body parts (Blanke, 2012). Embodied cognition theories assume that the "self" emerges from the integration of bodily and/or environmental information. This information consists of visual, tactile, proprioceptive, vestibular, auditory, olfactory, visceral, and motor inputs (Blanke, 2012). Thus, embodied cognition is, at least from a neuroscience perspective, closely connected to multi-sensory integration. A recent study by Collins et al. (2016) showed that synchronizing stimulation of the hand somatosensory cortex and observed touches of a corresponding prosthetic hand created the perception of ownership of the artificial limb. From a psychological perspective, there is agreement that cognitive functions can only be understood when considering their relevance for actions (Wilson, 2002). To sum up, embodied cognition approaches postulate that cognitive processes are embodied and hypothesize that an individual's bodily state (and its capacities and skills) and the environment interact (Rowlands, 2010).

Decision Making

Prior to acting, one needs to decide to do so. However, theoretical concepts of decision making often neglect the fact that cognitive and motor processes are intertwined. Some approaches describe decisions as heuristics, with strategies formally defined as building blocks, i.e., a search-, stop-, and decision-rule. The mere composition of cognitive building blocks reveals that the involvement of the sensorimotor system is widely ignored. An exception to this is the simple heuristic approach, which claims that a simple heuristic applied to option generation and decision making in complex sports behavior considers the building block of execution (de Oliveira et al., 2014). The execution rule addresses the question of which action to carry out and, more importantly, how to execute it with the motor system (Raab et al., 2005; de Oliveira et al., 2014). In our opinion, the intertwined motor and cognitive components of decisions, which have been theoretically discussed and coined in the light of motor control (Wolpert and Landy, 2012) or "embodied choices" (Raab, 2017), should be empirically studied and incorporated into theories of the psychophysiology of movement. To reach this goal, psychophysiological models of motor heuristics and embodied choices have to be formulated. Different models of the psychophysiology of movement have been studied in animals (Cisek and Kalaska, 2010) and humans (Wichary and Smolen, 2016) and can serve as a starting point for theory testing, integration, and development. Now, neuroscientific studies integrating different methodological challenges (Kyathanahally et al., 2017) target decision making (Chand and Dhamala, 2017; Muraskin et al., 2017), and find correlations of decision making and somatosensory networks (Harris and Lim, 2016), however, the aspect of movement or "real" (i.e., dynamic) action is still rarely taken into account. We return to this point when outlining current methodological developments.

Psychophysiology of Action and Cognitive Control

The literature concerning this topic is far too vast and complex to be laid down in detail here. Thus, we stick to the core mechanisms that seem relevant in this regard. From a neurophysiological point of view prefrontal cortex (PFC), motor cortex and basal ganglia networks and their corresponding neurotransmitter systems are crucial for action and cognition. More specifically, for task performance ("blocking and punching" to stick to the initial example) the stability of information in the PFC is crucial. Within these networks, there are structures and functions relevant for the evaluation of goal states. That is, for example, the allocation of attention to task-relevant features. On a rather simple level, the establishment of goals refers to efficient stimulus-response mappings concerning the task at hand, or, coming back to the initial example: "*Move right arm up if left shoulder of the opponent indicates a punch.*" But how do we keep track of our action goals on a neurophysiological level, and how are decisions implemented while acting? Working memory is crucial: the before-mentioned task-goal representations are being kept "online" within PFC networks (Jonides et al., 2008) via dopaminergic mediated activity states (Seamans and Yang, 2004). These assumptions match another idea: the reinforcement learning hypothesis (Holroyd and Coles, 2002). It assumes that within the PFC, dopamine (DA) is a kind of "gating signal" that is involved in keeping and adapting goal-state relations via reinforcement learning mechanisms (Miller, 2000). There exists considerable literature concerning connections of the PFC with parietal junctions (dorsolateral-prefrontal network) and how these networks control a variety of cognitive functions like motor planning, working memory, or allocation of attention. Ptak et al. (2017) have claimed that the core mechanism for motor planning (i.e., action planning) is action emulation. They argue that this emulation consists of a dynamic representation of abstract movement kinematics that sustains its internal manipulation. Thereby, it ensures its maintenance over short time periods. Further, it can be assumed that this dorsolateral prefrontal network has evolved from a motor control network to a general system supporting motor and cognitive functions. Related to the impact of actions, a recent account by Peterburs and Desmond (2016) suggests the cerebellum, the core structure for movement execution and motor adaptation, to play a crucial role in sensory prediction, error and conflict processing, response inhibition, as well as feedback learning. Here we return to the idea of embodied cognition: the key aspect of understanding cognition might be, not only from a psychological but also from a psychophysiological perspective, *action*. The neurophysiological mechanisms of action and the corresponding mechanisms related to the interaction with the environment are at the core of cognition.

Interoceptive and Exteroceptive Changes

Finally, using our example with Klitschko, interoceptive and exteroceptive changes produced by actions can be considered dynamically interacting. For instance, muscle tension cannot be maintained after a series of punches (interoceptive change), and Klitschko's opponent can positively influence the estimations of his chances to win by falling after a good punching sequence (exteroceptive change). One can argue that actions could be considered body movements which depend on external and internal factors. Such actions produce re-afferent feedback to interoceptive (generated within the body) and exteroceptive (generated outside the body) change. For instance, in a model of Schubotz (2007) these changes are meant to appear dynamically during movements. She defines interoceptive changes as proprioception (sense of the relative position of the body parts), visceroception (sense of the inner organs), equilibrioception (sense of balance) and nociception (sense from organs, joints, and bones). For complex actions, vision, audition, haptic and other senses are used to detect exteroceptive changes. Whereas we see a current trend in multi-sensory integration research (Greenlee, 2017), less knowledge is gained for the complex interaction of combining interoceptive and exteroceptive changes and their respective measures in one research program (Suzuki et al., 2013).

METHODOLOGICAL CHALLENGES RELATED TO INTEGRATING ACTION AND COGNITION

Besides the theoretical challenges that arise when taking the dynamics of actions into account, one of the core problems is the operationalization of the corresponding constructs. Nowadays there is a considerable amount of technical possibilities, however, only a few are used in dynamic contexts, or only in isolated paradigms measuring certain aspects. We think that more than static measurement of actions is required. For instance, in most classical experimental settings response times are measured or areas under the curve of a movement pattern are extracted, but temporal information provided by modern hard- and software is rarely taken into account. Further, these "static" measurements are often being analyzed independently of each other, e.g., response times are analyzed separate from EEG parameters, and are rarely integrated into attempts to solve theoretical questions (Debener, 2005; Hoffmann and Falkenstein, 2010; Plewan et al., 2016). Finally, many studies focus on central parameters like mean values or compare variances. However, in cognitive neuroscience a lot of measures have been developed which make it possible to describe the temporal dynamics of signals, e.g., time-frequency analysis, non-linear dynamics, or cross-coherence. We suggest a three-dimensional perspective integrating static and dynamic measurements, single and multiple measurements, and dynamics of statistics used. Anyway, the attempt to provide a comprehensive description of all possible methods would be too ambitious. In the following we will therefore describe essential aspects of this three-dimensional perspective and exemplify each aspect by selected methods.

From Static to a Dynamic Measurement of Action

The use of "static" measurements has a long tradition in psychology and is closely connected to the concept of the measurement error (Lord, 1959; Novick, 1966; Rozeboom et al., 1969). In experimental research (as in any empirical research) two types of errors, systematic and random error, might arise. By controlling the experimental setup, one hopes to control for errors or at least keep them constant. This has been achieved with rather static devices: The measurement error (of the device) in simple button presses can be easily controlled. Also, measuring psychophysiological variables can be quite tricky due to the sensitivity of the systems to movement artifacts or other artifact sources. In psychophysiology the term "signal-to-noise ratio" describes this relation of true value and error. To keep this ratio at optimum, the influence of artifacts can be kept low if the participant does not move strongly. Related to the aspect of how to deal with artifacts and how to report them, precise recommendations exist (Keil et al., 2013). Anyway, in former days, measurement instruments did not have the same high precision modern systems have, e.g., eye-tracking systems with high. Also, it was not possible to measure "online," that is, in more dynamic settings. This was due to the before mentioned problems, but also because it was not possible to measure remotely electromyographic or EEG data. In recent years solutions to these problems, for example, mobile EEG (Vos and Debener, 2014; Wascher et al., 2014) or even mobile brain/body imaging (Makeig, 2009; Banaei et al., 2017) have been put forward. Some of these systems show an excellent signal-to-noise ratio (Radüntz, 2018). However, many studies rather focus on "static" measurements like button presses to indicate choices. Only a few researchers integrate dynamic measures like eye-movements (Krajbich and Rangel, 2011). These dynamic measures could be highly relevant in order to model for example "true" action adaptation, like the change of direction of a movement during execution. We argue that due to this technical evolution more dynamic measurements should be taken into account since they provide a more fine-graded analysis of the mechanisms involved.

From Single to Multiple Measurements

If one takes into account dynamic measurements, it seems straightforward to make corresponding inferences concerning the number of dependent variables that are being taken into account. Obviously, one has to be aware of the problem that: (a) one has to carefully select variables meaningful for the research question at hand and (b) to control for the problem of alpha error inflation. However, recent advances in statistics and neurosciences promise to integrate measures that might not only bring together different approaches but also provide new insights. One of these developments is, for example, the increasing usage of multivariate statistics to model artifact and neural sources (Jung et al., 2000). With these techniques it is even possible to integrate different measurements like simultaneous EEG-fRMI (Debener et al., 2006; Diukova et al., 2008; Sajda, 2009; Hoffmann et al., 2013; Dizaji and Soltanian-Zadeh, 2017). For a detailed and extended overview of methodological advances, the reader might refer to a recent research topic edited by Gramann et al. (2014).

From Static to Dynamic Parameters

With "static" we refer to the assumption that the mean is an estimate of the "true" value of some operationalized concept. This assumption holds when any non-systematic variation is distributed normally around the "true" value and that with increasing sample size such variation approximates zero. Shortly described it is aimed to minimize the measurement error. For instance in response times experiments, the mean response times are assumed to estimate the "true response time" with respect to some experimental condition. The logic behind that is: If the cognitive (or neural) system responds to a stimulus, the response consists of the "true" response and the error. With increasing number of trials, this error is being statistically minimized. However, a vast amount of literature presenting alternative statistical parameters, capturing the variability of responses, has emerged. Indeed, this variability of responses might be modulated and might indicate variations in the processes of interest. One way to capture it are for example ex-Gaussians. They provide good fits of empirical response time distributions (Spieler et al., 1996; Matzke and Wagenmakers, 2009) and they allow descriptions of differences between conditions reflected in shifting and/or skewing of the RT distribution. Group differences can be more easily detected compared to classical approaches using Gaussian parameters like the mean. Other important approaches are drift-diffusion models (Ratcliff, 2013) and hierarchical drift-diffusion models (Lee and Wagenmakers, 2009; Wiecki et al., 2013). With drift-diffusion models one can basically model psychological parameters, e.g., information accumulation and decision threshold, by taking into account statistical parameters of response time distributions (Ratcliff, 2013). In sum, they have a long tradition in psychology, and recent advances integrate these accounts into neuroscience (Mulder et al., 2013; Forstmann et al., 2016).

A PERSPECTIVE ON INTEGRATING COGNITION AND ACTION

This headline promises much, and for sure a single, broad perspective will not provide a solution for "everything." However, we believe that a research program related to the integration of action and cognition, be it related to embodiment or cognitive control, should at least consider the literature of the fields mentioned herein but also consider methodological and theoretical advances from other fields. Indeed, more and more studies integrate concepts and methods from different fields (Cohen and Cavanagh, 2011; Cavanagh et al., 2011; Schneider et al., 2014; Stock et al., 2016). For instance, Kiverstein and Miller (2015) described how an integration of neuroscience and embodiment could be laid down but there was a focus on the integration of emotion and cognition. Hence, the core ideas of embodiment, that the body *and* actions are relevant for cognition (Wilson, 2002), has not been derived in detail yet. Coming back to the initial boxing example, it gets clear that the question of how Klitschko got to some strategic decisions cannot be answered without considering the interaction of interoceptive and exteroceptive information. Also, the effect of cognition during the fight cannot be investigated without using dynamic and multivariate measures, since the interaction of these intero- and exteroceptive changes might depend exactly on that setting. Also, this situation may affect neural mechanisms of cognitive control. Having a look at the different streams of literature in the research areas of multi-sensory integration, embodied cognition, decision making, and the neural base of cognitive control, one can only conclude that the fields have to become aware of advances in the respective other fields. For example, there is a huge amount of research related to what decision making *is* and *why it works as it does* but the investigation of *how our neural system processes decisions* and *how all the processes are integrated "online"* has not yet been developed in depth. We think *that a psychophysiological perspective* on actions *extends existing definitions by offering the opportunity to find an explanation of how internal and external factors interact*. Any perspective on integrating action and cognition should strive to find answers to the question about the relevant mechanisms that *initiate, guide, and evaluate action*.

AUTHOR CONTRIBUTIONS

This perspective has been developed during a group retreat by the "Performance Psychology" group in 2017. Note that though the corresponding author coordinated, integrated, and wrote the manuscript, all other authors contributed equally with respect to conceptualization of the manuscript, as well as revising it. Thus, the order of the authors is, except the corresponding author, in alphabetical order.

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REVIEW
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Neural Underpinnings of the Perception of Emotional States Derived From Biological Human Motion: A Review of Neuroimaging Research

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Research on the perception of biological human motion shows that people are able to infer emotional states by observing body movements. This article reviews the methodology applied in fMRI research on the neural representation of such emotion perception. Specifically, we ask how different stimulus qualities of bodily expressions, individual emotional valence, and task instructions may affect the neural representation of an emotional scene. The review demonstrates the involvement of a variety of brain areas, thereby indicating how well the human brain is adjusted to navigate in multiple social situations. All stimulus categories (i.e., full-light body displays, point-light displays, and avatars) can induce an emotional percept and are associated with increased activation in an extensive neural network. This network seems to be organized around areas belonging to the so-called action observation network (PMC, IFG, and IPL) and the mentalizing network (TPJ, TP, dmPFC, and lOFC) as well as areas processing body form and motion (e.g., EBA, FBA, and pSTS). Furthermore, emotion-processing brain sites such as the amygdala and the hypothalamus seem to play an important role during the observation of emotional body expressions. Whereas most brain regions clearly display an increased response to emotional body movements in general, some structures respond selectively to negative valence. Moreover, neural activation seems to depend on task characteristics, indicating that certain structures are activated even when attention is shifted away from emotional body movements.

Keywords: emotion, emotion recognition, body movements, fMRI, point-light displays, AON, mentalizing

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INTRODUCTION

As social beings, we spend the major part of our time interacting with others. Therefore, it is important for us to recognize and properly assess our conspecifics' emotions so that we can respond to them appropriately. This is advantageous, because it enables us to approach people who seem to be in a good mood while avoiding contact with those who are angry, threatening, or dangerous.

Emotions can be transmitted via very different channels. Most research on emotion perception and processing has focused on emotions expressed via facial expression and/or prosody. However, these emotional channels are not the only source of input conveying emotionally relevant information. Another important human-emotion-expressing system that plays a central role in person recognition has come into the spotlight in recent years: the human body; that is, body language and body movements (de Gelder, 2006; de Gelder et al., 2014). Human body movements can convey emotions, and observers can infer the emotional state of individuals or interacting partners from such movements even when these are still at a distance and their faces are not clearly visible (Michalak et al., 2009, 2011; Lorey et al., 2012; Kaletsch et al., 2014b,a). Furthermore, because emotions are closely linked to actions (Frijda, 1986), the bodily expression of an emotion can act as a direct cue as to what might serve as an adequate behavioral response (de Gelder, 2006; de Gelder and Hortensius, 2014).

On a neural level, research has demonstrated that the perception of emotional bodily expressions is linked not only to the activation of areas important for emotional processing such as the amygdala (Hadjikhani and de Gelder, 2003), but also to action representations and motor responses (de Gelder et al., 2004; for reviews, see de Gelder, 2006; de Gelder et al., 2010). This underpins the important linkage between emotions and adequate (re-) actions (Frijda, 1986; Panksepp, 1998).

The paradigms applied to investigate the perception of emotional body movements and the underlying neural substrate differ widely. However, what all paradigms have in common is that they present emotional body movements while excluding facial information and other distracting variables. Nonetheless, the stimulus material applied in research varies substantially with respect to the available information on the observed moving body, thereby providing different advantages and supporting different research perspectives. For example, point-light displays (PLDs) provide only kinematic information stemming from just a few points representing the joints of the body (Johansson, 1973). This ensures that perception is not affected by confounding variables in the stimulus material such as attractiveness, sympathy, and cultural aspects (Hoffmann et al., 2010). An avatar, however, provides further information on the shape of a moving body as well as depth cues, thereby creating a more complex percept and approximating the natural richness of emotional interactions.

Against this background, the present review examines the common methodology in the research field addressing perception of emotional body movements. We have chosen to describe results from studies using moving stimuli (i.e., full-light displays, PLDs, and avatars) because our theoretical focus lies on the perceived and represented differences between the different categories of moving human body stimuli that possess emotional content. We believe that whether the observer views static whole-body images or bodies in movement makes a qualitative difference because, as, for example, Atkinson et al. (2004) have stated, it is especially the perceived intensity of body gestures that relies more on movement than on static form information. Against this background, our aim is to analyze research that offers insight into the neural representation of the perception of emotional states derived from kinematic and bodily cues of biological (human) motion. We discuss how emotional movement stimuli of different quality may modulate the underlying neural substrate of the observer's perception. We further ask how depicted emotional valence (negative vs. positive) as well as different task instructions (implicit vs. explicit paradigms) might affect perception and its neural processing.

LITERATURE SEARCH

We identified and selected relevant studies (for selection process, see **Figure 1**) by searching in PubMed, Google Scholar, and Web of Science. We used several key terms in different variations, for instance fMRI, fNIRS, emotional brain, emotion, perception, point-light displays, body expressions, dynamic body, neural representation, body parts, biological motion, avatars, motion capture, emotional body language, kinematics, and emotion recognition. We then selected potential studies by examining their abstracts. Additionally, we scanned references retrieved from the selected literature for further articles on the topic. We included studies when (1) emotional body movements were used as stimulus material (i.e., full-light displays of whole bodies or body parts, point-light displays, avatars), (2) task requirements included emotion judgments or observation of emotional body movements, and (3) fMRI or fNIRS were used to assess brain activity. Based on these criteria, we selected a total of 16 studies for our review.

THE NEUROPHYSIOLOGY OF PERCEIVING EMOTIONS FROM EMOTIONAL BODY MOVEMENTS

Neuroimaging studies on the perception of emotional body movements investigate the brain structures that play a key role not only in perception *per se* but also during the processes of emotion classification, valence judgments, and social perception in response to such movements.

Regarding the observation of human actions, the last two decades have seen the accumulation of a broad body of neuroimaging studies assessing the brain networks underlying the respective observation processes. One widely discussed underlying neural substrate of human action observation abilities is the so-called action observation network (AON). This is supposed to play a crucial role when observing the actions of others (for a meta-analysis, see Caspers et al., 2010). The AON embraces all brain areas activated by the mere observation of actions. According to a meta-analysis of 104 studies, enhanced activation during the observation of human actions is found in the inferior frontal gyrus (IFG), the dorsal and ventral premotor cortex (dPMC, vPMC), the supplementary motor area (SMA), the inferior parietal lobe (IPL), the superior parietal lobe (SPL), and the primary sensory cortex (SI) (Caspers et al., 2010). The AON is believed to integrate the observed actions of others with an individual's personal motor repertoire. This suggests that the human brain understands actions by engaging in a motor simulation based on its own motor programs (Kilner et al., 2007). However, it has been asserted that understanding actions and

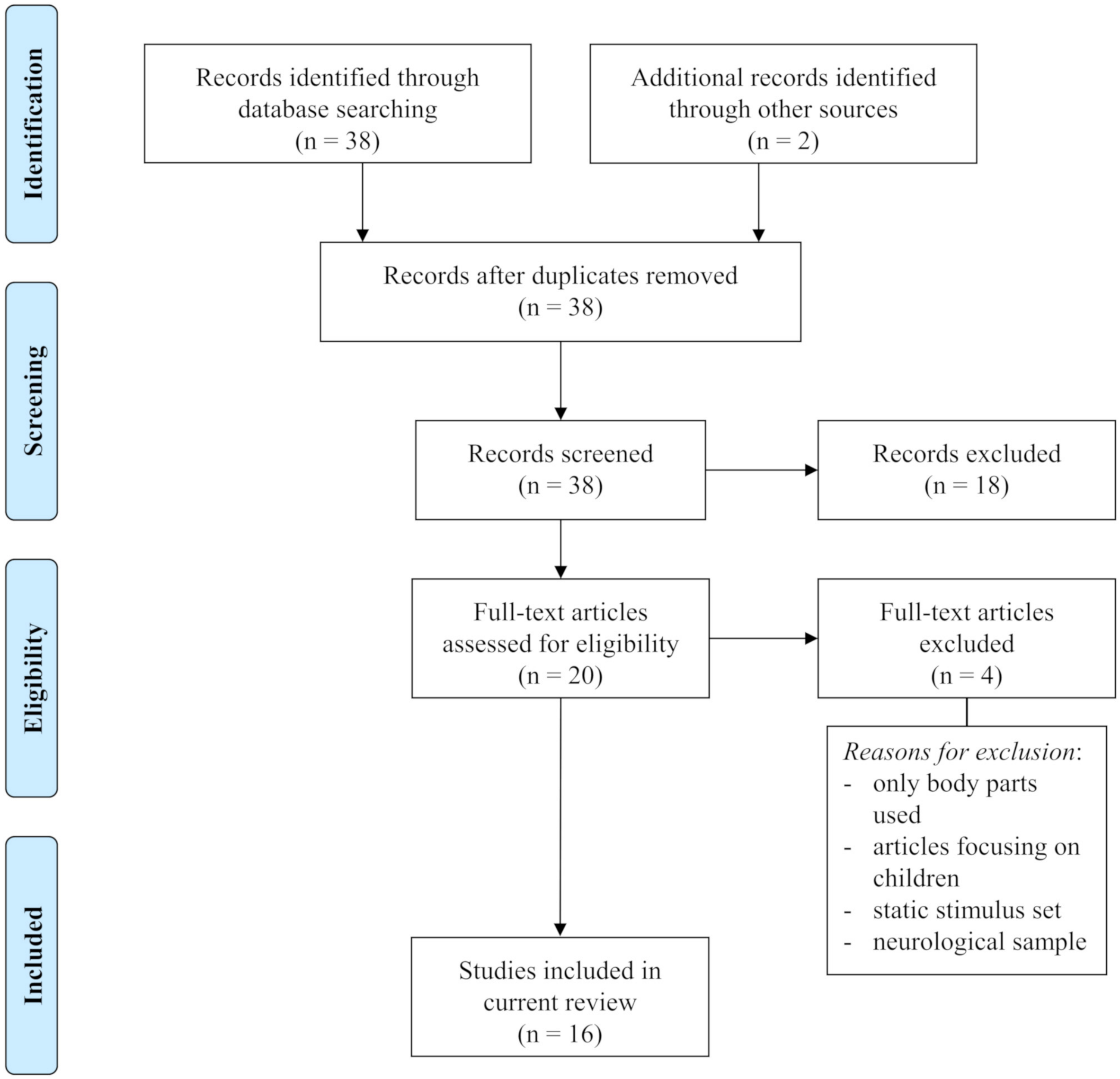

FIGURE 1 | PRISMA flow diagram of literature selection. Adapted from Moher et al. (2009).

their associated intentions cannot be purely motoric in nature. In addition, mental states such as a person's feelings, emotions, and desires are attributed to other people in order to understand the intentions underlying their actions (Frith and Frith, 2003). In this regard, Frith and Frith (2006) have suggested that simulating motor or affective processes is only the first step toward inferring the other's intentions and attitudes. Another process has been described as a mentalizing process or the employment of a "theory of mind" (ToM). This can be conceived as inferring another person's mental state, and it is thought to be subserved primarily by four brain regions: the ventromedial prefrontal cortex (vmPFC), the dorsomedial prefrontal cortex (dmPFC), the precuneus, and the temporo-parietal junction (TPJ) (Centelles et al., 2011). Further structures such as the anterior superior temporal sulci (aSTS), the lateral orbitofrontal cortex (lOFC), and the amygdala may also play a major role (Gallagher and Frith, 2003; Saxe, 2006; Frith, 2007; Bedny et al., 2009; Carrington and Bailey, 2009). Turning to the processing of human body form, further regions are thought to be involved in processing human body movements. These include the extra striate body area (EBA) and the fusiform body area (FBA). Both have been reported to respond selectively to human bodies and body parts (Downing et al., 2001; Schwarzlose et al., 2005).

In the following sections, we present neuroimaging research based on the observation and valuation of emotional body movements. More precisely, we discuss three different stimulus types of emotional body movements—namely, full-light displays (videos), PLDs, and avatars. Hence, the main focus of the current review is on the underlying neural substrate of the processing of emotional body movements and the possible modulatory effects of different stimulus categories. Furthermore, we discuss the influence of stimulus valences (e.g., angry, fearful, happy) on brain sites that are mostly valence-independent as well as on sites that react preferentially to specific valences. In a last step, we discuss effects of different task instructions (e.g., implicit vs. explicit tasks) on neural activation.

Stimulus Types

Full-Light Displays

Research on emotional body movements has frequently applied full-light displays of emotional body movements as stimuli. Although many studies have shown that emotional expressions can indeed be identified from the minimal kinematic information provided by, for instance, PLDs, Atkinson et al. (2004) have shown that the use of full-light displays leads to slightly better recognition accuracy rates for the specific emotional content. To construct stimuli, most studies asked non-professional or professional actors to enact different scenarios corresponding to emotional situations such as opening a door and reacting to someone or something that makes them angry (Pichon et al., 2008). Compared to more abstract displays of biological movements, this method clearly has greater ecological validity. However, it is harder to control and is therefore more susceptible to possible confounding factors such as the attractiveness of or sympathy toward the actor. Nonetheless, facial features and expressions are commonly removed and clothing is kept uniform (Grèzes et al., 2007) to ensure that these variables do not exert unwanted effects.

Neural correlates of observing full-light displays

Studies using full-light displays to investigate how emotional body movements are represented on a neural level have found an involvement of various structures across the brain (**Figure 2**). This network revolves around structures that code basal inputs such as form information and motor dynamics, but also ones on a higher cognitive level that evaluate the significance and meaning of actions as well as the intention behind the action.

Action observation network

Full-light displays of emotional movements activate several structures that are thought to be part of the AON. These include the inferior parietal lobule (IPL) and the inferior frontal gyrus (IFG) that both show increased activation for actions containing emotional expressions when contrasted directly with neutral actions (Sinke et al., 2010). Comparisons of the observation of emotional actions with the observation of neutral actions have also revealed increased activation within the premotor cortex (PMC), thereby indicating that this area also exhibits a particular sensitivity for emotional body movements (Grèzes et al., 2007; Pichon et al., 2008; Sinke et al., 2010). This involvement of AON-associated structures suggests that observing emotional movements might be mediated by a mental simulation process that draws on own motor representations of such movements in order to make sense of them. In this context, it is worth noting that a recent study by Jospe et al. (2018) has emphasized that this simulation process correlates with personality traits such as individual empathy levels. Their results showed that participants with high empathy scores utilize the embodiment or simulation process more optimally than participants with low empathy scores.

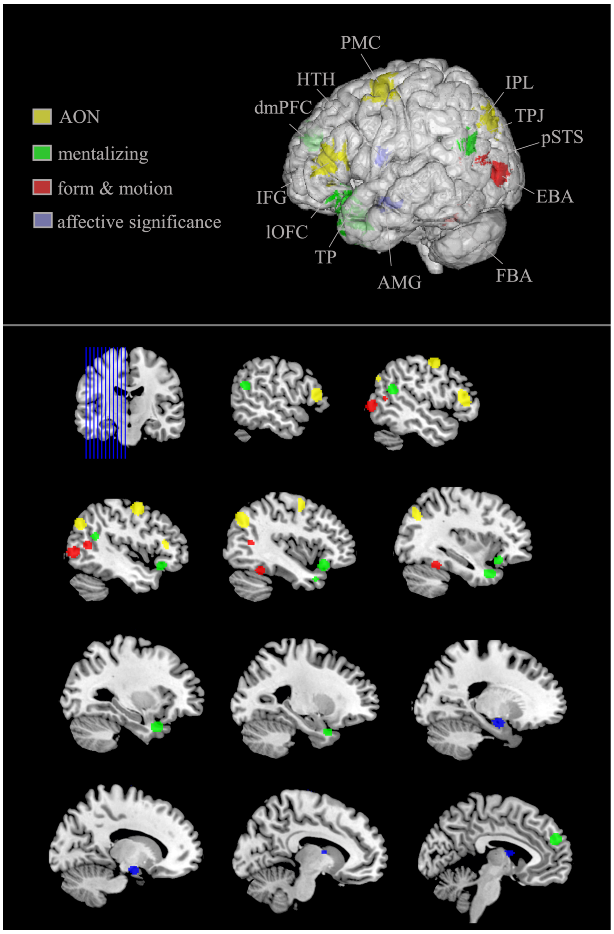

FIGURE 2 | Brain structures preferentially recruited by emotional (vs. neutral) body movements. Generic figure; upper image shows left hemisphere view. Increased surface transparency for visibility of subcortical structures (i.e., amygdala, hypothalamus). AON (yellow), action observation network; includes PMC, premotor cortex; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; mentalizing network (green) includes lOFC, lateral orbitofrontal cortex; dmPFC, dorsomedial prefrontal cortex; TPJ, temporoparietal junction; TP, temporal pole; form and motion associated areas (red) include pSTS, posterior superior temporal sulcus; EBA, extra striate body area; FBA, fusiform body area. Structures associated with affective significance and defensive reactions (purple) include AMG, amygdala; HTH, hypothalamus. Lower part of the image presents sagittal sections of the left hemisphere with each structure presented at least once.

The role of the mentalizing network

As stated above, although the AON is thought to be at the core of understanding another person's actions, the process of inferring the meaning behind actions has also been associated with so-called mentalizing processes (Frith and Frith, 2006). Within this framework, structures that commonly show an increased activation in response to emotional body movements compared to neutral actions include the temporo-parietal junction (TPJ) and the temporal pole (TP) (Pichon et al., 2008, 2009; Sinke et al., 2010). The TPJ is thought to be involved in reorienting processes, but has also been found to be active during mentalizing tasks and higher cognitive tasks such as perspective taking (Frith and Frith, 2006; Krall et al., 2015). It has been suggested that the temporal pole is a convergence zone in which knowledge from different modalities is integrated. For instance, knowledge about a person can be used to predict not only thoughts, feelings, and behavior that are most likely to occur within a given situation and vice versa, but also how moment-to-moment changes of a situation can alter these thoughts, feelings, and behavior (Frith and Frith, 2006). In this context, it is assumed that activation of the TP allows the observer to integrate the emotional behavior with the situational context in order to gain a meaningful understanding of it.

A more frontal region belonging to the mentalizing network, the medial prefrontal cortex (mPFC), has also repeatedly been found to be activated in persons observing and subsequently rating emotional body movements in terms of their emotional valence (e.g., neutral or angry) (Pichon et al., 2008, 2009, 2011; Sinke et al., 2010). The mPFC is considered to be associated with anticipating what another person is thinking or feeling. It has also been shown to be active when thinking about one's own mental state. It is therefore postulated that the mPFC is used to interpret what a person is likely to be feeling in a given situation (Frith and Frith, 1999).

Finally, increased activation of the lateral orbitofrontal cortex (lOFC) is found in response to the observation of emotional (vs. neutral) body movements (Pichon et al., 2008, 2009, 2011; Sinke et al., 2010; Van den Stock et al., 2011). Activation of the lOFC has also been associated with mentalizing and particularly with ToM processes (Völlm et al., 2006) as well as with comparing non-matching social-emotional cues (i.e., social violations) with stored representations (Moll et al., 2005).

Hence, the mentalizing network seems to be responsive toward emotional content when judging dynamic movements. Considering the simultaneous involvement of AON-associated structures, the increased sensitivity of the mentalizing network to emotional actions supports the idea that they serve a common purpose—that is, to infer and interpret affective states from body movements.

Areas encoding motion and form information

One further structure that is believed to be critical in decoding human motion (Blake and Shiffrar, 2007) is the (posterior) superior temporal sulcus (pSTS). In addition to its activation being elicited by human motion *per se*, the pSTS has also often been shown to be activated by dynamic emotional expressions (Grèzes et al., 2007; Pichon et al., 2009, 2011; Kret et al., 2011; Van den Stock et al., 2011). Moreover, it is worth noting that the pSTS has frequently been discussed as part of the AON. Urgen et al. (2016), for instance, pointed out that during the visual processing of actions, the pSTS pools information from the visual cortex and passes that information to higher levels of the AON (e.g., the PMC) that code higher aspects of actions.

Aside from motion information, emotional body movements also provide form information. Previous research suggests that the extra striate body area (EBA), located in the posterior inferior temporal sulcus/middle temporal gyrus, is linked to body representation in general and responds selectively to emotional bodies compared to a variety of other objects (Downing et al., 2001; Peelen et al., 2007).

Moreover, empirical studies have demonstrated a higher sensitivity of the EBA for emotional compared to neutral body movements (Grèzes et al., 2007; Peelen et al., 2007; Pichon et al., 2009; Kret et al., 2011). In this context, it is worth noting that the fusiform body area (FBA), a structure of the ventral fusiform gyrus, is also especially sensitive for emotional body movements compared to neutral body movements (Pichon et al., 2009; Sinke et al., 2010; Kret et al., 2011).

Hence, brain areas associated with motion and form processing show increased neural responses especially to movements with emotional content. It has been proposed that this is an outcome of the modulation by another brain structure—namely, the amygdala (Pichon et al., 2009).

Affective significance and action preparation

When observing emotional body movements, it is important to be able to judge the respective affective significance of the observed movement in order to know how to respond appropriately. This process is believed to be conducted by the amygdala, a structure that is also tightly connected with structures that play a pivotal role in defense reactions and action preparation such as the hypothalamus and the PMC (Barbas et al., 2003). Seeking support for this idea, Sinke et al. (2010) investigated whether small differences in body movements (i.e., threatening vs. teasing body movements) would lead to differential brain activation. Their results showed that threatening stimuli elicited greater amygdala and hypothalamus activation than teasing stimuli. This suggests that when a stimulus is evaluated as potentially threatening, this information is passed on to structures that modulate vegetative preparedness such as the hypothalamus (Sinke et al., 2010).

An extensive network recruited by full-light displays

To conclude, studies using full-light displays show that emotion perception from body movements is associated with increased activation in a broad network of cortical and subcortical areas. Moreover, this activation involves numerous subprocesses. While being composed of basal processes such as recognizing human form and motion, it is also associated with structures such as the EBA, the FBA, and the pSTS along with higher cognitive processes such as assigning meaning to what has been observed (IPL, IFG, and PM). Moreover, a related process of making sense of the movement observed is to recognize the intention of the person carrying out the movement. These mentalizing processes are assumed to be carried out mainly by the TPJ, TP, mPFC, and lOFC. Finally, and not to be neglected, because it plays a pivotal role in processing emotional movements, evidence reveals amygdala and hypothalamus activation in response to displays of emotional body movements (*for an overview*, see **Figure 2**).

Point-Light Displays

Back in the early 1970s, Johansson (1973) described a technique for studying perception from biological motion that reduces stimulus information to a minimum. By attaching reflective patches to several anatomical landmarks and carefully controlling the light settings, high-intensity signals from the reflective patches were visible and could be recorded while subjects performed movements. Nowadays, methods are more advanced, and using motion capture software to create so-called point-light displays (PLDs) has become a popular method for assessing social and emotion perception from biological movements in both behavioral and fMRI paradigms (Atkinson et al., 2004, 2012; Heberlein and Saxe, 2005; Lorey et al., 2012). Behavioral studies have shown a variety of inferences that can be made based on the observation of PLDs. These include attractiveness, affect, and vulnerability (Gunns et al., 2002; Provost et al., 2008; Centelles et al., 2011). Although PLDs may have restricted ecological validity due to their level of abstraction, the method seems to be highly suitable for investigating social perception while eliminating potential confounds in this domain such as gender and attractiveness.

Neural correlates of observing point-light displays

The evidence base from point-light displays is considerably smaller than that from the broader body of studies using full-light displays. In the following, however, we discuss whether a reduction of visual information, leaving purely kinematic stimuli, might affect neural activation in the discussed regions of interest (ROIs).

The action observation network

Because research has been shown that the mere observation of PLDs without explicit emotional content recruits action observation networks (Saygin et al., 2004), it is reasonable to assume that emotional body movements, depicted as PLDs, will also evoke activity in AON regions. In support of this assumption, the observation of, among others, emotional PLD interactions (Centelles et al., 2011) revealed activation in the PMC, and IFG. Alaerts et al. (2013), for example, carried out fMRI scanning with typically developed as well autistic individuals while they were performing an emotion recognition task using PLDs and a control task in which they observed the same PLDs but were instructed to direct their attention toward color changes rather than emotional states. Their results demonstrated that, compared to fixation, emotion recognition from PLDs activated several fronto-parietal regions of the AON as well as the IPL. These data underpin the notion that even after a reduction of visual information, activation is still elicited in fronto-parietal regions of the AON subserving action and/or emotion processing as well as embodied cognition (Rizzolatti and Craighero, 2004).

The mentalizing network

When inferring affective states from PLDs, it seems that the mentalizing network also plays a key role, as previously reported for full-light displays. For example, the TPJ has been identified repeatedly as being activated by the observation of emotional PLDs (Heberlein and Saxe, 2005; Centelles et al., 2011). Heberlein and Saxe (2005), for instance, asked their participants to rate the fit between an emotion or trait word and a previously observed point-light video. They found that the TPJ showed increased activation regardless of whether participants inferred either affective states or personality traits. Furthermore, the dorsal part of the mPFC (dmPFC) and the lOFC have also been found to be activated during the observation of emotional PLD movements (Heberlein and Saxe, 2005; Centelles et al., 2011), implying that these regions may not be specifically sensitive to the reduction of visual information.

In contrast to the literature on full-light displays, the studies using PLDs reviewed here do not report an increased activation of the TP. However, this should be interpreted with caution, because the TP might not have been a predefined ROI in the reviewed studies. However, on the basis of the evidence discussed in the present review, we cannot rule out the possibility that the TP is more sensitive to other stimulus properties such as visual context and ecological information in full-light displays, and therefore not activated successfully by point-light displays of emotional kinematics.

Motion and form information

Although PLDs do not include the same information on shape such as soft tissue form and motion, they show a similar pattern of neural activation within, for instance, areas associated with human body shape and motion. For example, Atkinson et al. (2012) compared neural responses to emotional (i.e., angry, happy) and non-emotional actions depicted as PLDs. They found that all human–motion- and form-information-associated areas (i.e., EBA; FBA, and pSTS) responded preferentially to emotional compared to non-emotional PLDs. Within this framework, it is worth noting that a study investigating neural responses to various complex motion stimuli showed that the STS reacted slightly more strongly to videos of humans performing different whole-body motions than to point-light displays of such motions (Beauchamp et al., 2003). However, a direct comparison between emotional full-light displays and PLD movements has yet to be conducted.

Affective significance and action preparation

Interestingly, no activation has been reported in either the amygdala or the hypothalamus when comparing emotional PLDs with neutral stimuli (Heberlein and Saxe, 2005; Centelles et al., 2011; Atkinson et al., 2012). Both groups of nuclei have been implicated in motor vigilance to support reflexive defensive behaviors, typically in response to threatening stimuli portraying, for example, anger (Pichon et al., 2011). Although the stimuli used in the present studies included negative emotional displays and the emotion could be categorized correctly, the lack of activation in these areas may be due to the level of abstractness of the stimuli. Another possibility is that predefined regions were used for the fMRI analyses and further activated regions may have been missed.

Similar activation pattern elicited by PLDs

Although PLDs contain only a minimum of kinematic information, studies using PLDs confirm that emotional point-light body expressions also modulate neural activation successfully in most of the areas that have previously been discussed as being relevant for the processing of emotional movements on the basis of findings using full-light body stimuli. These areas revolve around structures that are often associated with motion and form processing (pSTS, EBA, and FBA), the AON (IPL, IFG, and PMC), and mentalizing processes (dmPFC, lOFC, and TPJ). No activation has been reported in the amygdala and the hypothalamus, indicating that PLDs may not be suited to elicit defensive responses in the observer. However, it should be emphasized that most studies analyzed predefined ROIs and this limits their comparability.

Avatars

Recent years have seen increased interest in a third class of emotional movement stimuli. Whereas PLDs have been criticized because their level of abstractness may affect their ecological validity, full-light displays are restricted in their controllability with respect to confounding variables such as gender or age (Goldberg et al., 2015). Therefore, researchers developed an intermediate stimulus category: dynamic avatars. de Borst and de Gelder (2015) have argued that avatars may evoke differential processing (e.g., better discrimination), and this, in turn, may affect underlying brain activity. Because this is a relatively new paradigm, the body of neurophysiological research on emotion perception from avatars is still quite small. However, there are two studies that have investigated emotion perception by using avatars within a neurophysiological framework.

Neural correlates of observing avatars

Because only two studies have used paradigms including this type of stimulus, we decided to summarize their findings without subdividing this section according to different networks or brain regions.

Both studies used avatars displaying different emotional gait patterns (i.e., happy, angry, fearful, sad, or neutral). Participants were then asked to classify the presented emotional state during fMRI scanning (Schneider et al., 2014; Goldberg et al., 2015). Results showed that, in addition to regions previously associated with form and motion processing (i.e., EBA, FBA, and pSTS), there was activation within the fusiform face area (FFA) (Goldberg et al., 2015). The FFA is an area that responds selectively to faces (Atkinson et al., 2012). This result is quite surprising, in view of the fact that all avatars were "faceless." However, it could suggest that face completion effects may occur even when detailed facial information is missing (Goldberg et al., 2015).

Moreover, emotional gait patterns also elicited activation in two structures of the AON: the IPL and the IFG (Goldberg et al., 2015). However, no activation in the PMC was reported.

Regarding the mentalizing network, activation was observed in the TPJ and lOFC, yet no activation was reported in the dmPFC. Furthermore, emotional (vs. neutral) gait elicited an increase in activation in the amygdala but not in the hypothalamus (Goldberg et al., 2015).

Thus, observation of emotional gait patterns of avatars also elicited increased neural activation in the networks discussed within the framework of the processing of emotional body movements. However, it has to be considered that participants observed emotional gait patterns displayed by avatars instead of complex interactions or emotional gestures, as described previously. Therefore, the studies cannot be compared directly because they used different stimuli. However, the lack of activation in the PMC and hypothalamus support the notion that, perhaps, avatars displaying emotional gait are not able to elicit defensive behaviors in the observer, perhaps to the material's level of abstractness.

The Influence of Emotional Valence

The following paragraph describes possible modulatory effects of different emotional valences on the previously identified structures that appear to be involved in processing affect from body movements. Emotional valence means the intrinsic attractiveness (positive valence) or averseness (negative valence) of an event, object, or situation (Frijda, 1986). The term can also be used to characterize and categorize specific emotions. For example, anger and fear are considered to have *negative valence*, whereas joy, for example, has *positive valence*.

Moreover, it has been discussed whether some structures may even represent activation in favor of individual emotions (e.g., anger and fear) that can, for instance, be assigned to the same valence category (e.g., negative).

Valence effects

Indeed, several brain structures have been identified as responding more strongly to certain valences. One of these structures is the EBA. Schneider et al. (2014) reported that the EBA was not significantly more activated during the display of avatars showing a happy gait pattern compared to neutral gait. In contrast, an increase in activation was reported for angry, sad, and fearful stimuli (i.e., emotions with a negative valence) compared to neutral ones. However, Peelen et al. (2007) did not report such exclusiveness for negative valence in the EBA, because they found an increased activation elicited by not only angry, fearful, disgusted body movements but also happy ones during the observation of full-light videos. This is in line with Atkinson et al. (2012) findings reporting enhanced activation in the EBA for angry as well as happy (vs. neutral) body movements. Schneider et al. (2014) argued, however, that happy walks were the most difficult for their participants to identify. Moreover, there was a slightly positive correlation between recognition accuracy and activation in the EBA, suggesting that better emotion recognition was also associated with increased neural activation. Therefore, they concluded that happy avatar walks may have lacked emotional expressiveness and therefore failed to induce a significant increase in cortical activation (Schneider et al., 2014).

Regarding AON-associated structures, preferential activation for negative valence was found within the PMC as well as within the IPL. This effect was revealed by a direct comparison of threatening (i.e., negative) vs. teasing (i.e., positive) stimuli (Sinke et al., 2010).

A similar preference for stimuli with a negative valence (anger and fear vs. neutral stimuli) was found within the TPJ, a region associated with mentalizing processes (Centelles et al., 2011). In support of these findings, Schneider et al. (2014) also found a selectivity of the TPJ for negative stimuli—that is, avatars displaying an angry, sad, or fearful gait pattern. This is supported by a direct contrast between threatening and teasing stimuli in which threatening stimuli elicited greater activation (Pichon et al., 2008, 2009).

Differential Activation Between Emotions of One Valence Category?

Beyond a preferential activation for different valences (i.e., positive vs. negative), several studies have examined whether emotions of the same valence categories elicit differential neural activations. Against this background, the EBA and FBA present such a preference for certain emotions. For example, Peelen et al. (2007) showed that the EBA was modulated most effectively by anger, disgust, and, to a lesser degree, fear. The EBA, however, did not show increased activation in response to body movements portraying sadness. The FBA showed a similar pattern. However, fear and sadness both failed to elicit an increased response (Peelen et al., 2007). In support of this, Pichon et al. (2009) identified the FBA as being preferentially activated by anger compared to fear or neutral body movements.

Peelen et al. (2010) applied a multivariate approach to investigate whether neural patterns in the STS display emotion specificity. They found that neural pattern within the STS discriminated between different emotion categories, allowing for a distinction between emotions such as anger, disgust, fear, and sadness based on their neural patterns. This relatively new method of fMRI data analysis reveals that not only overall activity changes in brain regions but rather a more distributed response pattern within one brain region indicate the response to observed stimuli (Haxby et al., 2001; Haynes and Rees, 2005; Kriegeskorte et al., 2008).

Regarding areas belonging to the AON, evidence is quite sparse. Comparing anger and fear directly, the PMC, however, also reveals a preferential activation for angry body motion (Pichon et al., 2009).

Mentalizing-associated structures such as the TPJ show a preferential activation for angry compared to fearful body motion that becomes visible in the supramarginal TPJ. However, a reverse pattern has been identified in the superior temporal part of the TPJ, in which a greater response to fearful (vs. angry) stimuli was elicited (Pichon et al., 2009). For the temporal pole, evidence is also largely homogeneous.

Both studies that investigated emotion selectivity reported a preferential activation in response to angry body movements compared to fearful or neutral ones (Pichon et al., 2008, 2009).

The same holds true for frontal areas—that is, the dmPFC and lOFC. Both structures have been identified as displaying a greater BOLD response during the observation of angry compared to fearful stimuli (Pichon et al., 2009). This finding is in line with the results of multivariate analyses by Peelen et al. (2010) in which the individual emotions (i.e., anger, disgust, fear, and sadness) could be distinguished based on their activation patterns, thereby indicating an "emotion specificity" in the mPFC.

Finally, the amygdala showed increased activation during the observation of angry as well as happy body movements, whereas movements displaying disgust, fear, and sadness (all compared with neutral stimuli) had no effect (Peelen et al., 2007). The authors suggested that this effect might be attributable to low levels of arousal induced by disgust, fear, and sadness compared to happiness and anger. Arousal dimensions have been highlighted in the context of amygdala activation, indicating that higher intensities correlate with higher activation magnitudes (Anderson et al., 2003).

In sum, there is a clear trend toward preferential activation in response to negative stimuli and, presumably, stimuli that induce high levels of arousal. Such emotional modulation has been postulated to originate in subcortical structures such as the amygdala (Amaral et al., 2003). However, a combined continuous theta burst stimulation (cTBS)-fMRI study by Engelen et al. (2018) found that when regions belonging to the AON (i.e., PMC and IPL) were stimulated, activation of the amygdala increased during the observation of threatening compared to neutral stimuli. Without stimulation, amygdala activation did not differ significantly between the two conditions. The authors suggested that this effect could be attributable to functional connectivity processes between the amygdala and structures of the AON (Engelen et al., 2018). However, the exact circuits and feedback processes have yet to be established. From an evolutionary perspective, an argument in favor of a preferential activation caused by threatening stimuli seems plausible, because identifying negative emotions might be more relevant for the organism so that it can quickly initiate a defense response. However, it should be emphasized that multivariate studies are more likely to shed light on whether certain structures produce emotion-specific activations. Whereas emotions of the same valence category may not elicit significantly different activation magnitudes, they may well be represented within a different pattern of activation (Peelen et al., 2010).

Task Specificity

Experimental Paradigms

A variety of task paradigms using different types of stimuli and experimental instructions have been used to uncover the neural basis of emotion perception. For instance, within explicit observation paradigms, participants have been instructed to observe a short video clip displaying emotional body movements. In the next step, they are commonly asked to rate the video sequence they have seen in terms of its valence (emotional vs. neutral), or emotional intensity (e.g., "angry? 1: a little, 2: quite, 3: very much"), or make no judgment to ensure that the trials of interest are not confounded by motor responses. In the latter case, participants are instructed to press a button during control stimuli trials (e.g., upside down, oddball) to control for their attention.

Another popular method includes combined explicit and implicit observation paradigms. Within experimental runs, stimuli are blocked by task and alternate between series of explicit and implicit recognition. During explicit conditions, participants are asked to rate the emotion (e.g., fear/anger/neutral) displayed in the video sequence. During implicit conditions, they observe the same video sequences, but pay attention to colored dots or video frames that appeared during the videos. Following the sequence, participants are instructed to make a judgment about the color (Pichon et al., 2009; Alaerts et al., 2013).

Often, the implicit task condition serves merely as a control task. However, it does allow an investigation of the brain areas that may or may not be equally involved in conscious as well as non-conscious emotion processing.

Task Effects on Neural Activity

The extensive neural network involved in the perception of emotional body movements seems to be largely insensitive to a reduction of the visual properties of the observed moving stimulus. Nonetheless, modulatory effects regarding varying task requirements (implicit vs. explicit paradigm) can be observed.

Structures that appear to be preferentially activated during explicit emotion recognition include the pSTS and FBA (Pichon et al., 2011; Atkinson et al., 2012; Alaerts et al., 2013). For example, Alaerts et al. (2013) found that several regions, including bilateral pSTS, were activated more strongly during an explicit emotion recognition task compared to the implicit processing of emotional content during the control task. Further support stems from Atkinson et al. (2012) who directly compared an explicit emotion judgment task with a color naming control task. They also identified the pSTS as being more active during the explicit task. Thus, the STS seems to play a substantial role in the conscious perception of biological movement and dynamic emotional expressions (Pichon et al., 2008; Van den Stock et al., 2011).

Similarly, brain areas associated with mentalizing and ToM processes, such as the dmPFC, lOFC, and TPJ, responded preferentially during explicit emotion recognition (Sinke et al., 2010; Pichon et al., 2011). This may highlight that mentalizing processes are non-automatic and therefore require conscious attention.

When considering AON-related areas, the IFG also responded preferentially within explicit recognition trials across all study designs (Sinke et al., 2010; Pichon et al., 2011), whereas the PMC seemed to be equally responsive during both explicit and implicit trials. In contrast to brain structures in which activity seems to be modulated by explicit–implicit task demands, the PMC appears to be independent from attention control. This notion is underpinned in a study conducted by Van den Stock et al. (2011). They reported activity in the PMC also during conscious and non-conscious perception of emotions expressed via body movements in a patient with cortical blindsight.

Pichon et al. (2011) reasoned that especially the PMC may be involved in sustaining motor vigilance and also supporting reflexive defensive behaviors. The authors interpreted this finding as support for the view that emotions are essentially action tendencies that help the organism to adapt to environmental demands. Within this framework, recent evidence suggests that these activations more probably reflect automatic preparation for action (Pichon et al., 2008).

Two further structures are postulated to be involved in core processes of emotion recognition such as decoding affective significance and action preparation: the amygdala and the hypothalamus. Both have been shown to respond equally during attention and inattention (Pichon et al., 2011). In this regard, an interesting study on a patient suffering from cortical blindness (Van den Stock et al., 2011) investigated the neural correlates of residual visual perception for dynamic whole-body emotional actions that were presented in this patient's intact and blind visual hemifield. Activations specific for blind hemifield presentation of angry compared with neutral actions were found in subcortical areas (e.g., the amygdala), thereby showing a selective involvement of these subcortical structures in non-conscious visual emotion perception. This is underpinned by a recent review from Diano et al. (2017) suggesting that evidence tends to support an amygdala response during inattention. However, they also emphasized that the results depend strongly on the choice of paradigm. In fact, Van den Stock et al. (2011) also reasoned that the absence of significant activity in the amygdala during conscious perception of emotional movements does not necessarily mean that the amygdala is not involved in conscious processing, because standard fMRI methods might not be able to make a fine-grained distinction of the possibly different temporal profiles of activation occurring in various brain areas.

To summarize, the reviewed data show that the different cortical and subcortical areas involved in the processing of emotional body movements show a selective involvement in the explicit or implicit processing of emotional body movements.

CONCLUSION

The present review demonstrates that a variety of brain areas are involved in the perception and processing of emotional bodily expressions, indicating that the human brain is well adjusted to navigate in multiple emotional situations.

In general, it can be stated that all stimulus categories may induce an emotional percept and are associated with increased activation in a broad network of motor regions and/or in regions associated with emotional processing. It can be stated further that the emotional content of the moving stimuli matters. Thus, an emotional stimulus seems to elicit an enhanced neural response compared to a rather neutral one (Grèzes et al., 2007; Peelen et al., 2007; Pichon et al., 2008). The respective neural network seems to be organized around areas belonging to the so-called AON (PMC, IFG, and IPL), to the mentalizing network (TPJ, TP, dmPFC, and lOFC), and to areas processing body form and motion such as the EBA, FBA, and pSTS. Furthermore, emotion-processing brain sites such as the AMG and the hypothalamus seem to play an important role during the observation of emotional body expressions. For an overview of brain regions that are preferentially recruited during emotional (vs. neutral) body movements across all stimulus categories see **Supplementary Table 1**.

Regarding the different stimulus qualities, it can be concluded that both the perception and the associated neural activation pattern are partly modulated by the stimulus category in the following ways: (1) The observation of the most naturalistic full-light displays is linked to increased activation in the most extensive network including areas belonging to the AON (PMC, IFG, and IPL), the mentalizing network (TPJ, TP, dmPFC, and lOFC), body form and motion processing areas (EBA, FBA, and pSTS), and emotion-processing areas (amygdala and hypothalamus). (2) The observation of PLDs is associated specifically with increased activation in areas associated with processing motor (IPL, IFG, and PMC) and body information (EBA, FBA, and pSTS) as well as inferring mental states and intentions (dmPFC, lOFC, and TPJ). Increased amygdala activation, for example, was found only during the observation of full-light displays and avatars, indicating that the impression of animacy and body shape seems to have an increased impact on areas associated with emotional processing. Moreover, studies using PLDs and avatars did not report hypothalamus activation. This may suggest that, perhaps due to the level of abstractness or lack of realism, these stimulus categories do not elicit a preparation for possible defensive behaviors. However, this finding has to be viewed in light of the fact that all these PLD and avatar studies also used predefined ROIs for their analyses.

Regarding emotional valence, it is especially negative emotional content (such as anger or threat) that seems to be associated with increased activation of structures belonging to several networks (i.e., the STS, PMC, TPJ, dmPFC, and lOFC). This suggests that an adequate recognition as well as an adequate response to those who are angry, threatening, or dangerous may be of vital significance for self-protection and is therefore processed preferentially. Another possibility introduced by Peelen et al. (2010) is the idea that different emotions present different neural patterns, because the identified regions contain neurons that selectively represent emotion categories on an abstract level. Finally, attention matters. Whereas the PMC, the hypothalamus, and the amygdala have been shown to be equally responsive during explicit and implicit tasks, other structures, especially those associated with the mentalizing network (i.e., TPJ, dmPFC, and lOFC), respond only when participants have to judge emotional content explicitly.

However, it has to be noted that future studies need to investigate the different stimulus categories systematically within one design, because the results presented here stem from studies using a variety of designs, tasks, and statistics, and this indubitably contributes to their diversity. A further issue is that most studies used *a priori* defined search volumes. Therefore, it remains unclear whether further brain sites might process the observation and recognition of emotional body movements. Finally, the studies presented here used mostly traditional forms of fMRI data analysis that indicate only overall activity changes in brain regions in response to the observed stimuli. Newer approaches such as multivariate decoding (Haxby et al., 2001; Haynes and Rees, 2005; Kriegeskorte et al., 2008) might allow the investigation of the representational content of neuronal population codes and the identification of more distributed response patterns linked to a given stimulus. An increased usage of these methods will certainly further our understanding.

AUTHOR CONTRIBUTIONS

JB, JM, and BK contributed to the conception and design of the review. JB created and organized the database. All authors wrote the first draft of the manuscript, wrote sections and contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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Feedback-Related Electroencephalogram Oscillations of Athletes With High and Low Sports Anxiety

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We investigated the relationship between performance-related anxiety and the neural response to error feedback that was delivered during the execution of a time estimation task. Using the Sport Anxiety Scale (SAS-2), we selected university athletes high and low in sports anxiety. Participants executed a time estimation task where they were instructed to estimate 1 s by pressing a button after a sound cue. They performed this task while their performance was being evaluated by an experimenter (evaluation condition) and also while alone (in a no-evaluation condition). We tested whether feedback-related brain activities may increase in amplitude in the evaluation condition compared to the control condition – especially for athletes who report high performance-related anxiety. We focused on oscillations of sub-delta, delta, and theta frequency bands phase-locked to the feedback onset. Time-frequency analyses revealed that the magnitude of both the sub-delta component (0.3–1.2 Hz) and the theta component (4–8 Hz) were larger in incorrect than correct trials. In addition, the theta component was smaller for athletes high in sports anxiety than for athletes low in sports anxiety. The delta component was overall larger for correct than incorrect feedback. Further, athletes high in sports anxiety exhibited a larger delta component (1.5–3.5 Hz) for correct feedback in the evaluation condition than in the no-evaluation condition. Our results suggest that evaluation by others may increase the delta oscillation associated with correct feedback processing – especially among athletes high in sports anxiety.

Keywords: performance monitoring, delta oscillation, feedback-related negativity, sports anxiety, choking under pressure

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INTRODUCTION

Sport behavior is a dynamic and efficient form of action. Although elite athletes exhibit enhanced and sophisticated movements during sporting competitions, some are prone to choke under pressure (i.e., perform worse than usual) due to anxiety that occurs preceding or during an important competition (Baumeister, 1984). Indeed, we do not understand exactly why some elite athletes choke under performance pressure–and little is known about the neural basis of pressure-induced performance decrements, an understanding which might help develop improved coping techniques.

One previous study suggests that neural correlates of performance monitoring may differ among athletes who are prone to choking under pressure (Masaki et al., 2017). Masaki and colleagues focused on an event-related potential (ERP) referred to as the error-related negativity (ERN) (Falkenstein, 1990; Gehring et al., 1990). The ERN is obtained by averaging electroencephalogram (EEG) synchronized to the onset of erroneous responses, and reflects a generic neural system that implements performance monitoring (e.g., Ullsperger and von Cramon, 2001). The ERN peaks within 100 ms following the erroneous response over frontocentral regions, and is thought to be generated in the anterior cingulate cortex (ACC) (Dehaene et al., 1994). Previous studies have shown that the ERN amplitude is modulated through attentional control (e.g., Gehring et al., 1993; Tanaka et al., 2005; Ogawa et al., 2011) as well as anxious traits (Hajcak et al., 2003). Masaki et al. (2017) found that the ERN was increased among athletes high in sports anxiety when performance of a spatial Stroop task was being evaluated by an experimenter, whereas it was not increased by performance evaluation for athletes low in sports anxiety. These results were in line with previous findings that the ERN was larger when subjects' performance was being evaluated by others (Hajcak et al., 2005). Thus, sports anxious athletes may show higher ACC sensitivity to their errors during evaluation or pressure compared to when they are not being evaluated.

In tasks such as the spatial Stroop, participants are aware when they make mistakes. However, in some tasks, participants must utilize performance feedback to determine whether a response was correct. Previous studies have confirmed that processing of external feedback can be examined by the feedback-related negativity (FRN) that is elicited by incorrect feedback (Miltner et al., 1997). In the current study, we sought to investigate whether feedback processing is influenced by performance evaluation in anxious athletes. To our knowledge, no study has tested the relationship between feedback-related processing and sports anxiety that may relate to choking under pressure.

Given that the ERN and the FRN share apparent similar function and may rely on common ACC activity (Miltner et al., 1997; Gehring and Willoughby, 2002; Holroyd and Coles, 2002), it is reasonable to presume that the feedback-related brain activities would increase for individuals high in performance-related anxiety in an evaluation situation. Thus, we predicted that the feedback-related brain activities that include the FRN as well as other feedback-elicited positivities would be enhanced during the evaluation condition compared to the no-evaluation condition for athletes who are prone to choke under pressure.

In terms of frequency-band characteristics of feedback-related neural activity, theta frequency is increased following negative feedback, whereas the delta frequency band is increased following positive feedback (Bernat et al., 2008, 2011; Nelson et al., 2011; Foti et al., 2015). To examine feedback-related processing, we focused on oscillations of delta and theta frequency phase-locked to feedback onset, because these phase-locked oscillations can isolate error- and correct-related cognitive activities from other activities (Yordanova and Kolev, 2004; Yordanova et al., 2004). In this study, we applied time-frequency (TF) analysis to feedback-elicited EEG by focusing on three different frequency bands (i.e., 4–8 Hz theta, 1.5–3.5 Hz delta, and 0.3–1.2 Hz sub-delta) according to a previous study (Yordanova and Kolev, 2004). This allowed us to investigate individual components of feedback-related activities consisting of FRN in the theta frequency band, and both P300 and reward positivity (RewP) (Baker and Holroyd, 2011; Proudfit, 2015) in the delta frequency band, and slow wave or the late positive potential (LPP) that is modulated by outcome valence (Pornpattananangkul and Nusslock, 2015; Donaldson et al., 2016) in the sub-delta frequency band. We predicted that activity in these frequency bands would all be increased during evaluation compared to no evaluation condition for athletes who are prone to choke under pressure (i.e., both correct and incorrect feedback to be more salient among athletes high in sports anxiety).

To this end, we selected university athletes high in sports anxiety and low in sports anxiety using the Sport Anxiety Scale (SAS-2). All participants completed a time estimation task wherein participants estimate 1 s by a button press and receive feedback after each trial; this task was completed while performance was being evaluated by an experimenter and also during a control (i.e., no evaluation) condition. Thus, we tested whether individual frequency bands (i.e., theta, delta, and sub-delta) would be enhanced for athletes high in sports anxiety, as a function of performance evaluation.

MATERIALS AND METHODS

Participants

Two hundred sixteen undergraduate athletes from the Faculty of Sport Sciences in Waseda University completed the Sport Anxiety Scale (SAS-2), which assesses the competitive trait anxiety of athletes. We invited those students who scored above 34 (higher sport anxiety) and below 20 (lower sport anxiety) to participate in a laboratory experiment[1]. These criteria were determined on the basis of ± 1 standard deviation (SD) from the mean total SAS-2 score (*M*: 27.2, *SD*: 7.1). Consequently, 16 individuals with higher sports anxiety (7 females, mean age ± *SD* = 20.6 ± 1.26; SAS-2 range: 34–52) and 16 with lower sports anxiety (8 females, mean age ± *SD* = 21.1 ± 2.28; SAS-2 range: 15–20) participated in this study. A *t*-test comparing SAS-2 scores between individuals with higher (*M*: 37.4, *SEM*: 1.08) and lower sport anxiety (*M*: 17.4, *SEM*: 0.43) confirmed the difference between the two groups [$t(30) = 17.2, p < 0.0001, d = 6.09$].

Participants had normal or corrected-to-normal vision and were paid 3,200 yen (about 26 USD) for their participation. All participants gave written informed consent prior to the experiment. This study was approved by the Waseda University Ethics Committee.

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[1] We also recorded ERNs of these participants in a spatial Stroop task and reported the results in Masaki et al. (2017). It should be noted that participants tested in this study were not identical to the previous report (4 participants were excluded in Masaki et al., 2017 because of fewer response errors and artifact-contaminated trials).

Time Estimation Task

Participants performed a time estimation task where they were instructed to estimate 1 s by pressing a mouse button after the presentation of the sound cue (1,000 Hz, 65 dB, 200 ms duration) (**Figure 1**). Each trial began with a gray fixation cross that remained on the screen until feedback presentation. The sound cue was presented 2,500 ms after the onset of the fixation cross. Participants were asked to press the button with the right index finger whenever they thought 1 s elapsed following the sound cue. On each trial, visual feedback was either a smiley face (for correct response) or sad face (for incorrect response), and was presented at the center of the monitor to inform the participant of the outcome 1,200 ms after their estimation response. The visual angle and duration of the feedback was 3.8° × 3.6°and 1,500 ms, respectively. Estimation within the correct time range (i.e., 900–1,100 ms) at the beginning of the task was defined as a correct response. The correct range was expanded 20 ms when the previous trial was incorrect or shortened 20 ms when the previous trial was correct, which produced a total correct response rate of ∼50%. Although participants were paid for their participation, neither monetary reward nor punishment was contingent upon their individual performance.

Participants performed the task in two conditions. In the evaluation condition, the research assistant was behind the participant and pretended to evaluate the performance of the participant. In the no-evaluation condition, participants were left alone in a room to perform the task alone. Each condition consisted of two blocks (30 trials/block). The order of conditions was counter-balanced across participants using either ABBA or BAAB sequence.

Physiological Recordings

We recorded the electroencephalogram (EEG) from 128 scalp sites according to the Biosemi electrode coordinates (Biosemi Inc., Amsterdam, Netherlands). Participants wore a nylon mesh cap, in which Ag/AgCl electrodes were embedded. We also recorded the horizontal electrooculograms (HEOG) from the left and right outer canthi and the vertical electrooculograms (VEOG) from above and below the left eye. All these physiological indices were recorded with a bandwidth of DC to 205 Hz using the Biosemi Active Two system (Biosemi Inc., Amsterdam, Netherlands), which amplifies EEG signals via active electrodes. Both EEG and EOGs were digitized at a rate of 1,024 Hz and offsets were kept below 20, which is consistent with other studies using the Biosemi system.

Data Analysis

Event-Related Potential Analysis

Off-line preprocessing of EEG data was performed using the Brain Vision Analyzer 2 (Brain Products, Gilching, Germany). The EEG was re-referenced to the average activity from all 128 scalp electrodes. After down-sampling to 256 Hz, long epochs of 8,000 ms total (i.e., from 4,000 ms prior to and 4,000 ms after feedback onset) were extracted. For ERP averaging, the EEG was band-pass filtered with 0.1–30 Hz (roll-off: 24 dB/octave). Ocular-movement artifacts were corrected using the algorithm described by Gratton et al. (1983) and epochs in which EEG variations exceeded ± 75 μV were rejected from further analysis. Segmented EEG data were averaged, pooling four frontocentral electrodes (C11, C22, C23, and C24 Biosemi coordinates) including FCz. Baselines were corrected using a the time window of 100 ms prior to the feedback onset. The ERPs were measured as the mean amplitude within the time window of 100 ms, from 230 to 330 ms after the feedback onset.

Time-Frequency Analysis

For the TF analysis, the same procedures as the FRN analysis was conducted except that the EEG was band-pass filtered with 0.01–30 Hz (roll-off: 24 dB/octave). After the ocular-correction and artifact-rejection, segmented EEG data were exported for the follow-up TF analysis that was conducted using MATLAB R2012a (MathWorks, Inc., Natick, MA, United States). Based on Yordanova and Kolev (2004), we focused on three different frequency bands (sub-delta: 0.3–1.2 Hz, delta: 1.5–3.5 Hz, and theta: 4.0–8.0 Hz) using the continuous Morlet wavelet transform with a resolution of 0.1 Hz, ranging from 0.1 to 13 Hz. The TF analysis was applied to the averaged current source density (CSD) segments (Yordanova and Kolev, 2004) at the FCz of each participant. Mean amplitudes in a time window of 100 ms prior to the feedback onset were used as a baseline. TF components of theta bands were measured as mean amplitudes within the time window of 100 ms between a time point of 230 and 330 ms after the feedback onset. This time window corresponded to when the FRN was elicited in the current study. The TF activity of the sub-delta band was measured as the mean amplitude within the time window of 250 ms, from 200 to 450 ms after the feedback onset. The TF activity of the delta band was measured as the mean amplitude within time window of 200 ms, from 130 to 330 ms after the feedback onset.

The mean amplitudes of ERPs and each TF component were subjected to a mixed three-way analysis of variance (ANOVA) with the between-subjects factor of group (high/low in sports anxiety) and within-subjects factors of condition (evaluation/no-evaluation) and correctness (correct/incorrect feedback).

RESULTS

Performance

The mean correct rate was 54% (SEM = 1.9) in the evaluation condition and 53% (SEM = 1.5) in the no-evaluation condition for athletes high in sport anxiety, and 54% (SEM = 1.2) in the evaluation condition and 55% (SEM = 1.3) in the no-evaluation condition for athletes low in sport anxiety. As expected, the correct rate was approximately 50% for both groups. It did not differ between the evaluation and the no-evaluation conditions for either group (t's ≤ 0.92, p's ≥ 0.37, d's ≤ 0.24). No interaction was found [$F(1,30) = 1.06$, $p = 0.31$, $\eta_p^2 = 0.03$].

Feedback-Related Brain Activities

Event-Related Potential

Figure 2 depicts ERP waveforms of the feedback-elicited potentials, showing larger negative deflections (i.e., FRN)

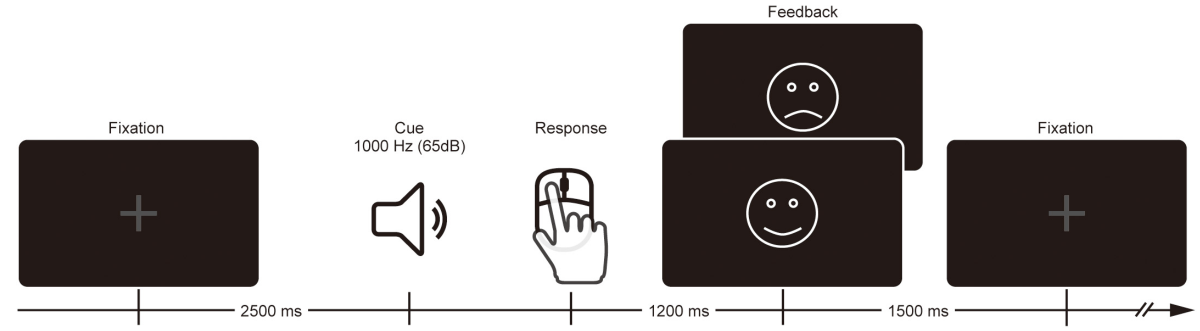

FIGURE 1 | Schematic illustration of the procedure.

at approximately 250 ms following incorrect feedback. A three-way ANOVA confirmed larger negative deflections for incorrect feedback than for correct feedback [$F(1,30) = 71.15$, $p < 0.001$, $\eta_p^2 = 0.70$]. Furthermore, a three-way interaction of Group × Correctness × Condition was significant [$F(1,30) = 4.58$, $p = 0.041$, $\eta_p^2 = 0.13$] (**Figure 3**). *Post-hoc* tests showed that FRN amplitude for incorrect feedback was more negative in the no-evaluation condition than in the evaluation condition among athletes low in sport anxiety [$t(15) = 2.22$, $p = 0.042$, $d = 0.24$]. It did not differ between two conditions among athletes high in sport anxiety [$t(15) = 0.25$, $p = 0.81$, $d = 0.04$]. In the evaluation condition, ERP amplitudes for correct feedback tended to be more negative for athletes low in sports anxiety than those high in sports anxiety [$t(30) = 1.83$,

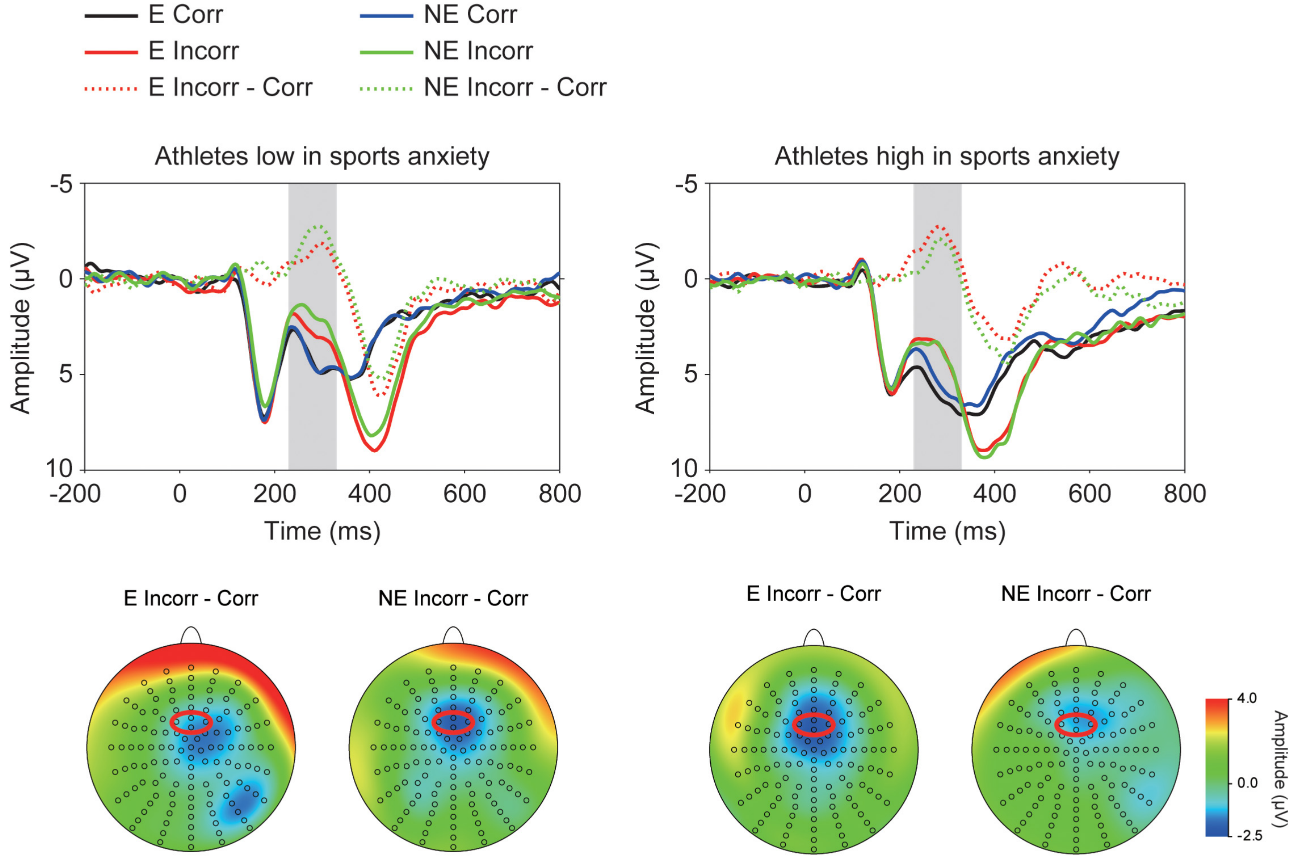

FIGURE 2 | Grand-averaged waveforms of the feedback-elicited potentials for athletes high and low in sports anxiety and their topographies. The waveforms were derived from frontocentral regions that are indicated by a red circle (pooled electrodes) on the topographical maps. E: the evaluation condition, NE: the no-evaluation condition, Corr.: correct feedback, and Incorr.: incorrect feedback.

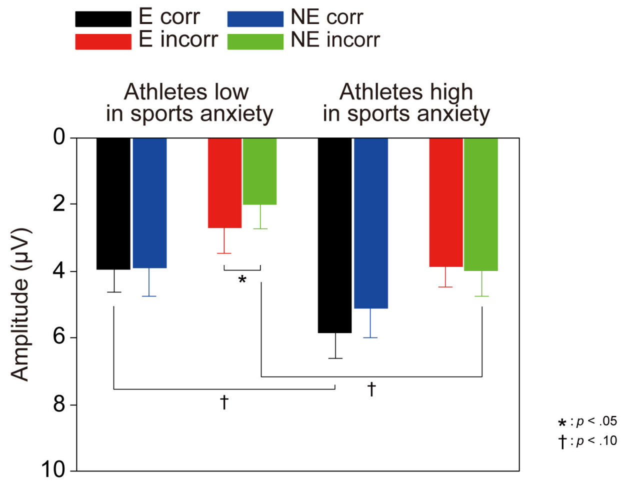

FIGURE 3 | Mean amplitudes of ERPs elicited by feedback signals. Error bars represent SEM.

$p = 0.076$, $d = 0.65$]. In the no-evaluation condition, FRN amplitudes for incorrect feedback tended to be more negative for athletes low in sports anxiety than those high in sports anxiety [$t(30) = 1.88$, $p = 0.070$, $d = 0.66$].

Current Source Density Derivation

Figure 4 (upper panel) illustrates CSD waveforms of the feedback-elicited potentials at FCz. The CSD transform was separately conducted prior to TF analysis. We applied the same three-way ANOVA to the CSD data as was done to the FRN. It only revealed a main effect of correctness, indicating larger negative deflections for incorrect feedback than for correct feedback [$F(1,30) = 33.09$, $p < 0.001$, $\eta_p^2 = 0.52$]. Neither the main effect of condition nor the interaction between condition and group was significant.

Time-Frequency Analysis

Figure 4 (lower panel) shows TF representations of the feedback-locked activities and suggest stronger activity in both the theta and sub-delta frequencies for incorrect feedback than for correct feedback, as well as increased delta frequency for correct feedback than for incorrect feedback. The TF plots of the feedback-locked activities also show larger activities of the theta frequency band (4–8 Hz) for incorrect feedback especially among athletes with low anxiety.

Figure 5 shows the grand averaged TF components of each frequency band at FCz. The sub-delta frequency band appears to represent the slow wave or the LPP that emerged about 300 ms after the feedback onset. A three-way ANOVA revealed a significant main effect of correctness, confirming larger

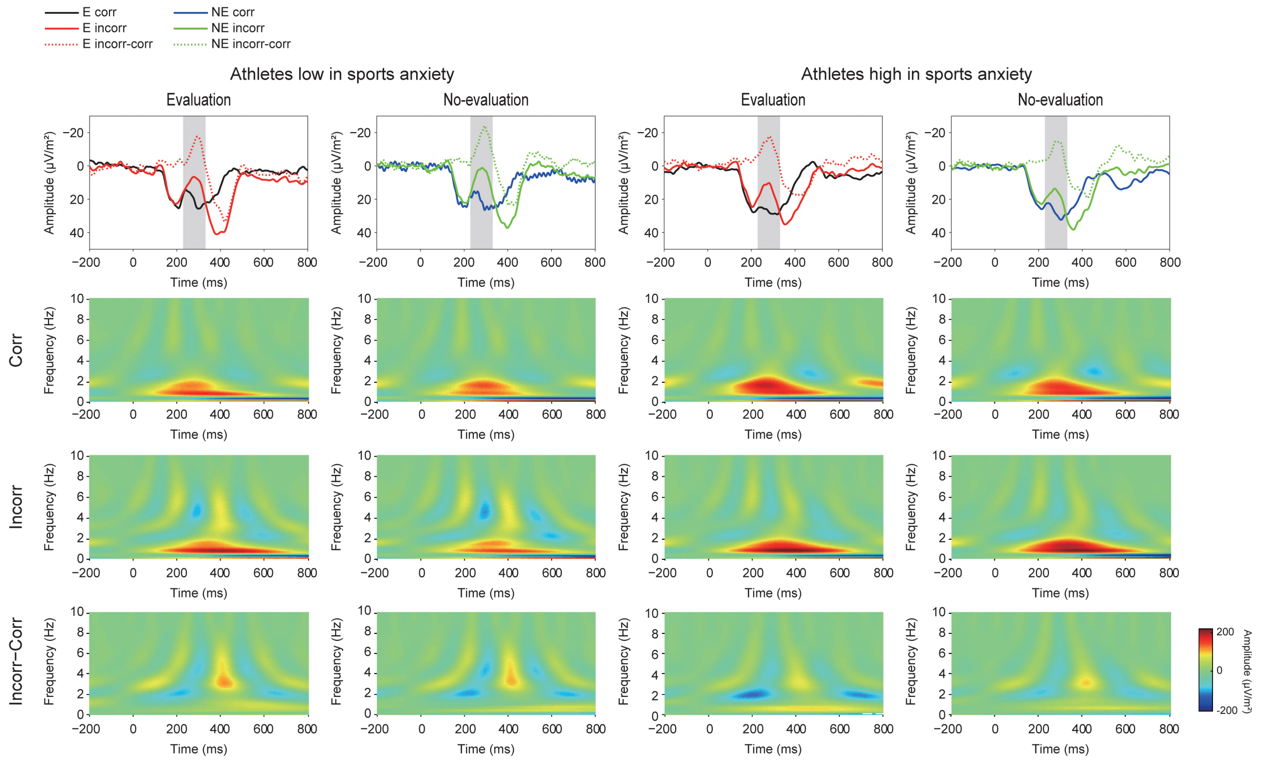

FIGURE 4 | Grand averaged Current Source Density (CSD) waveforms (upper panel) (E: the evaluation condition, NE: the no-evaluation condition, Corr.: correct feedback, and Incorr.: incorrect feedback). In the CSD waveforms, black and red lines represent correct and incorrect trials in the evaluation condition, respectively. Blue and green lines represent correct and incorrect trials in the no-evaluation condition, respectively. Lower panels show Time-Frequency plots of feedback-locked activities. The two left columns represent athletes low in sport anxiety and the two right columns represent athletes high in sports anxiety.

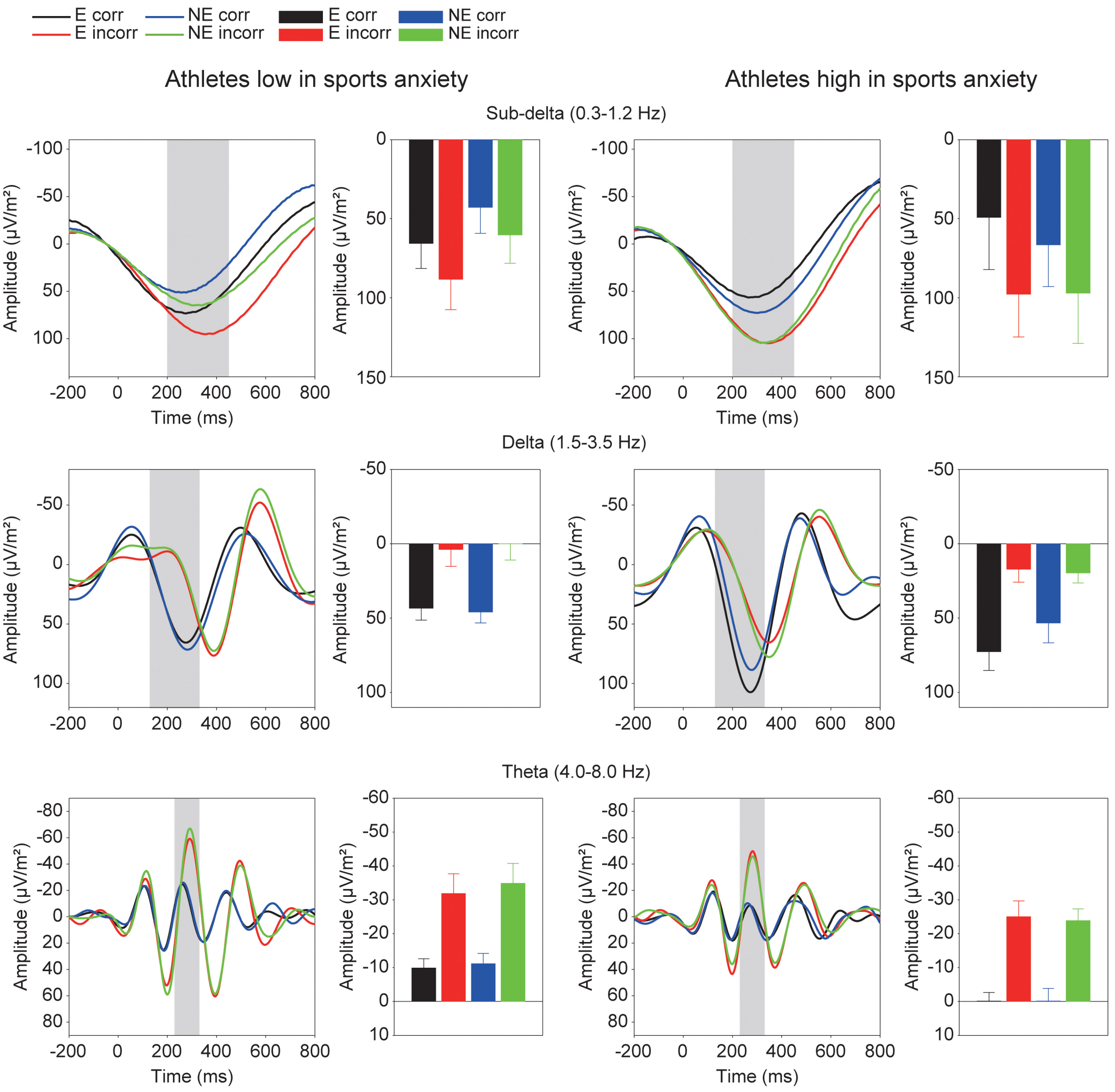

FIGURE 5 | Time-frequency components (sub-delta, delta, and theta) and mean amplitudes of these components in each condition. The two left columns represent athletes low in sport anxiety and the two right columns represent athletes high in sport anxiety (E: the evaluation condition, NE: the no-evaluation condition, Corr.: correct feedback, and Incorr.: incorrect feedback).

slow waves for incorrect feedback than for correct feedback [$F(1,30) = 9.86$, $p = 0.004$, $\eta_p^2 = 0.25$]. Neither main effect of condition [$F(1,30) = 0.78$, $p = 0.39$, $\eta_p^2 = 0.03$] nor group difference [$F(1,30) = 0.19$, $p = 0.67$, $\eta_p^2 = 0.01$] was found. No interactions were found (*F's* < 1.05).

For the delta frequency band, a three-way ANOVA revealed that delta activation was larger for correct than incorrect feedback signal [$F(1,30) = 58.85$, $p < 0.001$, $\eta_p^2 = 0.66$]. Furthermore, the three-way interaction of Group × Correctness × Condition was marginally significant [$F(1,30) = 2.97$, $p = 0.095$, $\eta_p^2 = 0.09$]. *Post-hoc* tests revealed that athletes high in sports anxiety had increased delta band activity for correct feedback in the evaluation compared to no-evaluation condition [$t(15) = 2.28$, $p = 0.038$, $d = 0.37$], and tended to show a more positive delta band activity for correct feedback in the evaluation condition compared to athletes low in sports anxiety [$t(30) = 1.95$, $p = 0.061$, $d = 0.69$].

For the theta frequency band, both groups showed larger oscillations for incorrect than correct feedback signal that was supported by a main effect of correctness [$F(1,30) = 54.04$, $p < 0.0001$, $\eta_p^2 = 0.64$]. In addition, the amplitude of the oscillation was larger among athletes low in sports anxiety than those high in sports anxiety [$F(1,30) = 4.83$, $p = 0.036$, $\eta_p^2 = 0.14$].[2]

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[2] We conducted an additional analysis in the same way as other studies (e.g., Foti et al., 2015; Proudfit, 2015) where the sub-delta frequency band (0.3–1.2 Hz) was combined with the delta frequency band. **Figure 6** shows the delta activity (<3.5 Hz) without decomposition. Mean amplitudes of the delta frequency band were scored within a time window of 200 ms (ranging from 130 to 330 ms following

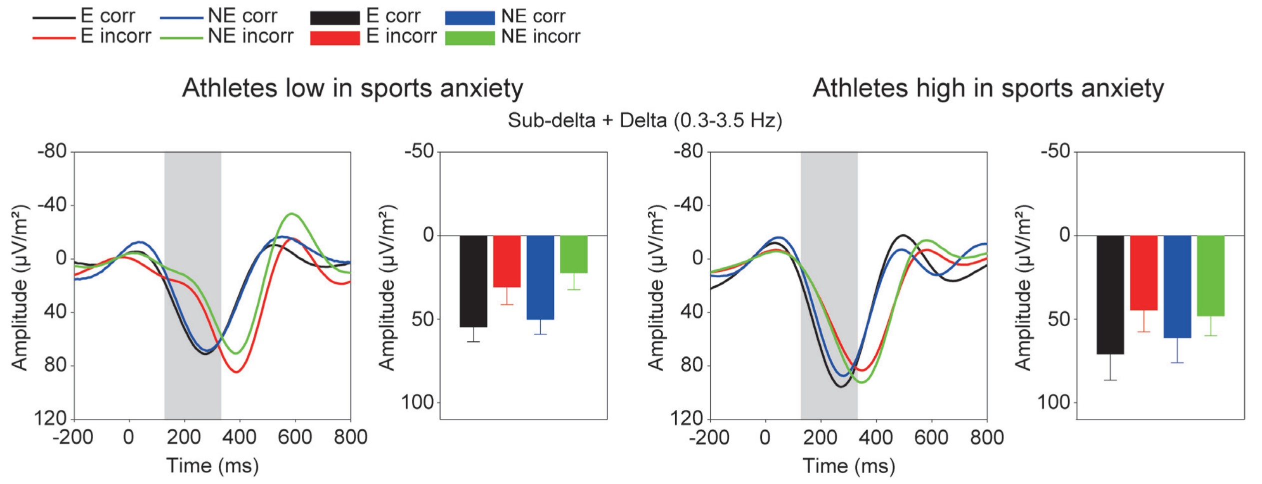

FIGURE 6 | Time-frequency component (0.3–3.5 Hz). See details in Footnote 2.

DISCUSSION

We examined the relationship between sports anxiety and neural responses to feedback signals in a time estimation task while performance was being evaluated and in a control condition. Across these conditions, we compared feedback-locked oscillations as well as ERP waveforms between athletes with high and low sports anxiety. Although ERP amplitudes were not modulated by evaluation in athletes with high sports anxiety, their decomposed delta band component for correct feedback was enhanced by evaluation. On the other hand, both the sub-delta and the theta frequency bands were associated with the correct/incorrect status (i.e., enhancement for incorrect feedback), but not associated with evaluation. For the theta frequency band, the amplitude was also larger among athletes low in sports anxiety than those high in sports anxiety.

Previous studies of the ERN found that performance evaluation potentiated the ERN among more socially anxious participants (Hajcak et al., 2005; Barker et al., 2015; Masaki et al., 2017). Contrary to our prediction, the FRN was not potentiated by evaluation in our study. Instead, a reduced FRN amplitude was observed in the evaluation condition for athletes with low sports anxiety. According to a recent assertion, both the ERN and FRN may increase in amplitude, reflecting the demands of attentional control (van Noordt et al., 2015, 2016, 2017). Thus, it is plausible that athletes who demonstrate low levels of sports anxiety were better able to avoid distraction in the evaluation condition resulting in a reduced FRN amplitude whereas highly anxious athletes failed to efficiently control their attention to feedback under evaluation.

The null effect of evaluation on the FRN among athletes with high sports anxiety might be due to the different tasks adopted in ERN and FRN studies. Masaki et al. (2017) used a spatial Stroop task where participants monitored their own responses that relied on inhibitory control in incongruent trials to avoid errors. The participants did not require a skilled motor control for the button press, because the task demands primarily relied on temporal perception. Furthermore, feedback information about outcomes was more important to improve performance in the current study.

Beilock and Carr (2001) asserted that attentional control may shift from external to internal attention while performance is being evaluated, impairing automaticity of movements. Thus, the inward attention is thought to be responsible for choking under pressure. In the time estimation task, however, the participants might have paid attention to feedback instead of attending inward even while their performance was being evaluated, because they had to know outcomes via external feedback. It is plausible that the difference in attentional control resulted in the null effect of evaluation on the FRN in the time estimation task.

On the other hand, the TF analysis provided perspectives different from the ERP results and a more direct way to isolate individual brain activities compared to traditional ERP methods. Athletes high in sports anxiety showed increased power in the delta frequency band (i.e., 1.5–3.5 Hz) for correct feedback than incorrect feedback in the evaluation condition. Contrary to our predictions, the impact of evaluation on feedback-related brain activities only affected the delta frequency band. In terms of differentiation of function, processing of incorrect feedback was represented in both the sub-delta (i.e., 0.3–1.2 Hz) and theta (i.e., 4–8 Hz) frequency bands; both components were enhanced for incorrect compared to correct feedback. Thus, it should be emphasized that athletes high in sports anxiety showed an evaluation effect for correct feedback only in the delta frequency band, but not in other frequency bands. In addition, analyses combining the delta and sub-delta frequency bands did not show any evaluation effect, suggesting that the error-specific sub-delta band activity may have obfuscated the impact of evaluation.

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the feedback). A 3-way ANOVA revealed that the amplitude of the delta frequency band was increased for correct response [$F(1,30) = 43.36$, $p < 0.0001$, $\eta_p^2 = 0.59$]. However, neither an interaction of Correctness × Group [$F(1,30) = 0.81$, $p = 0.37$, $\eta_p^2 = 0.03$] nor an interaction of Correctness × Group × Condition [$F(1,30) = 1.96$, $p = 0.17$, $\eta_p^2 = 0.06$] was obtained.

According to previous studies (Foti et al., 2015; Proudfit, 2015), it is reasonable to assume that the delta frequency band may include both P300 and RewP. As Proudfit (2015) proposed, the RewP may contribute to the feedback-related potentials over frontocentral regions more than P300. The RewP is attenuated (Foti and Hajcak, 2009; Foti et al., 2015) or even eliminated (Foti et al., 2011; Proudfit, 2015) when the outcome is bad, and as a result the FRN emerges. Although monetary reward was not contingent upon correct performance in our study, it is possible that success in the task provided participants with intrinsic reward especially in the evaluation condition, which might have elicited the RewP. Therefore, the enhanced delta activity in the evaluation condition might be a characteristic of athletes with high sports anxiety– they may be more sensitive to positive feedback under performance evaluation. A previous study of the ERN suggested that frequent presentation of feedback may have helped participants feel at ease, eliminating the relationship between anxiety and the ERN amplitude (Olvet and Hajcak, 2009). On the other hand, athletes low in sports anxiety did not show any enhanced delta activities for correct feedback, irrespective of evaluation. It is likely that neural response to correct feedback is not enhanced for athletes low in anxiety, because correct outcomes might not be an intrinsic reward for them.

It is well known that P300 amplitude represents the amount of attentional resources allocated to a given stimulus (Johnson, 1986). Given that the delta frequency band also includes P300 (Bernat et al., 2008, 2011; Foti et al., 2015), the present results suggest that athletes high in sports anxiety allocated attentional resources more to correct feedback in the evaluation than no-evaluation condition. This suggests that observation by others may exclusively influence feedback processing among athletes with high anxiety. However, the attentional resource might have been equally allocated to both correct and incorrect feedback processing among athletes low in sports anxiety.

Using TF analyses, Yordanova and Kolev (2004) extracted error-specific oscillations in the 1.5–3.5 Hz frequency window (delta) from multiple frequency components. They also found that the theta frequency oscillation occurred both for error and correct responses. They referred to the error-specific delta oscillation as performance monitoring system and referred to the theta oscillation as the movement monitoring system. Rather, we found correct-specific delta oscillations, that we did find error-specific sub-delta oscillation. This is not consistent with the assertion of Yordanova and Kolev (2004) that the sub-delta oscillation merely represents movement-related activities. On the other hand, we also found similar activities of the feedback-locked theta oscillation even when movement monitoring was not needed (i.e., feedback processing). That is, theta oscillation was enhanced for incorrect feedback. Thus, the feedback-locked theta frequency band may represent a more general process of outcome processing than movement monitoring.

We should also point out a limitation in our study. The three-way interaction among Group, Correctness, and Condition was marginally significant, probably due to the small sample size. Thus, further research is needed to test the delta frequency band in a larger sample of participants in order to rule out the possibility of Type I error.

Finally, in accordance with a previous report (Masaki et al., 2017), we also found that athletes low in sports anxiety were characterized by larger neural activities in the theta band than athletes with high sports anxiety irrespective of evaluation; The theta oscillations were larger for athletes low in sports anxiety than for those high in sports anxiety. These suggest that athletes with low levels of anxiety may have a distinct performance monitoring system that properly detects erroneous events. Given that lower sports anxiety results in better performance during a stressful sporting game, athletes low in sports anxiety might also have an advantage in motor skill acquisition that is consistent with a recent notion of performance monitoring during motor learning (Masaki and Sommer, 2012).

In sum, in terms of error processing, both the sub-delta and the theta frequency bands may differentiate incorrect and correct feedback activities. We found an evaluation effect on correct-feedback processing in the delta frequency band among athletes high in sports anxiety, although we did not find any evaluation effect in ERPs. This led us to conclude that decomposition of the feedback-locked activities using the TF analysis is a powerful method to reveal a small effect that is embedded in ERPs.

AUTHOR CONTRIBUTIONS

GH and HM designed the experiments. GH, YM, DF, and HM performed the experiments. TH and HM analyzed the data. HM, GH, YM, DF, and TH interpreted the data and wrote the paper. All authors have made direct contribution to the work and approved it for publication.

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Effects of Relaxing and Arousing Music during Imagery Training on Dart-Throwing Performance, Physiological Arousal Indices, and Competitive State Anxiety

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Music that is carefully selected to match the requirements of activities and the characteristics of individuals has been shown to produce significant impacts on performance enhancement (Priest et al., 2004). There is also evidence that music can enhance imagery (Grocke and Wigram, 2007), although few studies have investigated the effects of music on imagery in the context of sport skills. In the present study, the effects of relaxing and arousing music during imagery on dart-throwing performance, physiological arousal indices, and competitive state anxiety, were investigated among 63 novice dart throwers. Participants had moderate-to-high imagery ability and were randomly assigned to unfamiliar relaxing music (URM), unfamiliar arousing music (UAM), or no music (NM) groups. Performance was assessed by 40 dart throws at a concentric circles dartboard before and after 12 imagery sessions over 4 weeks. Measures of galvanic skin response (GSR), peripheral temperature (PT), and heart rate (HR) were taken during imagery sessions 1 and 12, and the Competitive State Anxiety Inventory-2 Revised (CSAI-2R) was administered prior to the pre- and post-intervention performance task. Dart-throwing gain scores were significantly higher for URM than for UAM and NM, with no significant difference between UAM and NM (URM = 37.24 ± 5.66, UAM = 17.57 ± 5.30, and NM = 13.19 ± 6.14, $F_{2,62} = 5.03$, $p = 0.01$, $\eta^2 = 0.14$). GSR, PT, and HR reflected lower arousal for URM than for UAM or NM. Significant decreases in somatic anxiety were evident for URM and UAM but not NM. Significant decreases in cognitive anxiety were evident for URM and NM but not UAM. Significant increases in self-confidence were evident for URM but not UAM or NM. Performance improved in all three conditions but URM was associated with the largest performance gain, the lowest physiological indices of arousal, and the most positive CSAI-2R profiles. Listening to relaxing music during imagery may have benefits for performance in other fine motor skills.

Keywords: physiological arousal, relaxing music, arousing music, imagery, fine-motor skill performance

INTRODUCTION

Imagery techniques have been acclaimed as a "central pillar of applied sport psychology" and are included in almost all psychological skills training programs for athletes (Perry and Morris, 1995, p. 339). Imagery has been defined as "the creation or re-creation of an experience generated from memorial information, involving quasi-sensorial, quasi-perceptual and quasi-affective characteristics, that is under the volitional control of the imager, and which may occur in the absence of the real stimulus antecedents normally associated with the actual experience" (Morris et al., 2005, p. 19).

Athletes report using imagery techniques for varied purposes, including learning and practicing skills, during pre-performance routines and game planning strategies, for previews and reviews of performance, for mental warm-ups and the development of psychological skills, for problem solving and stress management, for increasing concentration and confidence levels, and during injury rehabilitation (Morris et al., 2005; Strachan and Munroe-Chandler, 2006). Researchers have investigated several different aspects of imagery use in sport, including imagery objectives, types of imagery, measurement of imagery ability, psychophysiological factors, and performance enhancement imagery (Collins and Hale, 1997; Hall et al., 1998; Hall, 2001; Watt et al., 2004). Despite these extensive research efforts, understanding optimal imagery use in sport remains a challenge, requiring further investigations aimed at deriving greater benefit from imagery training. This represents a gap in imagery research that is yet to be examined comprehensively.

Music plays an influential role in many sports, being integral to performance in gymnastics, synchronized swimming, and ice dancing, or is used for motivational and entertainment purposes, to elicit patriotism and pride, and enhance the psychological state and performance of athletes (Terry and Karageorghis, 2011). Demonstrated benefits of music in sport and exercise include arousal control, enhanced affective states, lowered perceived exertion, improved performance, and greater physiological efficiency (Boutcher and Trenske, 1990; Terry et al., 2012; Bood et al., 2013; Hutchinson and Karageorghis, 2013). Music can clearly influence perceived relaxation and excitation levels, and its influence on physiological indicators, such as galvanic skin response (GSR), peripheral temperature (PT), and heart rate (HR), is also well established (Burns et al., 1999; Lundqvist et al., 2009; Salimpoor et al., 2009, 2011; Kuan et al., 2017).

Very few studies have investigated use of imagery accompanied by music as a way to enhance sports performance. Karageorghis and Lee (2001) compared the effects of motivational music, imagery, and a combination of both on an isometric muscular endurance task that required participants to maintain dumbbells in a cruciform position. The combination of music and imagery yielded greater endurance than music or imagery alone, although it was unclear if music and imagery interacted in some way to produce an ergogenic effect, or if enhanced endurance was due to the summation of the motivational impact of the music and the motivational impact of the imagery. Pain et al. (2011) examined the effectiveness of personalized pre-performance music and imagery scripts in facilitating flow states and performance. Results indicated that the use of asynchronous music and imagery when combined showed facilitative effects on flow and perceived performance. Kuan et al. (2017) investigated the effect of unfamiliar relaxing and arousing music during imagery on physiological and subjectively perceived arousal of elite shooters. Results showed that music used during imagery helped to manipulate arousal in the required direction, and also that researcher-selected musical excerpts were at least as effective for arousal control as participant-selected excerpts. Despite the burgeoning literature on the impact of music on sports performance, there is still little research on the potential of music to enhance the effectiveness of imagery and its consequential influence on athletic performance. Given the widespread use of imagery training by athletes to enhance performance, the paucity of research on the potential of music to enhance imagery effectiveness represents a significant gap in knowledge.

Terry et al. (2014) identified more than 80 studies investigating effects of music on sports performance. However, most of those studies focused on exploiting the motivational qualities of music, and there is little research investigating the effect of music on performance via use of imagery training, or investigating the characteristics of music associated with changes to physiological arousal. It is important for the development of optimal imagery training programs that the impact of music is investigated when imagery training is temporally distanced from performance. In the small number of studies investigating effects of music and imagery in sport (e.g., Osborne, 1981; Dorney et al., 1992), performance was assessed directly after completing imagery with music, whereas athletes more typically use imagery techniques (with or without music) over a period of time in the build up to competitions (Terry and Karageorghis, 2011). A more ecologically valid approach would be for participants to practice imagery with music on a number of occasions over an extended period, with the impact on performance assessed at a later time.

In the present study, we investigated the effects of unfamiliar relaxing and arousing music to augment imagery training, on dart-throwing performance, physiological indicators of arousal, and self-reported competitive state anxiety. Dart-throwing was selected to evaluate performance because it is a self-paced, closed skill involving fine muscle control, and hence is not influenced by time pressure, the involvement of an opponent, or physical exertion. Such task characteristics minimize extraneous effects on arousal, making it easier to detect physiological changes in arousal due to the effects of music. Recently, Kuan et al. (2017) tested the psycho-physiological effects of music on skilled shooters during imagery. Results for GSR, PT, and electromyography measures showed that unfamiliar relaxing music (URM) was most relaxing and unfamiliar arousing music (UAM) was most arousing. Based on the findings of Kuan et al. (2017), it was hypothesized (a) that imagery training would have a positive effect on performance for all music conditions, (b) the performance effect for relaxing music would be greater than for arousing music and no music (NM), and (c) that relaxing music would be associated with lower physiological indicators of arousal, lower somatic and cognitive anxiety, and higher self-confidence than arousing music and NM.

MATERIALS AND METHODS

Participants

Participants were 63 novice dart throwers (45 males, 18 females) aged 18–25 years (*M* = 20.21 years, *SD* = 3.20 years), recruited from students of sport and exercise science or physical education at a university in Melbourne, Australia. Participants had a minimum of one year's experience playing sports that included Australian football, basketball, cricket, handball, netball, soccer, softball, swimming, taekwondo, tennis, track running, or volleyball. Four potential participants reported they had competitive dart-throwing experience and were excluded from the study. Females participated during their late luteal phase (i.e., around the 25th day of the menstrual cycle) to minimize psycho-physiological variations induced by hormonal changes. All participants reported their hearing as normal. Sample size was determined, based on a mixed design ANOVA, by using G*Power 3.1.7. With an hypothesized effect size of 0.40, alpha of 0.05, power of 0.85, three groups, and two measurement occasions, the estimated sample size was 57. After adding the estimated drop-out rate of 10%, we required a total sample size of 63, with 21 participants in each condition.

Measures and Materials

Demographic Information

Demographic information was collected about current participation in sport and/or physical activity; previous experience in sport, competition, and dart-throwing; sport imagery experience; and hearing ability.

Sport Imagery Ability Measure (SIAM; Watt et al., 2004)

The SIAM assesses imagery ability in sport by having athletes imagine four generic sport scenes for 60 s each; namely, the home venue, a successful competition, a slow start, and a training session. Following imagery of each scene, athletes respond to 12 items with reference to that scene by placing a cross on a 100-mm analog scale. The 12 imagery ability items cover five imagery dimensions (control, vividness, ease, speed of generation, duration), and six sensory modalities (kinaesthetic, tactile, visual, auditory, olfactory, and gustatory). In addition, one item assesses imagery of emotion experienced during each scene. The 12 subscales appear in different orders for each scene to minimize order effects. During its validation process, the SIAM demonstrated Cronbach's alpha coefficients between 0.66 and 0.87 (Watt et al., 2004). We used the SIAM to ensure that participants had at least moderate imagery ability, to enable them to perform the dart-throwing imagery task. We asked participants to imagine their primary sport, rather than dart-throwing when completing the SIAM.

Imagery Script

A pre-recorded dart-throwing imagery script was developed and tested during a pilot phase of the study. The imagery script was checked for authenticity by two experienced darts players and minor changes implemented based on their feedback. The imagery script focused on the performance task, including feeling the weight of the dart, gripping the dart, looking at the bullseye, imaging the distance to the target and the height of the target from the floor, and releasing the dart accurately when ready. The imagery script also focused participants on the feeling in their arm muscles, the sensation of movement of the arm, and the need to keep their body still and stable as they threw. The script included instructions to picture successful performance with their darts hitting close to the bullseye, a strategy shown previously to build confidence leading to enhanced performance (Morris et al., 2005). Imagery training consisted of 12 sessions with an approximate duration of 9 min per session. Participants paced their own imagery and no instructions were provided about the frequency of imaging the dart throws.

Log of Imagery Sessions

Participants completed an adherence log to monitor the date, time, and duration of each imagery session, and added comments about their imagery experiences, such as how well they were able to concentrate and the emotions experienced. Completing the log provided an opportunity for participants to note changes in their experience over time and to comment on how strongly and vividly they experienced the music and imagery of dart-throwing. We established exclusion criteria, whereby participants with uncompleted logs and those who had missed more than two imagery sessions would be dropped from the main analysis. No participant met either criterion, indicating that all participants showed excellent adherence to the imagery intervention and completion of the log.

Music Conditions

Imagery training occurred under three music conditions using the same imagery script for all conditions. Unfamiliar music was used because it has been shown to generate similar levels of arousal to familiar music but minimizes the potential confounding effects of familiarity and past associations, which can lead to unpredictable effects on individual arousal level (Kuan et al., 2017). Music for the URM condition was taken from Frederick Delius's Florida Suite: III Sunset "*Near The Plantation,*" which was selected from music excerpts confirmed in a preliminary study to be both relaxing and unfamiliar (Kuan et al., 2017). Music for the UAM condition was Edmond De Luca's Conquerors of the Ages "*Attila The Hun,*" which was selected from music excerpts confirmed by Kuan et al. (2017) to be both arousing and unfamiliar. Participants in the NM control condition implemented imagery without music.

Physiological Signals

Physiological signal data were collected using the ProComp+ system and BioGraph software version 5.0 from *Thought Technologies*^{TM} (Montreal, Canada), which assessed participants'

GSR, PT, and HR. To prepare physiological data for analysis, signal filtering was performed to remove noise and artifacts. The raw GSR signal was detrended using a piecewise linear regression model when sudden drift was noticed through visual inspection. No filtering was required for the PT and HR signals as the outputs were clean. When measuring physiological data, it is important to consider baseline differences. Thus, recordings were compared with baseline physiological data collected over a 5-min period of silent relaxation in a sitting position.

Galvanic Skin Response (GSR)

Two sensors were placed on the non-dominant hand of participants, comprising Ag/AgCl electrodes on the medial phalanges of the second and fourth digits. GSR is a linear inverse correlate to relaxation, and reflects emotional responses as well as cognitive activity (Lang, 1995). As sweat is produced in response to sympathetic nervous system activity, the capacity of the skin to conduct an electric current is enhanced and measured conductance is increased. Higher GSR scores reflect increased conductivity, indicating increased arousal.

Peripheral Temperature (PT)

A thermistor was positioned on the ventral side of the little finger of the non-dominant hand of participants (threshold = 0.0, scale – 0.25). PT is a measure of the temperature of the skin extremities, which varies according to the amount of blood perfusing to the skin and reflects sympathetic arousal of the autonomic nervous system. When individuals are sympathetically aroused, muscle contraction occurs. This causes vasoconstriction, which reduces blood flow to the skin, and results in a decrease in temperature (Kluger et al., 1985). Therefore, as arousal increases, PT decreases. Increases in PT reflect greater relaxation.

Heart Rate (HR)

Heart rate (HR) was measured using an EKG receiver (Thought Technology) coupled to a Polar HR transmitter worn around the chest. EKG receivers use wireless transmission and are more stable and less prone to movement artifacts than a blood volume pulse measure (BVP).

Competitive State Anxiety Inventory-2 Revised (CSAI-2R; Cox et al., 2003)

The CSAI-2R was used to assess somatic state anxiety (five items), cognitive state anxiety (seven items), and self-confidence (five items) prior to dart-throwing performance. Respondents rated their feelings on the 17-item instrument (e.g., *I feel jittery, I am concerned about losing*) using a 4-point Likert scale from 1 (*not at all*) to 4 (*very much so*). Subscale scores were derived by summing item scores in each subscale, dividing by the number of items, and multiplying by 10. Score range is 10–40 for each subscale. The factorial validity of the CSAI-2R was established by Cox et al. (2003), using confirmatory factor analysis on data from 331 athletes, which showed a good fit to the hypothesized measurement model (CFI = 0.95, NNFI = 0.94, RMSEA = 0.05) and Cronbach alpha coefficients showed sound internal consistency (somatic anxiety = 0.88, cognitive anxiety = 0.83, self-confidence = 0.85).

Dart-Throwing Performance

Dart-throwing is a self-paced, closed skill, involving fine-motor control, meaning that performance occurred in a stable, predictable environment in which performers could choose when to execute the task. As such, arousal level during dart-throwing was largely unaffected by the physical aspects of the task, which assisted in isolating the influence of external factors, such as music. A modified international-standard competition dartboard and five precision steel tip darts were used for the performance task. The dartboard had 10 concentric circles with diameters of 2, 4, 6, 8, 10, 12, 14, 16, 18, and 20 cm. Concentric circles were used in preference to an unmodified competition dartboard to minimize the effects of strategy. Participants scored 10 points for hitting the center circle (known as the bullseye), nine points for the next circle, down to one point for the outermost circle, and zero if the dart hit outside the outer circle or missed the dartboard. Pre- and post-intervention performances were based on 40 darts thrown from a distance of 237 cm with the bullseye at a height of 173 cm from the floor. Possible scores were in the range 0–400 points. Participants were instructed to stand behind the throwing line, aim for the bullseye, and throw when ready. Five practice trials preceded each performance test of 40 trials.

Short Interview

On completion of dart-throwing assessment at the post-intervention stage, six participants (two from each experimental condition) completed a short interview to describe their subjective experience of the imagery training. Participants shared their imagery experiences, the effects of the music, challenges they faced during the imagery training, and recommendations for use of music with imagery. Questions related to music were not asked of the two NM interviewees.

Procedure

A pre-intervention – intervention – post-intervention design was used in this investigation, which ran over a 4-week period. First, participants provided written informed consent, completed a demographic information form, and were screened for imagery ability using the SIAM. Only participants who rated themselves as having moderate-to-high imagery ability participated in the study. Second, participants completed the CSAI-2R prior to the assessment of baseline dart-throwing performance. Third, participants were randomly assigned to three experimental conditions, termed URM, UAM, and NM, and undertook 12 sessions of imagery training while listening to their allocated music or NM over the 4-week period. Session 1 of the imagery training commenced 20 min after assessment of baseline dart-throwing performance.

For imagery sessions 2–11, participants listened to the 540 s imagery script on alternate days, using an MP3 player, and were prompted to do so via emails and telephone calls. Participants were instructed to follow the imagery script in a relaxed position while listening to the music and imaging the scene, and were asked to not conduct imagery training when tired. GSR, PT, and HR were monitored during sessions 1 and 12 of the imagery training, from 5 min before imagery commenced to 5 min after imagery ended. Fourth, after completing 12 sessions of imagery training, participants were retested on the dart-throwing performance task, having first completed the CSAI-2R. Finally, six participants (two in each condition) were selected to explore their subjective experiences using the interview protocol. All participants were debriefed and thanked for contributing to the study.

Data Analyses

Quantitative data were collated for analysis using SPSS Version 23, and checked for missing data and outliers (none were found). Assumptions of the statistical procedures used were confirmed. Descriptive statistics were calculated for all study variables and between-condition differences in baseline data were assessed using one-way analysis of variance (ANOVA). Performance gain scores for the three music conditions were compared using one-way ANOVA, plus follow-up Tukey tests. Gain scores were calculated as the difference between post-intervention performance and pre-intervention performance scores. Physiological measures (GSR, PT, HR) monitored during Session 1 and Session 12 were plotted graphically over the 540-s imagery period (t_0 to t_{540}) and between-group differences were assessed using a two-way, mixed design ANOVA (condition × session) plus follow-up Tukey tests. Music condition (URM, UAM, NM) was the between-subject factor, and time (Session 1 vs. Session 12) was the within-subject factor. We also examined the interaction between music during imagery conditions and time for the physiological variables. Paired samples t-tests were used to assess changes in CSAI-2R scores (somatic anxiety, cognitive anxiety, self-confidence) from Session 1 to Session 12. In all cases where we made multiple comparisons, we applied the Bonferroni adjustment to significance levels to reduce the risk of Type 1 errors (Hair et al., 1998).

Qualitative data from the short interviews were summarized using inductive content analysis. Content analysis refers to investigators searching text for recurring words and themes (Patton, 2002). This procedure allows researchers to organize raw data (e.g., direct quotations from participants) into interpretable and meaningful themes and categories as the inquirers come to understand patterns that exist (Hanton and Jones, 1999). Inductive content analysis was used because the purpose of the short interviews was to explore the experience of the participants during imagery with music or NM. Inductive content analysis has been widely used by sport psychology researchers (e.g., Pink et al., 2015; Ludlam et al., 2016; Partridge and Knapp, 2016).

RESULTS

Imagery Ability

Analysis of variance showed no significant between-condition differences on any SIAM subscale (see **Table 1**), indicating that participants in the three music conditions (URM, UAM, NM) did not differ in imagery ability at the start of the study. This result provides evidence that participants in the three music conditions were able to use imagery equally effectively as part of the intervention program.

Dart-Throwing Performance

One-way ANOVA showed no significant difference in dart-throwing performance among the three music conditions at the pre-intervention stage ($F_{2,62} = 1.15$, $p = 0.32$, $\eta^2 = 0.04$). Dart-throwing performance mean scores for URM, UAM, and NM, were 167.10 ± 37.97, 182.95 ± 49.46, and 186.05 ± 41.95, respectively, at the pre-intervention stage, and 204.34 ± 28.13, 200.52 ± 30.25, and 199.24 ± 32.64, respectively, at the post-intervention stage. The mean gain scores for dart-throwing performance from pre- to post-intervention are shown graphically in **Figure 1**. The URM group showed the greatest improvement in dart-throwing performance, followed by the UAM group, with the NM group showing the smallest gain.

Gain scores for the URM, UAM, and NM groups were 37.24 ± 5.66, 17.57 ± 5.30, and 13.19 ± 6.14, representing

TABLE 1 | Sport imagery ability measure (SIAM) subscale scores for three music conditions ($N = 63$).

	URM		UAM		NM			
SIAM	***M***	***SD***	***M***	***SD***	***M***	***SD***	$F_{2,62}$	***p***
Vividness	289.86	47.34	291.24	41.39	293.43	45.85	0.03	0.97
Control	287.24	51.58	279.67	42.31	282.62	50.52	0.13	0.88
Ease Generation	274.91	59.99	283.47	49.25	289.33	54.46	0.37	0.69
Speed Generation	280.57	53.71	285.47	42.63	288.62	47.41	0.15	0.86
Duration	274.14	58.92	276.24	49.36	282.47	59.07	0.13	0.88
Visual	292.38	46.22	291.81	37.60	294.95	49.41	0.03	0.97
Auditory	230.33	71.83	246.81	63.64	235.38	68.90	0.39	0.68
Kinaesthetic	252.57	53.42	235.28	53.78	253.76	53.92	0.78	0.46
Olfactory	168.33	74.16	121.38	60.64	144.00	61.53	2.68	0.08
Gustatory	156.24	85.44	114.86	69.53	133.09	71.32	1.57	0.22
Tactile	236.67	65.68	235.71	58.09	245.09	55.03	0.16	0.86
Emotion	247.05	61.46	261.95	47.99	247.95	52.39	0.43	0.66

URM, unfamiliar relaxing music; UAM, unfamiliar arousing music; NM, no music.

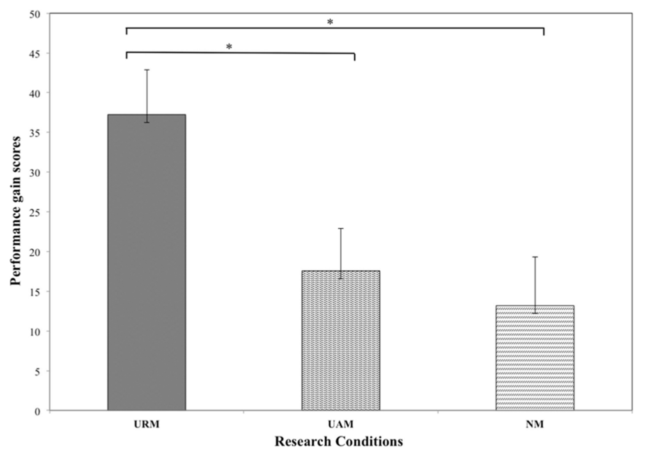

FIGURE 1 | Dart-throwing performance gain scores for unfamiliar relaxing music (URM), unfamiliar arousing music (UAM) and no music (NM) conditions. $*p < 0.05$.

performance improvements of 22.3, 9.6, and 7.1%, respectively. ANOVA indicated a significant between-condition difference in gain scores ($F_{2,62} = 5.03$, $p = 0.01$, $\eta^2 = 0.14$). Pairwise comparisons confirmed significant difference in gain scores between the URM group and the UAM group ($p = 0.04$) and NM group ($p = 0.01$), but no significant difference between the UAM and NM groups ($p = 0.85$).

Physiological Indices

Galvanic Skin Response (GSR)

One-way ANOVA showed no significant difference among music conditions for GSR at baseline ($F_{2,62} = 0.002$; $p = 0.99$, $\eta^2 < 0.001$). **Figure 2** shows mean values for GSR from t_0 to t_{540} for each of the three experimental groups (UAM, URM, and NM) during Sessions 1 and 12. The line graphs indicate that the URM condition was the most relaxing for participants, with GSR decreasing monotonically over time throughout the imagery periods. GSR for the NM condition also decreased during Sessions 1 and 12, but the extent and the rate of decrease were less than for URM. The UAM condition was associated with the highest arousal levels during Sessions 1 and 12, although a decrease in GSR was evident from the start to end of each session, notably so in Session 12. GSR levels at the start of Session 12 were lower than at the start of Session 1 for all music conditions.

Comparing t_0 values, a two-way, mixed design ANOVA (condition × time) showed a significant main effect of time ($F_{1,60} = 6.17$, $p = 0.02$, $\eta^2 = 0.09$), indicating that GSR was lower across conditions at the start of Session 12 than at the start of Session 1. There was no main effect for condition ($F_{2,60} = 0.05$, $p = 0.95$, $\eta^2 = 0.002$) and no significant condition × time interaction ($F_{2,60} = 0.049$, $p = 0.95$, $\eta^2 = 0.002$). Comparing t_{540} values, a mixed design ANOVA (condition × time) showed a significant main effect of time ($F_{1,60} = 10.05$, $p = 0.002$, $\eta^2 = 0.14$), indicating that GSR was lower across conditions at the end of Session 12 than at the end of Session 1. A significant main effect for condition was also evident ($F_{2,60} = 4.68$, $p = 0.013$, $\eta^2 = 0.14$). *Post hoc* Tukey tests confirmed a significant difference between URM and UAM ($p = 0.01$), but no difference between URM and NM ($p = 0.39$) nor between UAM and NM ($p = 0.20$). A significant condition × time interaction was evident ($F_{2,60} = 4.31$, $p = 0.02$, $\eta^2 = 0.13$). UAM was associated with significant reductions in GSR from end of Session 1 to end of Session 12, whereas GSR reduced only marginally for URM and NM over the same period (see **Figure 2**).

Peripheral Temperature (PT)

Results of one-way ANOVA showed no significant difference among music conditions for PT at baseline ($F_{2,62} = 0.03$, $p = 0.97$, $\eta^2 < 0.001$). **Figure 3** shows the mean values for PT from t_0 to t_{540} for the three experimental groups during Sessions 1 and 12. There were no between-group differences at the start of Session 1, although the groups diverged as the session progressed, with URM showing the highest level of PT, indicating the lowest level of arousal. This pattern repeated during Session 12. However, this divergence was not of sufficient magnitude to produce statistically significant differences between conditions at the end of Sessions 1 and 12.

Comparing t_0 values, a two-way, mixed design ANOVA (condition × time) showed no significant main effect of condition ($F_{2,60} = 0.21$, $p = 0.81$, $\eta^2 = 0.01$) or time ($F_{1,60} = 2.38$, $p = 0.13$, $\eta^2 = 0.04$), and no significant interaction between condition and time ($F_{2,60} = 0.19$, $p = 0.83$, $\eta^2 = 0.01$). Comparing t_{540} values, a mixed design ANOVA (condition × time) similarly showed no significant main effect of condition ($F_{2,60} = 1.32$, $p = 0.28$, $\eta^2 = 0.04$) or time ($F_{1,60} = 0.08$, $p = 0.77$, $\eta^2 = 0.001$), and no significant interaction between condition and time ($F_{2,60} = 0.16$, $p = 0.85$, $\eta^2 = 0.01$).

Heart Rate (HR)

One-way ANOVA showed no significant difference among music conditions for HR at baseline ($F_{2,62} = 0.02$; $p = 0.98$, $\eta^2 < 0.001$). **Figure 4** shows the HR means from t_0 to t_{540} for the three experimental groups during Sessions 1 and 12. The URM group showed the largest reductions in HR across Sessions 1 and 12, with HR decreasing monotonically from the start to the end of both sessions. Comparing t_0 values, a mixed design ANOVA (condition × time) showed no significant main effect of condition ($F_{2,60} = 0.22$, $p = 0.80$, $\eta^2 = 0.01$) or time ($F_{1,60} = 0.82$, $p = 0.37$, $\eta^2 = 0.01$), and no significant interaction between condition and time ($F_{2,60} = 0.27$, $p = 0.77$, $\eta^2 = 0.01$).

Comparing t_{540} values, a two-way, mixed design ANOVA (condition × time) showed a significant main effect of condition ($F_{2,60} = 4.28$, $p = 0.02$, $\eta^2 = 0.13$). *Post hoc* Tukey tests confirmed that HR values were significantly lower for the URM group than the UAM group at the end of Sessions 1 and 12 ($p = 0.01$), but no significant differences were found between URM and NM ($p = 0.44$), or UAM and NM ($p = 0.22$). No significant main effect was found for time ($F_{1,60} = 1.94$, $p = 0.17$, $\eta^2 = 0.03$), and no significant interaction between condition and time was found ($F_{2,60} = 0.20$, $p = 0.82$, $\eta^2 = 0.01$).

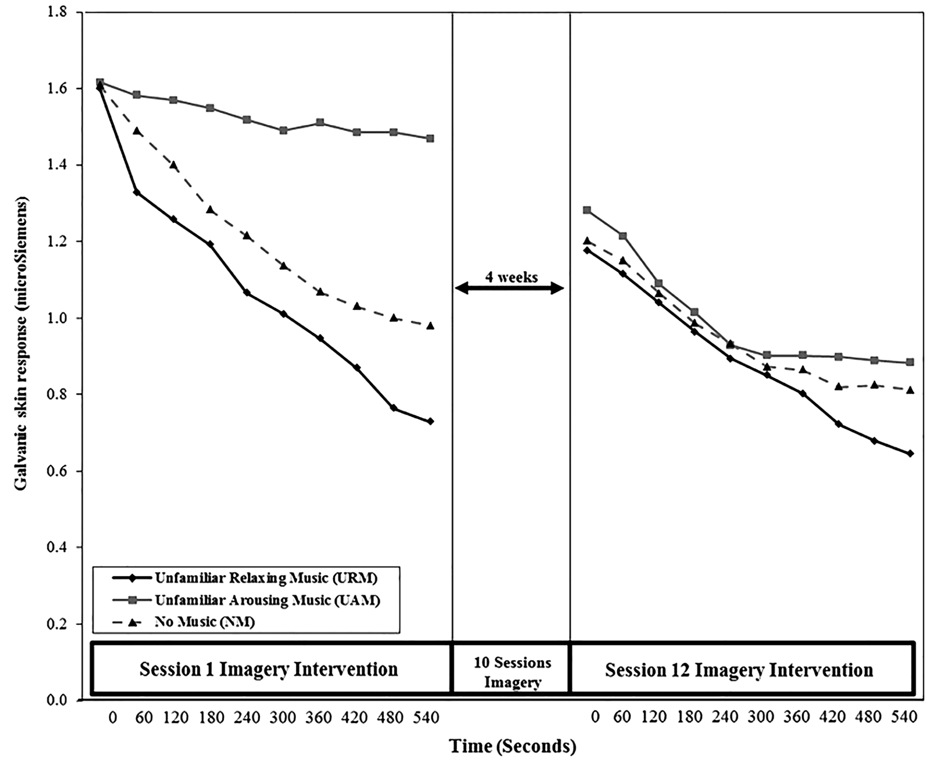

FIGURE 2 | Mean galvanic skin response (GSR) from t_0 to t_{540} across Sessions 1 and 12.

Competitive State Anxiety

Descriptive statistics for the CSAI-2R among participants in the three music conditions prior to the pre- and post-intervention assessments of dart-throwing performance are shown in **Table 2**. One-way ANOVA showed no significant difference among music conditions at baseline for somatic anxiety ($F_{2,62} = 0.03$, $p = 0.97$, $\eta^2 < 0.001$), cognitive state anxiety ($F_{2,62} = 0.20$, $p = 0.82$, $\eta^2 = 0.01$), self-confidence ($F_{2,62} = 1.78$, $p = 0.18$, $\eta^2 = 0.06$). In paired-samples t-tests, we identified significant reductions in somatic and cognitive anxiety, and a significant increase in self-confidence, among the URM group (see **Table 2**). Cohen's d values indicated that these changes from pre- to post-intervention represented very large effects. The UAM group reported a significant reduction in somatic anxiety, of moderate magnitude, but no significant changes in cognitive anxiety or self-confidence. The NM group reported a significant reduction in cognitive anxiety, of moderate-to-large magnitude, but no significant changes in somatic anxiety and self-confidence.

Short Interview Data

All participants completed each of the 12 sessions of imagery training. Six participants reported on their overall imagery training experiences, and four participants commented on their experience of music during imagery. Participants also reported any challenges they faced during imagery training and recommendations for future sessions. Pseudonyms have been used to ensure participant anonymity. The participants, with corresponding research condition, were Christian (URM), Anna (URM), Andrew (UAM), Jackson (UAM), Matthew (NM), and Johnna (NM).

All six respondents indicated they had made a sustained effort throughout the imagery training and dart-throwing trials. Further, five of the six participants indicated that the intervention had improved their dart-throwing performance. Participants felt more relaxed, positive, confident, and experienced greater flow following the imagery intervention compared to during the pre-intervention dart-throwing trials, as exemplified by Christian's comments:

> The imagery showed some effects on the dart-throwing, I felt confident and great… it not only had helped my capacity to hold more images in my head, but it also affected my mood and the positive outcome… my body had less tension… I was able to imagine more flow state within the imagery…I felt in control of my task knowing what to react to and able to concentrate on my task.

Anna said, "After the imagery, I was relaxed… I felt my body was not tensed… I have more confidence to throw the darts on target and to improve my score… I am surprised this imagery could make a difference in my skills." Andrew indicated he had experienced reduced anxiety and less concern about his performance: "I improved in my scoring… I felt less nervous compared to the initial competition… I was not

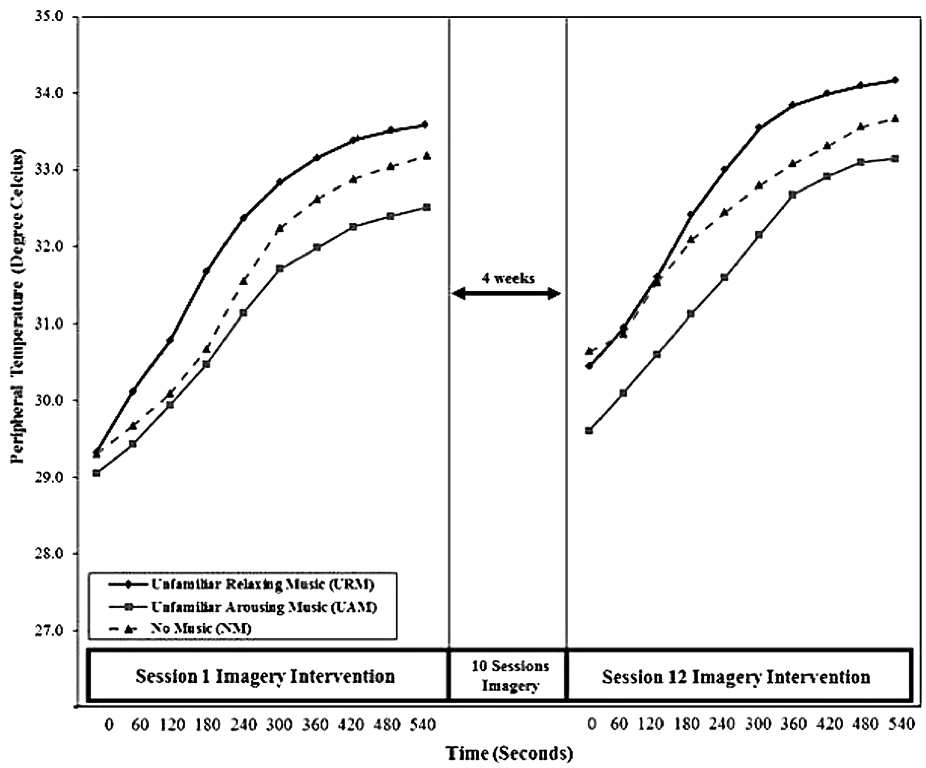

FIGURE 3 | Mean peripheral temperature (PT) from t_0 to t_{540} across Sessions 1 and 12.

worried… my confidence increased…" Matthew also indicated that, during the intervention phase, he had felt more relaxed, but it was after the third imagery training session that he began to note significant changes; "I was able to visualize the dart-throwing more efficiently after the third attempt… I began to feel relaxed… my body was not tense as before… I began to feel more focused and had more concentration… I felt good." Similar responses were provided by Johnna: "Imagery works…my body was relaxed… I had complete concentration and focus… I was not worried about the scoring… I was not concerned about performing poorly."

On the impact of music for imagery training, all four participants reported that they enjoyed having music as a facilitator to imagery training. For example, Anna expressed the view that during the imagery training, she felt more excitement and motivation, and the music had prompted her to remember the imagery: "I like the (relaxing) music … the rhythm was good… I am in a relaxed mood… it makes the imagery a more interesting, motivating and exciting experience… it helped me to remember the imagery during the post-performance." Andrew also expressed excitement and motivation: "I found it an interesting and rather exciting experience… I experienced a motivating experience visualizing with high beat music… slowly I got used to the music and began to visualize my throwing more efficiently." Jackson used the music to energize his imagery, "I used the music to 'pump me up' and make me perform better… it makes me more excited, want to do it better, getting more aroused, but then 'turn them off' to focusing on throwing the dart… I think it is a fun experience."

As for the challenges faced, two participants reported difficulties trying to concentrate, occasionally feeling tired, and finding suitable times to complete the imagery sessions. For example, Matthew expressed the following thoughts:

> I nearly missed one or two sessions due to tiredness… I have assignments and a lecture in the morning…. it was rather hard to concentrate if I was tired… However, the follow-up on contacting me and completion of the logbook did help me to remember to do my training.

Johnna reported similar concerns: "I was distracted twice… waking up too early made me de-motivated and tired… it was hard to manage my time for the imagery."

Finally, participants suggested recommendations, including longer imagery periods (Christian, Matthew), shorter imagery periods (Andrew), weekly follow-ups (Matthew), having a performance test between imagery sessions (Anna), measuring HR in every session (Matthew), adding a breathing exercise before imagery (Johnna), using their own earphones (Jackson), and increasing the frequency of imagery sessions (Anna, Matthew). Matthew said, "I think it should be more, as 12 sessions is not enough for me. I suggest 20 sessions will be ideal…"

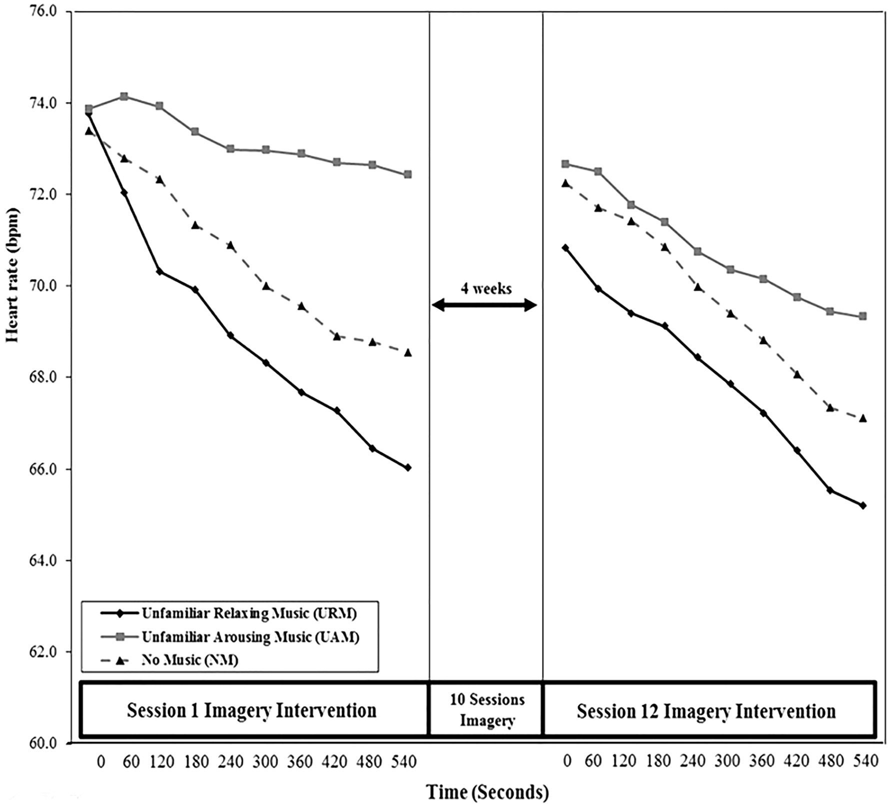

FIGURE 4 | Mean heart rate (HR) from t_0 to t_{540} across Sessions 1 and 12.

TABLE 2 | Pre- and post-intervention scores for somatic anxiety, cognitive anxiety, and self-confidence ($N = 63$).

Source		Pre-intervention	Post-intervention	t_{20}	*p*	*d*
Somatic anxiety						
URM	*M* (*SD*)	16.38 (3.53)	12.67 (2.76)	5.06	<0.001	1.10
UAM	*M* (*SD*)	16.05 (5.14)	14.38 (4.49)	2.34	0.03	0.51
NM	*M* (*SD*)	16.14 (4.93)	14.43 (4.49)	2.00	0.06	0.44
Cognitive anxiety						
URM	*M* (*SD*)	20.10 (5.78)	13.62 (4.63)	5.09	<0.001	1.11
UAM	*M* (*SD*)	20.86 (8.31)	17.90 (6.24)	2.05	0.06	0.45
NM	*M* (*SD*)	19.52 (6.13)	17.05 (6.68)	3.23	0.004	0.70
Self-confidence						
URM	*M* (*SD*)	26.29 (3.70)	33.33 (3.60)	6.97	<0.001	1.52
UAM	*M* (*SD*)	28.57 (5.63)	29.05 (7.23)	0.45	0.66	0.10
NM	*M* (*SD*)	28.86 (5.00)	30.76 (4.62)	2.12	0.06	0.46

URM, unfamiliar relaxing music; UAM, unfamiliar arousing music; NM, no music.

DISCUSSION

We investigated effects of unfamiliar relaxing and arousing music during imagery training on subsequent dart-throwing performance, physiological arousal indices, and competitive state anxiety. Imagery ability was confirmed as being sufficiently well developed and equal across groups, prior to participants completing 12 sessions of imagery training accompanied by one of three music conditions (URM, UAM, NM) over a 4-week period. Dart-throwing performance was assessed before and after the intervention. Differences in mean performance scores among the music conditions at the pre-intervention stage were not statistically significant. Performance gain scores among the music conditions were evaluated rather than comparing specific pre- and post-intervention scores, as recommended by Huck and McLean (1975), as a statistical strategy to minimize the effect of pre-intervention differences between groups. As hypothesized, imagery training had a positive effect on performance for all music conditions and URM was associated with the highest performance gain scores. Participants who listened to URM improved significantly more (22.3%) than those in the UAM (9.6%) and NM (7.1%) groups.

Improvement by the NM group can be attributed to the combined benefits of the imagery intervention and the practice effect of completing the dart-throwing task twice. The additional improvement by the UAM group can be attributed to the augmentation of imagery with arousing music, whereas the much greater improvement by the URM group highlights the importance of using relaxing rather than arousing music to accompany imagery in order to maximize the performance benefit in fine motor skills, such as dart-throwing. Dorney et al. (1992) reported that music did not enhance the benefits of imagery on dart-throwing performance, although the methodological limitations of that study have been noted (Karageorghis and Terry, 1997). Other studies are more aligned with our findings. A triangulation interview study on NCAA Division 1 collegiate athletes concluded that music is an important facilitator of imagery (Sorenson et al., 2008), becoming an essential element in athletes' pre-performance imagery routines. Athletes reported that music enabled them to focus on their imagery routine, block out distractions, and reduce anxiety. Further, in his seminal work on visuo-motor behavior rehearsal, Suinn (1976) proposed the benefits of preceding imagery rehearsal with a relaxation exercise. Our results support Suinn's proposition by demonstrating that performance benefits were greater when imagery was used in conjunction with relaxing music.

Results from the physiological measures indicated consistent changes in GSR, PT, and HR that reflected greater reductions in arousal for the URM group than for either the UAM or NM groups. Visual inspection of **Figures 2–4** shows consistent patterns of responses, wherein the three groups commenced the imagery sessions at similar levels of arousal but steadily diverged during the 9 min that the imagery sessions lasted. Relaxing music, as hypothesized, was associated with the greatest reductions in arousal, arousing music was associated with the smallest reductions in arousal, with the NM group falling in between the two music conditions. Although these trends are unsurprising, it is noteworthy that the combination of imagery and arousing music produced a clear relaxation effect, rather than increasing arousal, during the imagery training sessions. It is also noteworthy that imagery produced a relaxation effect over the course of the sessions even in the absence of music. A practice effect was apparent, in that all three groups commenced and finished Session 12 at lower levels of arousal than the equivalent time in Session 1. The significant interaction effect between condition and time for GSR may indicate habituation to the UAM by the UAM group. In essence, the unfamiliar may have become familiar over the course of 12 imagery sessions, reflected in arousal declining only marginally during Session 1 due to the novelty of the arousing music, but declining significantly during Session 12 as the music became more familiar and its arousing qualities declined. This effect is more apparent for GSR measures compared to PT and HR, suggesting that among the three psycho-physiological indices used, GSR is the most sensitive indicator of autonomic nervous system activity. Kuan et al. (2017) reported similar results for GSR compared to PT and HR.

Self-report measures were included in the present study to assist interpretation of physiological changes in arousal level. Greater improvements in CSAI-2R scores were evident for the URM group than the other two groups from the pre- to post-intervention dart-throwing assessments. These results provide support for the proposition that reductions in physiological arousal were associated with relaxation rather than boredom or drowsiness. It is likely that both the imagery process and the music contributed to the observed changes in state anxiety and self-confidence scores. According to Morris et al. (2005), numerous studies in sport have shown that imagery training can decrease anxiety and increase self-confidence, often resulting in enhanced performance. For example, Hanrahan and Vergeer (2001) demonstrated that an imagery intervention provided for modern dancers reduced state anxiety and increased self-confidence, as well as helping to clarify goals and focus attention.

Most imagery studies that recorded state anxiety and self-confidence scores did so because the imagery intervention was designed specifically to reduce anxiety or enhance confidence. Although this was not the primary focus of our study, participants were encouraged to imagine successful performance outcomes, a strategy previously shown to enhance self-confidence (e.g., Wesch et al., 2016). The use of relaxing music during imagery in the present study may have played an important role in reducing state anxiety. For example, Elliott et al. (2012) provided support for the application of relaxing music in reducing competitive state anxiety and Seaward (2002) recommended that listening to relaxing music for 1 h a day could significantly reduce anxiety.

Researchers have reported that increases in self-confidence tend to accompany reductions in state anxiety (Woodman and Hardy, 2003). Our results supported the proposal that listening to relaxing music during imagery was effective in decreasing competitive state anxiety and increasing self-confidence for fine motor skill performance. The subjective experiences of participants derived from the interviews at the end of the study indicated that they benefited from imagery regardless of research condition. Imagery was associated with improvements in performance, enhanced relaxation, and a more positive mindset. In addition, all four interview participants who completed imagery with music reported that the music created more motivation, fun, and excitement, which motivated them to perform the imagery training.

One limitation of the present study was that we provided no instructions to participants about the number of times they should imagine throwing a dart at the target during each session. Instead, participants paced their own imagery. Hence, there was inconsistency in number of throws imagined, which may have influenced performance. However, we found no study in the literature that had assessed the impact of number of imagery repetitions on performance. The evidence we gleaned from observing participants and inviting their feedback in logs and interviews suggested there were no systematic differences in number of imagery repetitions between the three experimental conditions. Nevertheless, we recommend that the number of imagery repetitions is controlled in future studies in this area of investigation.

Given that we interviewed only two participants from each music condition, their responses have limited generalizability and we recommend that additional qualitative investigations be conducted to explore the effects of music on imagery more fully. Differences in dart-throwing performance among the three music conditions at the pre-intervention stage are also noted. Although these differences were not significant and use of gain score analysis ameliorated their potential effects, we recommend that future studies allocate participants to music conditions using matched pre-intervention performance scores.

Future Research

Our results raised a number of considerations that warrant further investigation. For example, some researchers (e.g., Karageorghis and Priest, 2012) have emphasized the benefits of music for sport performance as part of pre-competition routines, and Terry (2004) provided specific examples of how elite athletes have used music within pre-competition routines to regulate mood and arousal. However, we found no studies that examined effects of music presented in contexts temporally removed from performance. Given that some sports prohibit athletes from using any form of music player in the competition venue, it may be difficult for performers to use music as part of their pre-competition routines during events. Therefore, further investigations of the extent to which a program of imagery with music completed well in advance of competition might benefit subsequent performance, would be worthwhile.

One benefit of examining the impact of imagery on novices is that they have greater scope for improvement than more experienced performers. Some researchers have reported that novices may benefit more than elite performers from listening to music in the context of sporting performance (e.g., Karageorghis and Priest, 2012) whereas others have argued that imagery is more effective with skilled performers than novices (Blair et al., 1993; Morris et al., 2005). A challenge for future research would be to clarify whether imagery conducted in combination with music provides performance benefits for highly skilled performers and therefore we recommend that the present study is replicated among elite athletes using context-specific performance tasks rather than dart-throwing. In particular, it would be worthwhile to investigate the impact of imagery with different music conditions on the performance of gross motor skills of a more dynamic nature rather than the fine motor skill used in the present study.

CONCLUSION

Results provided strong support for using imagery training accompanied by URM to enhance performance of a fine motor skill. Further examination of the effects of relaxing and arousing music on other sports tasks and among participant groups of varying performance levels, is recommended.

ETHICS STATEMENT

The study was carried out in accordance with the recommendations from the Victoria University Human Research Ethics Committee with written informed consent from all participants. All participants gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the Victoria University Human Research Ethics Committee.

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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Physiological Response to Facial Expressions in Peripersonal Space Determines Interpersonal Distance in a Social Interaction Context

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Accurate control of interpersonal distances in social contexts is an important determinant of effective social interactions. Although comfortable interpersonal distance seems to be dependent on social factors such as the gender, age and activity of the confederates, it also seems to be modulated by the way we represent our peripersonal-action space. To test this hypothesis, the present study investigated the relation between the emotional responses registered through electrodermal activity (EDA) triggered by human-like point-light displays (PLDs) carrying different facial expressions (neutral, angry, happy) when located in the participants peripersonal or extrapersonal space, and the comfort distance with the same PLDs when approaching and crossing the participants fronto-parallel axis on the right or left side. The results show an increase of the phasic EDA for PLDs with angry facial expressions located in the peripersonal space (reachability judgment task), in comparison to the same PLDs located in the extrapersonal space, which was not observed for PLDs with neutral or happy facial expressions. The results also show an increase of the comfort distance for PLDs approaching the participants with an angry facial expression (interpersonal comfort distance judgment task), in comparison to PLDs with happy and neutral ones, which was related to the increase of the physiological response. Overall, the findings indicate that comfort social space can be predicted from the emotional reaction triggered by a confederate when located within the observer's peripersonal space. This suggests that peripersonal-action space and interpersonal-social space are similarly sensitive to the emotional valence of the confederate, which could reflect a common adaptive mechanism in specifying theses spaces to subtend interactions with both the physical and social environment, but also to ensure body protection from potential threats.

Keywords: peripersonal space, interpersonal space, facial expression, electrodermal activity, physiological response

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INTRODUCTION

The space around the body is essential to interact physically and socially with the environment. Conceptualized as the peripersonal space, it is conceived as a multisensory interface between the body and the environment where objects can be reached and are naturally coded in terms of potential actions (Rizzolatti et al., 1997; Previc, 1998; Berti and Frassinetti, 2000;

Holmes and Spence, 2004; Coello and Delevoye-Turrell, 2007; Cardellicchio et al., 2011; Iachini et al., 2014; Wamain et al., 2016). Dominant theories of spatial cognition consider that the peripersonal space is represented as an action space depending on the spatial properties of the environment and the dynamic characteristics of the body (Cléry et al., 2015; Coello and Iachini, 2016a; di Pellegrino and Làdavas, 2015). As a consequence, modifying arm length in the body schema through tool-use (Cardinali et al., 2012; Bourgeois et al., 2014) or biasing the spatial outcome of manual reaching action (Bourgeois and Coello, 2012), also modifies the representation of the peripersonal space. Likewise, changing the value of objects in the environment through reward expectations also alters the representation of the peripersonal space (Coello et al., in press). Due to its motor nature, increased activation in the sensorimotor brain areas has been reported when manipulable objects are presented in the peripersonal instead of extrapersonal space, even with tasks focusing on perceptual (Culham et al., 2008; Proverbio, 2012; Wamain et al., 2016), semantic (Wamain et al., 2018) or conceptual information about objects (Coventry et al., 2008; Coello and Bonnotte, 2013).

More recently, peripersonal space has also been described as a safety space contributing to protect the body from external threat (Iachini et al., 2014, 2017; Coello and Iachini, 2016a). In agreement with this, it has been reported that the presence of a threatening stimulus near the body alters the representation of the peripersonal space (Graziano and Cooke, 2006; Coello et al., 2012; Valdés-Conroy et al., 2012; Ferri et al., 2015). Likewise, an object of interest that is at hand could be ignored if it assumes a threat value due to the social situation. Consistently, in a monkey study, Fujii et al. (2007) showed that the parietal activity associated with the presence of a manipulable object within peripersonal space significantly reduced when another monkey, with a dominant status, was looking for the same object. This suggests that a manipulable object can be included or not in the peripersonal space depending on its value and the social context, which implies a specific modulation of the neuronal activity in the pre-frontal cortex in relation with the posterior parietal cortex (Fujii et al., 2009).

As a consequence, the peripersonal-safety space may influence the adjustment of interpersonal distances in social contexts (Hall, 1969; Hayduk, 1978; Teneggi et al., 2013; Knapp et al., 2014), suggesting that social and action spaces share common mechanisms (Iachini et al., 2014; Ruggiero et al., 2016). As evidence, Quesque et al. (2017) revealed an increase of the minimum interpersonal comfort distance after using a long tool, a typical enlargement effect known for peripersonal space (Bourgeois et al., 2014). This indicates that the representation of the peripersonal space constrains the spatial dimension of social interactions (but see, Patané et al., 2016). Interpersonal distances can thus be viewed as the physical space between people where social interactions occur on the basis of their emotional and motivational relevance (Lloyd, 2009), but in relation with the representation of self and others' peripersonal space (Coello and Iachini, 2016a). However, interpersonal distances may diverge from peripersonal space depending on the degree of affiliation with the interlocutor, defined by different variables such as gender, ethnicity, age, and also previous social experience (Leibman, 1970; Tajfel et al., 1971; Iachini et al., 2016). For instance, Iachini et al. (2016) showed that participants select larger comfort distance than reachability distance, in particular female participants when perceiving an approaching male confederate.

Identifying others' emotional state is an essential aspect of interpersonal social interactions, for which facial expressions may play a crucial role (Darwin, 1872; Ekman and Friesen, 1971; Buck et al., 1972). Indeed, positive facial expressions generally foster approaching behavior whereas negative ones induce avoidance behavior, which means that the size of interpersonal distances perceived as comfortable may depend on the emotional context (Lockard et al., 1977; Ruggiero et al., 2016). In agreement with a link between peripersonal-action and interpersonal-social spaces, invasion of others' peripersonal space is usually experienced negatively and can cause intense discomfort and anxiety (Horowitz et al., 1964; Hayduk, 1978; Lloyd, 2009). Furthermore, psychological disorders such as social anxiety (Dosey and Meisels, 1969; Brady and Walker, 1978), claustrophobia (Lourenco et al., 2011), borderline personality disorder (Schienle et al., 2015), autistic spectrum disorders (Gessaroli et al., 2013; Perry et al., 2015; Candini et al., 2017), or anorexia (Nandrino et al., 2017) are characterized by a prevalence of enlarged interpersonal distances for comfortable social interactions. In an fMRI study, Kennedy et al. (2009) reported a bilateral activation of the amygdala, a subcortical brain structure known to play a crucial role in emotion regulation, when the experimenter remained in the participants' peripersonal space during the scan acquisition. Increase of cortisol level and electrodermal activity (EDA) has also been reported in the context of uncomfortable social distances (McBride et al., 1965; Aiello et al., 1977; Evans and Wener, 2007). Complementary evidence linking emotional, social, and spatial processes came from the observation that surgical resection of amygdala associated with temporal tumor surgery produced a severe deficit in the adjustment of interpersonal distances (Kennedy et al., 2009).

Stimuli valence and action system appear thus to contribute to the representation of both the peripersonal-action space and the interpersonal-comfort distance. However, little is known about the link between the body response to the presence of a confederate in the peripersonal space and the interpersonal comfort distance when socially interacting with the confederate. The previous study by Ruggiero et al. (2016) has shown that peripersonal-action space and interpersonal-social space are both sensitive to the emotional valence of a virtual confederate approaching with different facial expressions. Depending on their valence, facial expressions may carry different emotional states and trigger different physiological responses in the observer, which can be detected in the sympathetic nervous system activation associated with the level of physiological arousal (Lang et al., 1993; Boucsein, 2012). Accordingly, physiological responses triggered by a confederate's facial expression could be modulated by the peripersonal or extrapersonal position of the confederate. Furthermore, the physiological responses triggered by the confederate's facial expression in peripersonal space could be predictive of the interpersonal comfort distance in a social interaction task. In the present study, we tested these hypotheses by measuring the EDA triggered by a human-like virtual stimulus carrying different facial expressions, and by evaluating whether the interpersonal comfort distance during social interactions can be predicted on the basis of this physiological activity. A reachability judgment task toward the stimuli placed in either the peripersonal or extrapersonal space or at their boundary was used during the EDA recording. Then, a comfort distance judgment task was used to determine the minimum interpersonal comfort distance with stimuli carrying also different facial expressions. We expected that the presence in the peripersonal space of a confederate displaying a negative facial expression should produce a higher EDA in comparison to a confederate displaying a neutral facial expression, more particularly with male confederates who are usually maintained at a larger distance. Moreover, we expected the interpersonal comfort distances to increase in relation to the individual physiological response, in agreement with the protective role of the peripersonal space.

MATERIALS AND METHODS

Participants

Thirty-seven healthy participants (17 women, *M* age = 21.7 years, *SD* age = 2.79) with normal or corrected-to-normal vision participated in the experiment. Participants gave written consent to take part in this study. The protocol received approval by the local Institutional Ethics Committee (Reference No. 2016-2-S41) and conformed to the principles of the Declaration of Helsinki (World Medical Association, 2013).

Materials and Stimuli

A schematic representation of the apparatus is presented in **Figure 1A**. Participants were standing at a distance of 1 m from a 4 m × 2 m screen, on which 3D visual stimuli were projected using rear projection from a stereoscopic video projector (Christie Mirage 4K25 DLP 3D projector). The visual stimuli consisted of human-like point like displays and were projected at 120 Hz with a 4 K spatial resolution (3840 × 2060 pixels). Active 3D eyewear (Christie) was used for producing 3D image perception. Stereoscopic images were displayed with off-axis projection by using non-symmetrical camera frustums in order to prevent vertical parallax while providing comfortable stereo pairs. The images were generated according to the participants' height and inter-pupillary distance. Thus, each eye received a different image for each stimulus alternately displayed at the rate of 8.33 ms. Normal fusion allowed perceiving the 3D moving visual stimuli and distances through relative size and binocular disparity.

The stimuli consisted of human-like point-light displays (PLDs) representing adult males or females oscillating in place or walking toward the participants (Johansson, 1973). The PLDs were generated from adult models captured with a Vicon motion capture system, recording by means of six MX F20 near-infrared cameras (frequency 240 Hz) the position of 39 infrared markers distributed on the body and limbs (see Mouta et al., 2012 for a detailed description). The positions of 13 white dots (54 cd/m^2) on a black background (0.4 cd/m^2) were calculated by interpolation from the location of the markers, and signalized the motion of head as well as the left and right ankles, knees, hips, wrists, elbows, and shoulders. Pictures of human faces with different expressions were selected from the NimStim battery (Tottenham et al., 2009) and were associated with the dot representing the head on the PLDs. Geometrical characteristics of the head-picture were computed online to match the distance and size of the PLDs. 72 facial expressions were selected from the NimStim set of facial expressions: 12 female and 12 male faces each associated with a happy, angry, and neutral expression (see **Figure 1B**). For each participant, a set 24 facial expressions was pseudo-randomly selected, including 12 female and 12 male faces each being associated with one single emotion resulting in 8 happy, angry, and neutral expressions. This selection process was used in order to avoid any specific effect of a particular expression associated to a particular face.

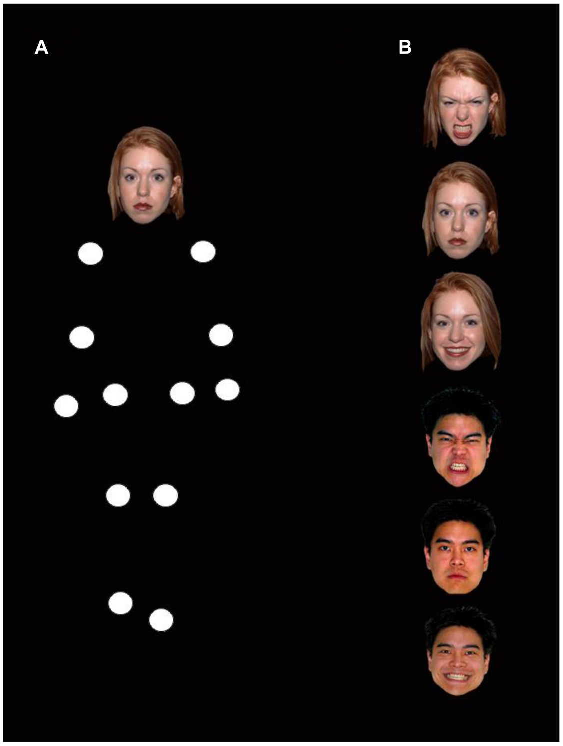

FIGURE 1 | (A) Illustration of the PLD used in the experiment (with a neutral facial expression). **(B)** Illustration of the facial expressions used in the experiment.

The stimuli were used in two tasks: a reachability judgment task and an interpersonal comfort distance task. In the reachability judgment task, the 24 PLDs with facial expressions were presented in both the participants' peripersonal space (at 65 cm) and extrapersonal space (at 250 cm, see **Figure 2A**). To allow their perception in 3D, they were oscillating in place without moving their feet. The oscillation activity consisted in a rotation of the whole body around the vertical axis with an angular rotation of about 20 to 30° at a frequency of 0.5 Hz. Another set of 10 PLDs with neutral facial expressions was presented during the reachability judgment task at the boundary of peripersonal space. This boundary was established from a pilot study ($N = 20$) consisting in indicating by pressing on a keyboard key when an approaching PLD (two males, two females, presented twice each) with different facial expressions (angry, neutral, happy) was at a reachable distance (mean: 150 cm, *SD*: 49 cm). In the experiment, the stimuli used were different than the one used in the pilot study and PLDs presented at the boundary of the peripersonal space were essentially used for the purpose of the reachability judgment task.

In the interpersonal comfort distance judgment task (**Figure 2B**), the same set of 24 PLDs with facial expressions were moving toward the participants and the displacement of the PLDs was perceived through the stereoscopic perception of the 13 white dots moving on the black background. In each trial, the PLDs appeared at a distance of 7 m from the participants, walking toward them at a constant speed of 1.2 m/s (simulated looming velocity was constant) and disappeared after having covered a distance of 5 m (thus, at a distance of 2 m from the participants). The PLDs could start walking from a side position located ±30° according to the participants straight ahead (minus sign for left locations). For each starting location, the PLDs could pass the participants' fronto-parallel plane either on their left or right side. For each side, 10 distances could separate the participants' and the PLDs' shoulders at the crossing location, from −8 up to 64 cm by step of 8 cm (negative signs representing collision with the body, see **Figure 2B**). The 0 cm condition was defined according to individual distance between the participants' mid-sagittal plane and shoulders. Since the PLDs disappeared at 2 m from the participant, the latter had to represent the end of the trajectory mentally until they represent the PLDs passing their fronto-parallel plane.

In the reachability judgment task, physiological responses were registered from EDA through a physiological amplifier BIOPAC MP36 (BIOPAC Systems, Inc., Goleta, CA, United States). Two Ag-AgCl electrodes filled with GEL101 electrolytic mixture were tied on the distal phalanges of the index and major fingers of the non-dominant hand of participants. The temperature of the room during the experiment was maintained at 21°C for all participants and the signal was recorded at a sample rate of 1000 Hz.

Procedure

Before starting the experiment, the participants were requested to fill a self-administered battery of questionnaires in order to control for exclusion criteria (no recent drug and alcohol consumption or excessive stimulating beverage, no previous history of neurological or psychiatric disorders). They also completed the State-Trait Anxiety Inventory STAI-YB (Spielberger et al., 1983; French version by Bruchon-Schweitzer and Paulhan, 1993) and none of them highlighted depressive symptom (average score for anxiety-state: 31 and anxiety-trait: 41). Then, the experimenter placed the electrodes on the participant's non-dominant hand and provided instructions concerning the experiment. The participants were placed in front of the vertical screen as described earlier and watched few examples of the human-like PLDs walking toward them from a straight-forward location (0°), and disappearing when reaching the distance of 20 cm from the participants. This practice session was performed in order to familiarize the participants with the virtual environment, the stereoscopic display and the PLDs. It was also performed to assess the correct 3D perception of the stimuli. Then, the participants started with the reachability judgment task and then performed the interpersonal comfort task.

Reachability Judgment Task

The reachability judgment task started with a 2 min baseline recording of the EDA while the participants were still staring at a black screen. Then, the reachability judgment task started and the 24 PLDs with different facial expressions were randomly presented in the peripersonal and extrapersonal space (thus 48 stimuli), intertwined with the 10 PLDs with neutral facial expressions presented at the boundary of peripersonal space. Thus, a total of 58 stimuli were randomly presented, articulated in two blocks of trials separated by a rest period. Because we used human-like PLDs, the stimuli were animated with an oscillatory movement so that they were perceptible with a 3D structure. Participants were requested to keep a stable posture and to estimate if the presented PLD was reachable with their dominant hand or not, but without performing the related arm movement. The PLDs were presented for a duration of 6 to 7.5 s (randomly selected), then a question mark appeared on the screen informing the participants that they had to provide their response. Reachable-unreachable responses (i.e., yes–no dichotomous responses) were provided with the index and major fingers of the dominant hand (counterbalanced across participants) using a computer keypad placed on a table located on the participants' side. A black screen appeared then for a duration of 4 to 5.5 s following the participant's response.

Interpersonal Comfort Distance Judgment Task

Participants had to judge whether the distance at which the PLDs crossed their fronto-parallel plane was comfortable or not (yes–no responses) by pressing one of two keys on the computer keypad with the index and major fingers of their dominant hand (counterbalanced across participants). The PLDs started walking 7 m from the participants, either at +30° or at −30° (for the left side) of eccentricity according to the participants' straight-ahead. For each starting location, the PLD crossed the participants' fronto-parallel plane with one of the 10 possible inter-shoulders distance (−8, 0, 8, 16, 24, 32, 40, 48, 56, 64 cm), randomly selected, and disappeared when reaching the distance of 2 m from the participants. The participants provided comfortability judgment after the PLD disappeared and when it had virtually reached the level of their (right

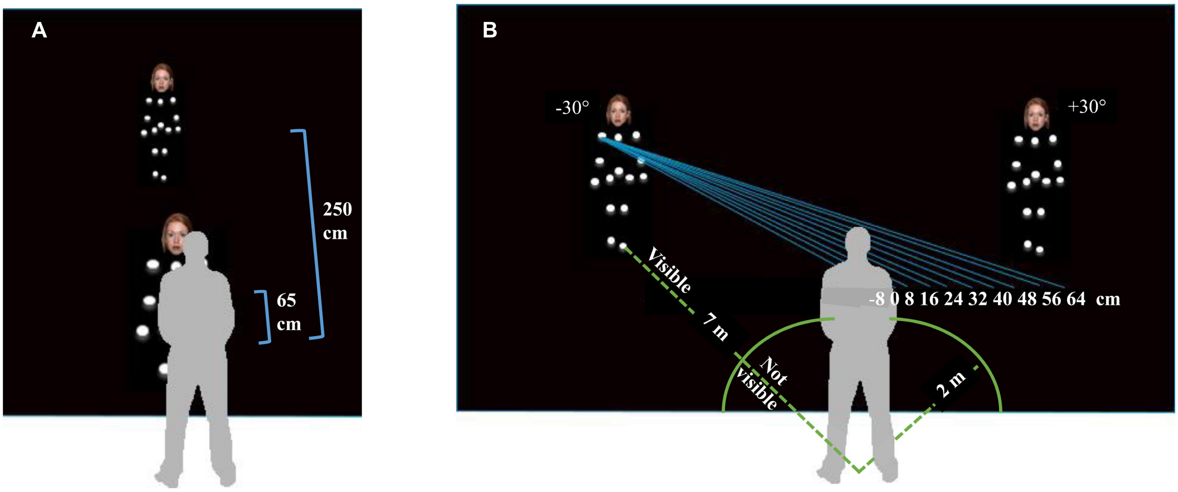

FIGURE 2 | (A) Location of the PLD (with a neutral facial expression) when presented in the participants' peripersonal space (at 65 cm) or extrapersonal space (at 250 cm). PLD located at the boundary of peripersonal space (at 150 cm) is not represented. **(B)** Schematic representation of the within-subjects experimental conditions (not scaled for distance). The PLD started from two different locations (7 m, ±30°), crossed the participants' mid-sagittal axis, and disappeared at 2 m before virtually passing his/her fronto-parallel plane with an inter-shoulders distance of –8 to 64 cm on the right or left side.

or left) shoulder. Thus, 480 trials were performed, divided in three blocks of 160 trials with resting period between the blocks.

Post-experiment Stimuli Evaluation

Following the experiment, the participants were involved in a post-experiment debriefing and had to evaluate the different facial expressions in terms of emotion (arousal and valence) using the self-assessment manikin (SAM, Bradley and Lang, 1994). The evaluation was presented on a 30′′ computer screen using Limesurvey's software. Overall, the experiment lasted around 2 h.

Data Analysis

Participant's responses and EDA were analyzed using MATLAB R2015b software (MathWorks, Inc., Natick, MA, United States) and statistical analysis was performed using R (version 3.4.1) and R Studio softwares (version 1.0.143). In the *reachability judgment task*, the dichotomic (yes–no) responses were recorded by the computer and the frequency of reachable responses was analyzed through a Space (peripersonal, extrapersonal) × Facial expression (angry, neutral, happy) ANOVA with repeated measures on both factors. The EDA was processed only for the PLDs presented in the peripersonal and extrapersonal spaces. Using the LEDALAB toolbox of MATLAB (version 349, Benedek and Kaernbach, 2010), the physiological signal was down-sampled at 20 Hz and smoothed using the gauss-method with a 32 samples window. We first decomposed the physiological signal into tonic and phasic components using continuous decomposition analysis, then we analyzed the average of the phasic activity over each epoch (CDA.SCR). The time window of interest was 0.5 to 6 s after stimulus onset. Linear mixed-effect model was used to analyze the phasic activity (μS) as a function of Facial expressions (angry, happy, neutral), Space (peripersonal, extrapersonal), PLD Gender (male, female) and Participant Gender (male, female). This data analysis takes into account interpersonal variability as random variables (lme4 1.1-13 package, Bates et al., 2015). According to the full model:

$$\begin{aligned}\text{PhasicActivity} = {} & (\text{Facial expression} * \text{Space} + \text{Facial expression} \\ & + \text{Space} + \text{PLD gender} + \text{Participant} \\ & \text{gender} + (1 \mid \text{Participant}))\end{aligned} \tag{1}$$

Reduced models (i.e., when removing fixed effects of interest) were compared using Likelihood Ratio test distributed like χ^2 with degrees of freedom corresponding to the parameters estimate of each model. When significant, parameters of the models were associated with the corresponding t-value; p-values were obtained using normal approximation of the corresponding t-values. We also tested the phasic activity as a function of PLDs arousal and valence evaluation (SAM questionnaire). According to the models used:

$$\begin{aligned}\text{Phasic Activity} = {} & (\text{Arousal} * \text{Space} \\ & + (1 \mid \text{Participant}))\end{aligned} \tag{2}$$

$$\begin{aligned}\text{Phasic Activity} = {} & (\text{Valence} * \text{Space} \\ & + (1 \mid \text{Participant}))\end{aligned} \tag{3}$$

Concerning the *comfort judgment task*, the participants' responses were pooled for PLDs starting from the left and the right position (see Quesque et al., 2017, for details). Perceived minimum interpersonal comfort distance was determined using a maximum likelihood fit based on the second-order derivatives (quasi-Newton method) to obtain the logit regression model that best fitted the comfortable/uncomfortable responses (see Bourgeois and Coello, 2012 for details). We used the equation:

$$y = e^{(\alpha+\beta X)}/(1 + e^{(\alpha+\beta X)}) \tag{4}$$

in which y is the participants' (yes, no) response, X is the crossing distance, and $(-\alpha/\beta)$ is the critical value of X corresponding to the transition between comfortable and uncomfortable stimuli, thus expressing the perceived minimum comfortable distance. Statistical analyses were carried out using linear mixed-effects model to analyze the variation of minimum comfortable distance (cm) as a function of the condition. According to the full model:

$$\begin{aligned}\text{Comfort Distance} = {} & (\text{Facial expression} + \text{PLD gender} \\ & + \text{Participant gender} + (1 \mid \text{Participant}))\end{aligned} \tag{5}$$

We also tested the comfort distance as a function of PLDs arousal and valence evaluation (SAM questionnaire), according to the model:

$$\text{Comfort distance} = (\text{Arousal} * \text{Valence} + (1 \mid \text{Participant})) \tag{6}$$

With respect to our hypotheses, the relation between the minimum comfort distance (interpersonal comfort distance judgment task) and the EDA (reachability judgment task) was analyzed for the PLDs with different facial expressions when located in the peripersonal space. Then, we used linear mixed-effect models in order to analyze the relation between the EDA phasic activity and the minimum comfort distance, according to the model:

$$\text{Comfort distance} = (\text{Phasic activity} + (1 \mid \text{Participant})) \tag{7}$$

Finally, PLDs arousal and valence evaluations depending on the facial expression (angry, neutral, happy) were analyzed from the SAM questionnaire responses using linear mixed-effects models, as follows:

$$\text{Arousal} = (\text{Facial expression} + (1 \mid \text{Participant})) \tag{8}$$

$$\text{Valence} = (\text{Facial expression} + (1 \mid \text{Participant})) \tag{9}$$

RESULTS

PLDs Arousal and Valence Evaluations (SAM Questionnaire)

Concerning arousal evaluation, the value attributed to the PLDs was on average 1.57 (*SD* = 1.20) and depended on the facial expression [$\chi^2(2) = 390.31$, $p < 0.001$; angry PLDs: 2.23 (*SD* = 1.08); neutral PLDs: 0.47 (*SD* = 0.59); and happy PLDs: 2.01 (*SD* = 0.99)]. The evaluation of angry PLDs differed from the evaluation of happy PLDs (estimate = 1.80, *SE* = 0.08, *t* = 10.2, $p < 0.001$) and neutral PLDs (estimate = 1.94, *SE* = 0.07, *t* = 25.42, $p < 0.001$).

Concerning valence evaluation, the value attributed to the PLDs was on average 1.90 (*SD* = 1.40) and depended on the facial expression [$\chi^2(2) = 1195$, $p < 0.001$; with for angry PLDs: 0.23 (*SD* = 0.40); neutral PLDs: 1.92 (*SD* = 0.19); and happy PLDs: 3.53 (*SD* = 0.47)]. The evaluation of angry PLDs differed from the evaluation of happy PLDs (estimate = 3.31, *SE* = 0.04, *t* = 78.28, $p < 0.001$), but not neutral PLDs (*t* = 1.2, *p* = 0.22).

Reachability Judgment Task

Concerning the reachability estimates, PLDs presented in the peripersonal and extrapersonal space were respectively judged as reachable (94.4%) and unreachable (99.10%). Furthermore, reachability judgment for PLDs presented in the peripersonal and extrapersonal space was not influenced by the facial expression [$F(2,34) = 1.16$, $p = 0.31$], and there was no interaction between the two factors [$F(2,34) = 0.61$, $p = 0.55$]. PLDs at the boundary of peripersonal space with neutral facial expression were predominantly judged as unreachable (94.5%).

Concerning the EDA phasic activity, statistical analysis revealed a main effect of Space [$\chi^2(1) = 7.615$, $p = 0.006$] and an interaction between Facial expression and Space [$\chi^2(2) = 6.92$, $p = 0.031$, see **Figure 3**]. PLDs in the peripersonal space led to an increase of the phasic activity in comparison to PLDs in extrapersonal space (estimate = 0.0006, *SE* = 0.0002, *t* = 2.78, *p* = 0.0054) and the effect was higher for PLDs with angry facial expression than for PLDs with neutral facial expression (estimate = 0.002, *SE* = 0.0006, *t* = 2.95, *p* = 0.0032). Finally, in the peripersonal space PLDs with angry facial expression led to a higher phasic activity in comparison to PLDs with neutral facial expression (estimate = 0.0012, *SE* = 0.0004, *t* = 3.11, *p* = 0.0018). Statistical analysis also revealed an interaction between PLDs arousal evaluation and Space [$\chi^2(1) = 7.57$, $p < 0.01$]. Stimuli evaluated as highly arousing resulted in a higher phasic activity in

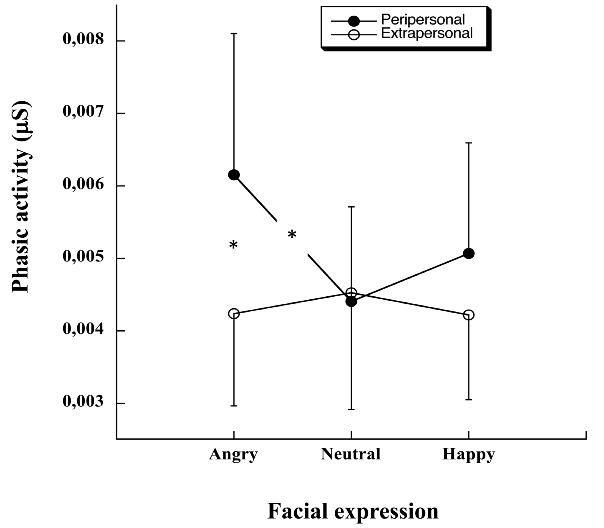

FIGURE 3 | Mean phasic activity (µS) and standard error as a function of the PLDs' facial expression (angry, neutral, happy) when located in either the participants' peripersonal or extrapersonal space.

the peripersonal space (estimate = 0.0004, *SE* = 0.0002, $t = 2.01$, $p = 0.045$). No other effect was significant.

Comfort Interpersonal Distance Judgment Task

Concerning the minimum interpersonal comfort distance (29.70 cm on average), statistical analysis revealed a main effect of Facial expression [$\chi^2(2) = 87.15$, $p < 0.01$], with an increase of the minimum interpersonal comfort distance for angry facial expressions in comparison to neutral (estimate = 9.29, *SE* = 1.10, $t = 8.43$, $p < 0.001$) and happy facial expressions (estimate = 10.17, *SE* = 1.20, $t = 8.43$, $p < 0.01$, see **Figure 4**). Statistical analysis also showed a main effect of PLDs Arousal evaluation [$\chi^2(1) = 73.71$, $p < 0.001$] and an interaction between Arousal and Valence [$\chi^2(1) = 5.74$, $p = 0.0.02$]. PLDs evaluated as highly arousing led to an increase of minimum interpersonal comfort distance (estimate = 3.54, *SE* = 0.70, $p < 0.001$) and the effect was modulated by the valence rating (estimate = −0.76, *SE* = 0.32, $p = 0.02$). No other significant effect was observed.

Relation Between the EDA Triggered by PLDs in Peripersonal Space and the Interpersonal Comfort Distance

When considering facial expressions producing differences in EDA in the peripersonal space (angry and neutral facial expressions), we observed that the modulation of the phasic activity predicted the modulation of the minimum comfort distance [$\chi^2(1) = 7.22$, $p < 0.01$], with a gain of 5.14 cm (estimate) per increase of 0.01 µS phasic activity (*SE* = 1.88, $t = 2.74$, $p < 0.01$, see **Figure 5**).

DISCUSSION

The aim of the present study was to examine how individual physiological response was modulated by human-like stimuli with different facial expressions in the participants' peripersonal space, and to demonstrate a relation between the individual physiological response and the interpersonal distances felt as comfortable when interacting with the same human-like stimuli. For this purpose, we used a reachability judgment task and an interpersonal comfort distance task, both performed with PLDs displaying happy, angry, or neutral faces.

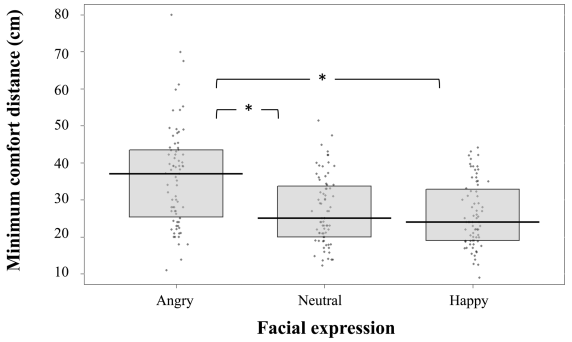

FIGURE 4 | Pirateplot (median and interquartile) representing the variation of minimum comfort distance (cm) as a function of the PLDs' facial expression (angry, neutral, happy).

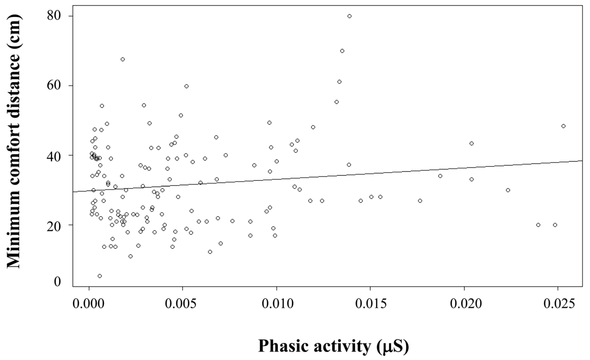

FIGURE 5 | Individual minimum comfort distance (cm) as a function of individual phasic activity (µS) for PLDs with angry and neutral facial expression presented in the peripersonal space. The linear relation indicates that 0.01 µS increase of phasic activity corresponds to an increase of 5.14 cm of minimum comfort distance.

With respect to the physiological responses in the *reachability judgment task*, we observed that angry, neutral and happy facial expressions triggered different EDAs in the participants. A significant increase of physiological response was registered for PLDs carrying an angry facial expression (arousal: 2.23; valence: 0.23) when located in the participants' peripersonal space in comparison to participant's extrapersonal space (gain of 45%) and for those same PLDs in comparison to PLDs carrying a neutral facial expression (arousal: 0.47; valence: 1.92) in participants' peripersonal space (gain of 40%). These results confirm the protective role of peripersonal space (Kennedy et al., 2009; Coello et al., 2012; Valdés-Conroy et al., 2012; Iachini et al., 2014, 2016; Ruggiero et al., 2016) and suggest that an invasion of the peripersonal space may trigger defensive behavior (Graziano and Cooke, 2006; Cléry et al., 2015; di Pellegrino and Làdavas, 2015). The need of maintaining a safety space around the body is particularly important in the presence of angry individuals who might be potentially harmful (Horstmann, 2003; Graziano and Cooke, 2006; Kennedy et al., 2009; Seidel et al., 2010; Iachini et al., 2015a). Supporting this view, previous work on the role of the stimuli valence has revealed that the presence of a dangerous object near the body produces shrinkage of the peripersonal space (Coello et al., 2012). Furthermore, Ruggiero et al. (2016) reported an increase of the peripersonal space when an angry avatar was approaching a participant in a virtual reality display. Both results are compatible with a peripersonal space representing a multimodal interface to interact safely with the physical and social environment (de Vignemont and Iannetti, 2015; Coello and Iachini, 2016b). In accordance with this view, unexpected invasion of peripersonal space may produce intense discomfort and anxiety (Horowitz et al., 1964; Hayduk, 1978; Lloyd, 2009). Furthermore, high trait anxiety is usually associated with an extended peripersonal space (Iachini et al., 2015b). In the present study, the protective role of peripersonal space is also highlighted by the observation that the PLDs located in the participants' peripersonal space modulate the EDA, confirming the established link between threat and associated physiological response. In accordance with this, the more the participants rated stimuli as arousing, the more their physiological responses increased when the PLDs were in their peripersonal space (Sequeira et al., 2009; Bach et al., 2010). These results confirm thus the safety role of the peripersonal space and show how threatening stimuli have an impact on the physiological activity (McBride et al., 1965; Coello et al., 2012; Ferri et al., 2015; Rossetti et al., 2015; Szpak et al., 2015; Ruggiero et al., 2016).

As regards reachability judgments, the participants judged, as expected, almost all PLDs in peripersonal space as reachable (94.4%) and almost all PLDs in extrapersonal space as unreachable (99.10%). Concerning the PLDs located at the boundary of peripersonal space, the participants judged them as unreachable in 94.46% of the cases. This bias toward unreachability for stimuli located at the boundary of peripersonal space could be explained by the fact that the latter was determined in a pilot study using approaching stimuli. Previous studies have indeed shown that peripersonal space increased when a confederate approached a passive participant, in comparison to a situation where the participant was moving toward the confederate (Iachini et al., 2014; Ruggiero et al., 2016). The fact that the boundary of peripersonal space was specified in our study on the basis of approaching PLDs could explain the prevalence of unreachable responses when judging afterward the reachability of stationary PLDs.

With respect to the *interpersonal comfort distance*, the minimum distance was on average 30 cm (inter-shoulder distance), which is in agreement with previous studies (e.g., 32 cm in Quesque et al., 2017). We found that the minimum comfort distance increased with PLDs carrying angry facial expressions in comparison to PLDs with neutral ones (34%) and in comparison to PLDs with happy facial expressions (39%). The present data confirm the effect of valence of facial expressions on comfortable interpersonal distances (Lockard et al., 1977; Ruggiero et al., 2016). Facial expressions rated as negative (e.g., angry facial expressions) led to an increase of the comfortable interpersonal distance in comparison to those rated more positively (neutral and happy facial expressions). We also found that the more facial expressions were rated as arousing by individuals, the more the minimum comfort distance increased and that this relation was modulated by the valence evaluation of the same stimuli. The increase of minimum comfort distance in relation to the increase of arousal was indeed lower when the valence was rated positively. These findings corroborate the previous observation that spatial distance enlarges in the presence of angry faces compared to neutral and happy faces, with no difference between the last two (Ruggiero et al., 2016). However, the present study went further by demonstrating that this enlargement was also associated with the subjective evaluation of the faces (including both valence and arousal).

Surprisingly, neither the participants' nor the PLDs' gender was found to modulate the minimum comfort distance in the social interaction task, which contrasts to what was reported in previous research (e.g., McBride et al., 1965; Iachini et al., 2016). For instance, Iachini et al. (2016) described an increase of the minimum comfort distance from male virtual confederates in comparison to female ones. The main findings were that peripersonal space and interpersonal distances shrank with humans as compared to objects (Iachini et al., 2014), and both spaces were affected by age and gender, i.e., decreased with children and females as compared to adult males, thus reflecting, respectively, affiliative and attraction mechanisms (Iachini et al., 2016; see also Argyle and Dean, 1965; Aiello, 1987; Uzzell and Horne, 2006). The different effect of gender on interpersonal social space observed in these studies and the present one could be due to the importance of facial expressions, which may have prevented or reduced the effect of gender (see also Ruggiero et al., 2016). Although facial expressions and gait were gendered, the emotions displayed might capture most of the attention available while putting aside less relevant features such as gender.

Another important point raised by the present study concerns the relation between the physiological response associated with PLDs in the participants' peripersonal space and the minimum comfort distance accepted with the same stimuli. When considering PLDs with angry and neutral facial expressions (i.e., the ones statistically different in the two tasks), we found a significant relation between the change of the EDA (reachability judgment task) and the change of the preferred social distance (comfort interpersonal distance judgment task), associated with the different valence of the facial expressions. We also observed that the more the physiological response increased in the presence of a negative facial expression, the more the interpersonal distance of comfort widened. Precisely, a gain of 0.01 μS for the phasic activity for stimuli presented in the peripersonal space corresponded to an increase of the comfort distance of 5.14 cm. Information regarding the emotional state of a confederate in a social context would trigger physiological automatic response likely to help adapting distance to the confederate in order to feel safe. It is worth noting that EDA was acquired during the reachability judgment task only and not also during the comfort interpersonal distance judgment task in order to avoid any habituation effect of the emotional stimuli on EDA, but which represents a limitation of the present study. Another extension of the present work would be to compare these data to the postural stability of participants while threatening stimuli are approaching them. This might indeed inform us about the implicit behavioral withdrawal strategy adopted along with the physiological responses. An additional interesting aspect would be to manipulate the characteristics of the PLDs in order to study whether other characteristics of the human-like stimuli (size, status, previous experience...) are taken into account to specify the spatial component of social interactions.

Taken together, these results confirm the protective role of peripersonal-action space and support its role in the adjustment of interpersonal comfort distances for appropriate social interactions (Iachini et al., 2014; Coello and Iachini, 2016a; Ruggiero et al., 2016; Quesque et al., 2017). The increase of the physiological response to PLDs with angry faces may represent an automatic avoidance reaction to the violation of the near body space, as a consequence of arousal regulation and the necessity to ensure a stable self-protection (Dosey and Meisels, 1969; Hayduk, 1983; Siegman and Feldstein, 2014). The strong physiological response in the presence of angry faces is consistent with neurofunctional and behavioral studies showing that negative stimuli yield stronger body response than positive stimuli (Öhman, 1987; Cacioppo et al., 1993; de Gelder et al., 1999; Strack and Deutsch, 2004; Vuilleumier and Pourtois, 2007; van Dantzig et al., 2008; Cole et al., 2013). Thus, the proximity of a threatening confederate obviously leads to avoidance mechanisms in the form of an increase of the social distance, with the consequence that non-appropriate social distance leads to physiological warning signal inducing defense behavior (Lockard et al., 1977; Evans and Wener, 2007; Kennedy et al., 2009; Ruggiero et al., 2016). In contrast, positive elements such as happy facial expressions might foster social interactions (Lockard et al., 1977; Cole et al., 2013; Ruggiero et al., 2016).

CONCLUSION

The present study showed that both peripersonal-action space and interpersonal-social space are similarly sensitive to the emotional meaning of stimuli, which suggests that they may rely on common mechanisms in relation to the motor action system. It also brings new information regarding the emotional coding of threat in terms of distances and how safety can be quantified physiologically and spatially.

AUTHOR CONTRIBUTIONS

AC, GR, TI, and YC conceived and planned the experiments and contributed to writing the manuscript and interpretation of the results. AC, YC, and LO carried out the experiments and analyzed the data.

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Task-Specificity of Muscular Responses During Motor Imagery: Peripheral Physiological Effects and the Legacy of Edmund Jacobson

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Motor imagery has become a key issue in cognitive neuroscience and particularly in fMRI research. However, peripheral physiological effects of motor imagery were already being studied a century ago with some research hypotheses even tracing back to Washburn (1916). This review focuses on research by Edmund Jacobson in the early 1930s. Jacobsen demonstrated that peripheral physiological effects rely on task-specific instructions: Bending the right arm elicits muscular responses in the right biceps, but not in the muscles of other limbs. This review discusses how Jacobsen examined this issue in a series of studies. This scientific spadework is worth recalling here because of its methodological innovations and its forward-looking discussion that even today, continues to be relevant for prospective research on this topic.

Keywords: Jacobson, motor imagery, embodiment of cognition, electromyographic recording, psychophysiology

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INTRODUCTION

Edmund Jacobson was one of the first researchers to study the physiological effects of mental motor imagery in detail. Indeed, in this context, he is often cited as one of the basic references on the peripheral physiological effects of motor imagery. However, despite being cited frequently within the framework of motor simulation phenomena, the full extent of his research is rarely recognized. For example, few people know that he published not just one basic article on this topic (Jacobson, 1930a) but a body of six articles that systematically build on each other. This neglect of his work might be due to the strong recognition of his legacy in the field of relaxation techniques and specifically "progressive relaxation" (Jacobsen, 1929), also known as "progressive muscular relaxation." This article presents a historical review of Jacobson's early and experimentally farsighted work on motor imagery. The aim is to show how modern imagery research is built on the basic research he conducted in the 1920s and 1930s.

Edmund Jacobson (1888–1983) gained his Ph.D. in 1910 at Harvard University where he came into contact with William James. However, this contact seems to have had little influence on his own work. After receiving his Ph.D. at Harvard, he moved to Cornell University for 1 year where he joined Edward Titchener as a research fellow. Afterward, he taught physiology in Chicago until 1937. During this time, he also started to run his own laboratory in which he focused mainly on relaxation methods and their clinical applications[1].

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[1] Biographical data have been taken broadly from Gessel (1989).

One of Jacobson's central interests was in understanding how introspection might work. In principle, introspection procedures can be viewed as an intrinsic part of imagery research. However, the different research paradigms in imagery research indicate that interest does not always focus merely on introspective reports on the quality of imagery. Indeed, in most experimental settings, imagery procedures start normally with an explicit instruction to imagine a certain motor act (Munzert and Zentgraf, 2009). This implies at least some conscious effort (coupled to introspection) to produce and to control the respective image. However, this conscious effort can be reduced notably when imagery is instructed more implicitly, for instance, in mental rotation tasks for body parts (see Parsons, 1987). Participants in mental rotation experiments have to give a response after completing the mental rotation. Thus, even in this implicit method, there is a residual introspective component that is essential for the experimental procedure. The importance of introspection can be demonstrated more clearly for mental timing tasks in which the basic idea is to simulate a motor task internally and to signal the end of the action, for example in walking different distances (Decety et al., 1989; Munzert et al., 2015). Jacobson applied a similar paradigm within his experiments. He used a buzzer and instructed participants to imagine a specific movement upon hearing the first sound and to relax upon hearing the second sound (Jacobson, 1930a, p. 579). Hence, pairs of sounds signaled the start and end of the given motor imagery. To rule out the possibility that physiological effects were caused by the mere occurrence of the sound, on some control trials, he also instructed participants to relax between both signals.

As a physiologist, Jacobson was especially interested in measuring bodily reactions in response to mental activities. In his first 1930 paper, he argued that "if the study of mental phenomena is ever to become a true science, it would appear to be the task of the physiologist to bridge the gap to physics" (Jacobson, 1930a, p. 567). This led him to combine his genuine interest in mental activities, which were analyzed at least partly through introspective methods, with his interest in basic research in physiology and physics. Hence, Jacobson can also be viewed as an early promoter of embodied cognition phenomena.

FUNDAMENTAL EXPERIMENTS ON MOTOR IMAGERY

When appraising Jacobson's experimental approach, one has to bear in mind that he was a true pioneer in the field of psychophysiology. Knowledge about psychophysiology in the early 1930s was far from the present understanding, and his attempt to bridge the gap between mental activities and peripheral physiological processes was ambitious, pioneering, and far ahead of its time. In his first 1930 paper, he followed a short theoretical introduction (referring to Weber, Fechner, and Wundt) by outlining the technical aspects of psychophysiological measurement on more than 11 pages. He elaborated the construction of his device extensively, referred to other measurement methods that were being introduced at that time, and discussed the meaning of the signals that were relevant in his experiments. Electrophysiology was a new and future-oriented approach, and Jacobson really pushed this approach in a new direction by, for example, discussing the properties of the string galvanometer (also known as the Einthoven galvanometer). In 1924, the Dutch physician Willem Einthoven (1860–1927) had received the Nobel Prize for Physiology and Medicine for developing this electrocardiological device. Metaphorically speaking, psychophysiological methods were appearing on the radar at that time.

The aim of the 1930 study was "to secure electrical records of neuromuscular states during specific acts of imagination" (Jacobson, 1930a, p. 569). Jacobson addressed this issue by using a sophisticated experimental device, as outlined above, and also by controlling task-related instructions. The basic experimental task contained the instruction to imagine bending the right arm continuously for some seconds. The start and the end were signaled by a buzzer. This condition was contrasted with several control conditions, for example, imagery of bending the left foot, the left arm, the relaxed or the paralyzed right arm; or extension of the right arm and general free imagery. Active movements of bending the left arm and the left foot were also included. When the specific conditions were assessed, 96% of the specific imagery trials (imagery of bending the right arm) were accompanied by significant electrical changes in the muscles of the right arm. In contrast, this effect was negative for 93% of the control conditions. When actual flexion was compared to imagined flexion for the right arm, actual flexion showed more electrical activity than the imagined contraction. This relation varied inter-individually, producing between 33 and 410% of stronger activation for active trials. The article presents averaged data for each single participant and also exemplary photographic records of electrophysiological measurements. Mere imagery of bending of the right arm elicited significant changes in the electrophysiological signal at the biceps area that was similar, but also weaker to that found in active trials for the same movement. This result demonstrated for the first time that the peripheral physiological effects of motor imagery are movement-specific and not a result of motor intentions in general.

In the following paper (Jacobson, 1930b), Jacobson reported electrophysiological data extending the range of tasks in which the right biceps was involved. He asked participants to imagine lifting a ten-pound weight with the right forearm. Control conditions referred to the instruction either not to imagine this task or to imagine the lifting movement with the other (left) arm. In 93% of experimental trials, he found a significant increase of muscular activation in the biceps, whereas no additional activation was found in control trials. Averaged for all participants, he found roughly a 450% increase of muscular activation in experimental trials compared to relaxation. This magnification ratio is higher than that in the bending task. This can be taken as supporting the argument that effort plays a significant role in motor imagery. Results are therefore in line with the work of Bakker et al. (1996) who showed that the imagined weight during a movement has an effect on EMG activity (see Mizuguchi et al., 2013 for a similar argumentation taking cerebral effects into account). A closer inspection of the time course of the electrophysiological data revealed an average time delay of about 400 ms, which can be interpreted as a reaction time (Jacobson, 1930b, p. 27). This might indicate that participants started to imagine the respective action shortly after the buzzer signal.

Additional data are reported in summary for very different imagery instructions such as writing one's own name, boxing, or engaging in other actions using the right arm. The data demonstrated that the recordings from the biceps were stronger in imagining than in relaxation, but weaker than in bending the arm. There are also some references to recordings of alternating rhythmical movements such as climbing a rope, but the data are not reported in detail. These results underline once more the movement specificity of peripheral physiological effects relying on motor imagery.

In a subsequent series of control experiments, Jacobson tried to investigate whether the electrical signal recorded during imagery is a result of muscle contraction (Jacobson, 1930d). He presented data from four participants who were instructed to imagine bending the right or the left arm and lifting a ten-pound weight with the right or left arm. This time, he examined not only the electrophysiological effects in the biceps but also micro-movements of the right arm. The electrophysiological data underpinned the results of former studies, showing increased activation in the right biceps only for right-handed imagery. Furthermore, the movement recordings showed small microscopic flexions of the right arm that can be ascribed to contractions of the biceps muscle. Additional evidence is provided indicating that it is not possible to relax completely while simultaneously imagining a flexion. This conclusion differs from more recent studies that examined neural mechanisms of strength increases as a result of motor imagery and controlled for movement artifacts during imagery (Yue and Cole, 1992). More specifically, when examining mental strength training, it is mandatory to rule out any muscle contraction that could be connected to potential muscle hypertrophy (Reiser et al., 2011).

In a further study, Jacobson (1930c) reported electrophysiological recordings of eye muscles during visual imagery of large objects (the Eiffel Tower in Paris). He found that the recordings of the imagery data were similar to those for active movements. Jacobson reasoned that eye movements also occur during visual imagery (Jacobson, 1930c, p. 701). Reference values were again derived from relaxation phases; in this case, relaxation of the oculomotor system. As an early antecedent of oculomotor research in the context of motor imagery, results demonstrated task-specific eye movements during motor imagery with the eyes open and with closed eyes (Heremans et al., 2008). The results of his research on oculomotor effects led Jacobson to think about effects of visualizing motor acts such as bending the arm (Jacobson, 1931a). He invited three participants to take part in this study who "gave characteristically positive results in the form of action-potentials from the right biceps, when the instruction was merely, 'Imagine bending the right arm'" (Jacobson, 1931a, p. 119). Here it becomes clear that he used "imagination of bending the arm" in a way that focused on what we now define as motor imagery in contrast to visualization of a movement (see Munzert et al., 2009, for a discussion of motor imagery from a neuroscientific perspective). In the case of visualization of the movement, action potentials were absent from the biceps. On the other hand, instructions to visualize the motor action did elicit electrophysiological effects in the oculomotor region. Further control experiments showed that instructions for imagining bending the arm resulted in persistent activation of the biceps and movements of the eye in some but not all trials (Jacobson, 1931a, p. 120). It becomes unclear whether the latter effect was due to technical aspects of placing the needles close enough to the ocular muscle, or whether other systematic effects have to be considered. However, as a main result of this study, it can be seen that Jacobson (1931a) provided evidence for a fundamental difference between visual and motor imagery of movements.

We end our presentation of Jacobson's imagery research with a single-case study. Here, Jacobson examined a patient who had suffered from a left arm amputation above the elbow (Jacobson, 1931b). Testing imagery for the right intact hand showed mixed results including 8 out of 12 trials showing a clear activation in the right biceps. A *post hoc* review revealed that this result could probably be ascribed to visualizing strategies especially in the first imagery trials (Jacobson, 1931b, p. 123). For imagery of bending the left affected hand, he reports results for electrodes placed at the left and the right arm. Imagery of bending the left arm showed significant action potentials in the left biceps on 13 out of 14 trials. Several control conditions elicited no or only minor electrophysiological activities in the left stump. This was different for imagining right-hand activities. Here, activities were also found for the left stump, indicating a more or less bilateral activation in both arms. A *post hoc* explanation that the participant mirrored right-hand mental activities to the left hand should be considered carefully. Bakker et al. (1996) also report some cross-talk of EMG activity to the contralateral limb while imagining lifting a weight. Research using functional magnet resonance imaging (fMRI) in amputees has shown a clear lateralized activation in motor areas for imagery and execution in both the intact and the phantom limb (Raffin et al., 2012). These and other recent studies on motor imagery with amputees can help to reinterpret Jacobson's idea on mirroring mental movement activities. Whereas neural activation in cortical areas is clearly lateralized, there are also indications for a cross-talk to the opposite limb. It should be noted that Jacobsen was ahead of his time even in speculating about imagery of phantom limbs. He was the first to show that imagining a movement that cannot be performed due to amputation will still elicit the neural signals that would be necessary for its actual performance.

DISCUSSION

First, we have to point out that Jacobson did not aim to analyze motor imagery in a narrower sense. He was more interested in examining the peripheral physiological effects of differences between mental activities and relaxation states. Imagery of motor acts was the central task he used to specify the very broad term of mental activities. If today, we interpret his results as basic research on motor imagery, we should take this context carefully into account. His focus on the relaxation topic is underlined by the fact that he preferred to invite participants trained in relaxation techniques to perform his experiments. This does not influence the imagery strategies directly. In this perspective, it affects primarily the control condition of relaxation. The result is to increase the difference between experimental conditions (imagining of motor acts—general, mental activities) and control conditions (relaxation) by reducing muscular activity during relaxation. However, it has to be noted that studies investigating the influence of individual differences in imagery ability have found that participants with high imagery ability report significantly more relaxation than low imagers in relaxation tasks. Thus, imagery ability might be related to greater subjective responses to relaxation (Rickard et al., 1985; Johnsen and Lutgendorf, 2001). It can therefore be reasoned that Jacobson examined participants who might also have had the ability to create vivid mental images of the motor acts he was investigating.

A further interesting and experimentally farsighted manipulation was to implement different imagery modalities in his experiments. In contemporary literature, this is discussed as visual versus motor imagery (see Ruby and Decety, 2001, for a reference). In most of his studies, Jacobson implemented instructions that seem to aim toward imagery of the core motor act. However, in one study (Jacobson, 1931a), he focused on instructions that differed in terms of imagery modality. He compared motor-oriented instructions to instructions that were obviously focused on the visual imagery of a motor act. It is especially the "motor interpretation" of instructions that is clearly validated by electrophysiological data. In contrast, visual imagery of movements elicited activity in the oculomotor system, but showed no further activation in the target muscles that had proven to be activated during motor imagery. Furthermore, his data showed that it might sometimes have been difficult for his participants to clearly distinguish between motor and visual imagination.

However, the principal merit of his studies is that they revealed task-specific electrophysiological activation for imagery in those muscles that were active during actual execution of the specific motor task. He was not the first to formulate hypotheses on this issue (see Washburn, 1916). However, he developed methods with which to examine peripheral physiological effects. Modern research has underlined this effect of task-specific muscle activation during motor imagery (Bakker et al., 1996; Gandevia et al., 1997; Guillot et al., 2007, 2012). In particular, Guillot et al. (2007) have extended this issue by demonstrating that motor imagery is accompanied by subliminal EMG activity not only in the prime mover but also in related antagonists, synergists, and fixator muscles that work commonly as a muscle synergy. It has been further argued that this subliminal EMG activity results from central neural activation that is inhibited incompletely (Guillot et al., 2012).

Regarding recent neuroscientific research within the field, task specificity has become a key topic in research on motor imagery and action observation. In this context, newer approaches like multivoxel pattern analysis enable to identify task-specific neural patterns within one area of interest in fMRI studies (Gallivan et al., 2013; Filimon et al., 2014; Pilgramm et al., 2016). For example, it has been demonstrated that different actions as well as their modality (motor imagery, observation and execution) can be decoded from neural patterns in frontal and parietal motor cortices (Filimon et al., 2014; Zabicki et al., 2017). Again, this progress in neuroscientific research can be interpreted as a further underpinning of the forward-looking perspective that Jacobson offered so many years ago.

Jacobson interpreted the task-specific EMG activity as the outcome of a specific mental activity that he then could contrast with peripheral effects during relaxation. He was not concerned with the nature of motor imagery as we are nowadays when we refer to Jacobson's pioneering work. Nevertheless, his experimental approach had great predictive power, because his results fit in nicely with such concepts as mental simulation theory (MST) based on the work of Jeannerod (1994). Jeannerod proposed that motor imagery is processed by an internal simulation of a motor act on the basis of motor representations in the motor-related cortical and subcortical brain areas (Munzert et al., 2009; Munzert and Zentgraf, 2009; Guillot et al., 2014; Eaves et al., 2016). Subliminal EMG activation, as demonstrated in Jacobson's early experiments, is then interpreted as incomplete inhibition of the motor commands generated for simulation (Jeannerod, 1994; Bonnet et al., 1997; Guillot et al., 2007, 2012). MST offers a later neurophysiological explanation of the experimental results that Jacobson had collected in a series of experiments nearly 90 years ago. Jacobson's great contribution was to acknowledge the central origin of the peripheral physiological signals collected during mental activities.

AUTHOR CONTRIBUTIONS

JM defined the aims of the research question and wrote the manuscript. BK contributed to all parts of the research question and to all parts of the manuscript.

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Transcutaneous Vagus Nerve Stimulation (tVNS) Enhances Response Selection During Sequential Action

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Transcutaneous vagus nerve stimulation (tVNS) is a non-invasive and safe technique that transiently enhances brain GABA and noradrenaline levels. Although tVNS has been used mainly to treat clinical disorders such as epilepsy, recent studies indicate it is also an effective tool to investigate and potentially enhance the neuromodulation of action control. Given the key roles of GABA and noradrenaline in neural plasticity and cortical excitability, we investigated whether tVNS, through a presumed increase in level of these neurotransmitters, modulates sequential behavior in terms of response selection and sequence learning components. To this end we assessed the effect of single-session tVNS in healthy young adults ($N = 40$) on performance on a serial reaction time task, using a single-blind, sham-controlled between-subject design. Active as compared to sham tVNS did not differ in terms of acquisition of an embedded response sequence and in terms of performance under randomized response schedules. However, active tVNS did enhance response selection processes. Specifically, the group receiving active tVNS did not exhibit inhibition of return during response reversals (i.e., when trial N requires the same response as trial N–2, e.g., 1-2-1) on trials with an embedded response sequence. This finding indicates that tVNS enhances response selection processes when selection demands are particularly high. More generally, these results add to converging evidence that tVNS enhances action control performance.

Keywords: tVNS, implicit motor sequence learning, response selection, GABA, cognitive enhancement

INTRODUCTION

Non-invasive methods of brain stimulation have become an increasingly popular approach to probing the relationship between neurochemistry and cognitive-behavioral performance. Although transcranial direct current stimulation (tDCS) is currently the subject of great scientific interest (Plewnia et al., 2015), it has recently been suggested that transcutaneous (through the skin) vagus nerve stimulation (tVNS) may be a novel technique to investigate and potentially enhance the neuromodulation of action control (van Leusden et al., 2015). Converging evidence from animal and clinical studies suggests that tVNS increases levels of GABA (Ben-Menachem et al., 1995;

Marrosu et al., 2003) and noradrenaline (NA) in the brain (Roosevelt et al., 2006; Raedt et al., 2011). Consistent with this literature, tVNS has been shown to increase intracortical inhibition in healthy adults (Capone et al., 2015), supporting the idea that tVNS might alter and potentially enhance performance related to the GABAergic and noradrenergic systems. Given the crucial role for GABA in the neuromodulation of response selection (Bar-Gad et al., 2003; Munakata et al., 2011; de la Vega et al., 2014) and motor learning (Floyer-Lea et al., 2006; Stagg et al., 2011), we investigated the effects of tVNS on implicit sequence learning and response selection processes underlying sequential action.

The neurochemical effects of tVNS have the potential to alter cortical excitability and synaptic plasticity, which are shaped by brain GABA concentration (Nakamura et al., 1997; Werhahn et al., 1999; Floyer-Lea et al., 2006; Boy et al., 2010; Stagg et al., 2011; Ziemann et al., 2015). Consistent with this neuromodulatory role, individual differences in GABA level have been related to response selection and inhibition (Snyder et al., 2010; Munakata et al., 2011; de la Vega et al., 2014), impulsivity (Boy et al., 2011), error detection, and conflict monitoring (van Veen and Carter, 2006), as well as implicit motor learning (Stagg et al., 2011; de Beaumont et al., 2012). The effects of GABA on response selection and inhibition are commonly explained by its role in a "winner-takes-all" mechanism, in which GABA enhances the mutual inhibition of competing response options (Bar-Gad et al., 2003; Plenz, 2003). This is thought to facilitate the suppression of incorrect response alternatives and aid in selection of the appropriate response (Munakata et al., 2011; de la Vega et al., 2014). Given this facilitatory effect of GABA on action control, it is possible that tVNS, via a transient increase in GABA concentration, modulates, and potentially enhances response selection processes (c.f. van Leusden et al., 2015).

Recent studies support this hypothesis by showing that tVNS can indeed improve cognitive-behavioral performance. These effects of tVNS were not related to sequenced action specifically, defined here as a sequence of movements that are serially ordered to achieve a task goal (Sakai et al., 2004; Abrahamse et al., 2013). However, previous work has demonstrated that tVNS can enhance processes thought to underlie motor sequence performance and learning. For example, Beste et al. (2016) demonstrated improved inhibitory control from tVNS. As robust response selection is crucial to sequenced actions (Deroost and Soetens, 2006), enhanced inhibition from tVNS might facilitate selection of the target response through suppression of competing non-target alternatives (Munakata et al., 2011; de la Vega et al., 2014; Colzato et al., 2018). Consistent with this notion, Steenbergen et al. (2015) reported that tVNS enhanced response selection when two responses were executed in succession.

Importantly, tVNS affects not only GABA but the NA system as well (Roosevelt et al., 2006; Raedt et al., 2011). In line with this finding, tVNS has been reported to enhance processes that (i) are associated with the acquisition of sequenced movements, and (ii) are thought to be mediated by NA transmission. For example, tVNS has been shown to enhance the formation of associative memory (Jacobs et al., 2015). When responses follow an implicit sequential structure, associative memory allows for development of an integrated representation of the sequence or sequence elements based on formed associations between responses (Hommel, 1996). Consistent with this notion, tVNS has been argued to improve associative memory via a presumed increase in NA transmission from the locus coeruleus to hippocampal areas (and the amygdala in the case of emotional memory formation) (Jacobs et al., 2015). Furthermore, increased post-error slowing is thought to be an important component of sequence learning (Ruitenberg et al., 2014) as it reflects upon rule-based performance (Tam et al., 2013). Sellaro et al. (2015) demonstrated that tVNS increased post-error slowing, which depends on catecholamine activity, i.e., dopamine (Moeller et al., 2012; Wardle et al., 2012) and NA (Ullsperger et al., 2010; Colzato et al., 2013). Taken together, the aforementioned findings support the hypothesis that tVNS can enhance response selection processes during sequential action.

In contrast to these expectations, there is also the possibility that tVNS results in suppression of sequential learning. Sequence acquisition is typically associated with an *increase* rather than a *decrease* in cortical excitability (Lin et al., 2011), and indeed, some have demonstrated that increased GABA predicts reduced implicit motor sequence learning (Stagg et al., 2011; de Beaumont et al., 2012). In light of these previous studies, the effect of tVNS on sequence acquisition remains uncertain. Therefore, the present study set out to clarify the effect of tVNS on sequence acquisition and response selection during sequential action.

The Present Study

In more general terms, with the present study we set out to extend the literature on tVNS enhancement of cognitive-behavioral performance by investigating its potential to improve sequential action control. Given that tVNS increases brain GABA, which is crucial to the modulation of action control processes (Bar-Gad et al., 2003; Floyer-Lea et al., 2006; Munakata et al., 2011; Stagg et al., 2011; de la Vega et al., 2014), we tested the hypothesis that tVNS might enhance sequential action as assessed on a serial reaction time (SRT) task (Nissen and Bullemer, 1987). The SRT task is a 4-choice reaction time task that involves response selection, inhibition of non-target responses and implicit formation of response sequence structures, each of which may be sensitive to GABA and NA changes from tVNS. Typically, a second-order conditional (SOC) response sequence is embedded in the task unbeknownst to the participants. Implicit acquisition of the sequence structure results in increasingly shorter response latencies and less response errors as the task progresses (Nissen and Bullemer, 1987; Abrahamse and Noordzij, 2011; Schwarb and Schumacher, 2012). However, there is potential difficulty in disentangling the nature of these improvements (Jongkees et al., 2017a) as performance improvements might not necessarily be due to implicit learning processes but rather reflect general practice effects (Abrahamse and Noordzij, 2011). For this reason, a transfer approach is used to judge the extent by which performance improvements rely on the practiced sequence (Willingham, 1999; Robertson, 2007; Abrahamse and Noordzij, 2011). In the SRT task variation employed in the present experiment, each block of trials included both an embedded SOC sequence as well as a transfer sequence based on a pseudo-random stimulus presentation schedule. In addition to evaluating performance improvement across practice, this approach allowed for comparisons between sequenced trials and randomized trials as an index of sequence learning. Post-error slowing was also evaluated for trials under sequenced and random schedules to investigate the effects of tVNS on sequence learning processes. As tVNS might not enhance sequence learning but rather improve response selection processes, overall task accuracy and reaction time (RT) performance was assessed under the view that increased accuracy or reduced response latency under tVNS reflects efficiency of selecting the target response. To probe inhibitory processes that are relied upon to select target responses, we applied the concept of inhibition of return (Posner and Cohen, 1984; Lupiáñez et al., 1999 for reviews; see Klein, 2000) to the SRT paradigm to further investigate response selection processes under tVNS. In the SRT task, inhibition of return is evaluated by comparing RT on reversal trials to non-reversal trials (Vaquero et al., 2006). A reversal trial is defined as occurring when the target response location for trial *N* is a repetition of the target response location for trial *N−2* (e.g., 1-2-1; Vaquero et al., 2006). Longer response latencies for reversal trials as compared to non-reversal trials reflect inhibition of an action that has been recently performed (Klein, 2000). Increased GABA levels due to tVNS might result in suppression of inhibition of return as well as the inhibition of competing response options, thereby allowing efficient selection of a response even when it has been recently performed.

MATERIALS AND METHODS

Participants

Forty undergraduate students from Leiden University were offered partial course credit for participation in a study on tVNS. Participants were randomly assigned to either the active ($N = 20$) or sham ($N = 20$) tVNS group. The groups were comparable with respect to age ($M = 22.3$ vs. 22.5 years, $SD = 2.7$ vs. 2.5, respectively), $t(38) = 0.244$, $p = 0.809$, and gender distribution, ($F{:}M = 14{:}6$ vs. 18:2, respectively), $X^2(1, N = 40) = 2.50$, $p = 0.114$. Participants were screened individually using the Mini International Neuropsychiatric Interview (MINI), a short, structured interview of approximately 15 min that screens for several psychiatric disorders and drug use (Sheehan et al., 1998), and has been used previously in neuromodulation research (Jongkees et al., 2017a,b). Participants were included if they met the following criteria: (i) between 18 and 30 years; (ii) no history of neurological or psychiatric disorders; (iii) no history of substance abuse or dependence; (iv) no chronic or acute medication; and (v) no implants or cardiac disorders for safety reasons concerning the tVNS. Before the start of the study, participants were informed of the procedure and potential side-effects of the tVNS (i.e., itching, stinging, or burning sensation from the electrodes, reddening of the skin and head ache). None of the participants reported major side-effects. The study conformed to the ethical standards of the declaration of Helsinki with written informed consent from all subjects and the protocol was approved by the local ethical committee (Leiden University, Institute for Psychological Research).

Transcutaneous Vagus Nerve Stimulation

tVNS stimulates the afferent auricular branch of the vagus nerve, which is located medial of the tragus at the entry of the acoustic meatus (Kreuzer et al., 2012). In order to avoid stimulation of fibers to the heart, tVNS is safe to be applied to the left but not the right ear (Sperling et al., 2010; Kreuzer et al., 2012). The tVNS device consisted of two titan electrodes mounted on a gel frame and connected to a wired neurostimulating device (CMO2, Cerbomed, Erlangen, Germany), see **Figure 1**. Following the suggestions by Dietrich et al. (2008) for optimal stimulation, the tVNS® device was programmed to a stimulation intensity of 0.5 mA, delivered with a pulse width of 200–300 μs at 25 Hz. Both active and sham stimulation constantly alternated between active stimulation for 30 s, followed by a break of 30 s. Consistent with Kraus et al. (2007), sham stimulation was applied by placing the electrodes over the center of the left ear lobe instead of the outer auditory canal, as the ear lobe is free of vagus innervation (Peuker and Filler, 2002) and its stimulation produces no activation in the cortex and brain stem (Kraus et al., 2013).

Serial Reaction Time Task

To assess response selection and sequence learning, participants performed an adapted SRT task (Vaquero et al., 2006) presented using E-Prime 2.0 software (Psychology Software Tools, Inc., Pittsburgh, PA, United States). In this task four horizontally aligned empty squares are presented in the center of the screen. On each trial one of the squares turns red and the participant must press a corresponding button on the QWERTY keyboard (from left to right: V, B, N, M) using the index and middle fingers of the left (V, B) and right (N, M) hand. An error sound is presented if the wrong button is pressed, along with the Dutch words “Verkeerde toets!” (“Wrong button!”). RT is measured in milliseconds as the latency in the key press to the stimulus and if RT exceeds 3,000 ms, the Dutch words “Te langzaam!” (“Too slow!”) are presented. Following the response, the four

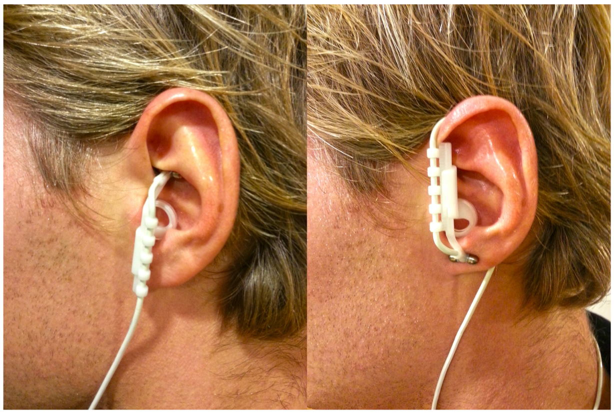

FIGURE 1 | Positioning of the tVNS electrodes in the active (left) and in the sham (right) condition.

empty squares appear for a 50 ms response-stimulus interval before the next stimulus is presented. Participants were instructed that accuracy and response speed were equally important in the task.

Participants completed 3 task familiarization blocks of 120 randomly sequenced trials prior to stimulation, and then performed 15 experimental blocks each consisting of 10 cycles of 12 trials while stimulation was applied. Each experimental block alternated between a cycle of random trials and two cycles of SOC trials (R-SOC-SOC-R-SOC-SOC-R-SOC-SOC-R), with each SOC cycle containing the same 12-item response sequence (VBVNMBNVMNBM) (Reed and Johnson, 1994). Whereas performance gradually improves on SOC trials as the response sequence is implicitly learned, the random response sequence prevents anticipation of responses and thus requires stimulus-oriented control. Hence RT and response errors are expected to be higher on random cycles (Willingham et al., 1989) but performance is expected to recover on SOC trials. After completion of each block, performance feedback indicated the number of errors and mean RT followed by a 30 s rest interval. The task took approximately 30 min to complete.

The random response sequences were generated prior to the study and held constant across all participants, to avoid chance-based group differences in the structure of the random cycles. For example, performance artifacts may occur due to differences in the number of reversal trials (Reed and Johnson, 1994; Vaquero et al., 2006). A reversal trial occurs when the third trial of any three consecutive trials involves the same target response as the first trial (e.g., V-B-V). Random cycles were generated to match SOC cycles on the number of reversals and hand switches (left-to-right and right-to-left) across trials (Jongkees et al., 2017a) and immediate response repetitions were not allowed within a random cycle nor at the transition between a random and SOC cycle. As such, any group difference in performance is not confounded by chance-based differences in the structure of random cycles.

Procedure

Upon entering the lab, informed consent was obtained and participants practiced the SRT task to familiarize themselves with the task. Subsequently tVNS was applied and after 15 min of stimulation the experimental SRT task was started. Stimulation was applied throughout the entire task, which took on average 30 min. After the task participants were asked to rate, on a five-point (1–5) scale, to what extent they experienced (i) headache, (ii) neck pain, (iii) nausea, (iv) muscle contraction in the face and/or neck, (v) stinging sensation under the electrodes, (vi) burning sensation under the electrodes, (vii) uncomfortable (non-specific) feelings, and (viii) other sensations or adverse effects. None of the participants reported major side-effects.

Statistical Analyses

The percentage of response accuracy (ACC) and mean RT for SRT task familiarization performance was calculated for each individual participant. RT calculation was based on correct trials only. ACC and RT for task familiarization were submitted separately to univariate analysis to test for any Group performance differences prior to stimulation conditions.

For performance in SRT task experimental blocks, ACC was calculated for each individual according to Sequence Type (SOC, random) and Trial Type (non-reversal, reversal) factors and submitted to a 2 (Group: active, sham) × 2 (Sequence Type: SOC, random) × 2 (Trial Type: non-reversal, reversal) analysis of variance (ANOVA) with repeated measures on the last two factors. RT was calculated based on correct trials according to Sequence Type, Trial Type and Block (1–15) factors. RT was then submitted to a 2 (Group) × 2 (Sequence Type) × 2 (Trial Type) × 15 (Block) ANOVA with repeated measures on the last three factors. For the purpose of the present experiment, a significant Group × Sequence Type × Block interaction was identified as being a critical test of enhanced sequence learning during active stimulation. A significant main effect of Group or a significant Group × Sequence Type interaction represented key identifiers of response selection efficacy. Enhanced response selection during active stimulation based on suppression of inhibition of return was expected to be revealed either as a significant Group × Trial Type interaction or a Group × Sequence Type × Trial Type interaction. Analysis for inspection of post-error slowing involved aggregating correct trial RT separately for post-error trials (a correct trial that was preceded by an error trial), post-correct trials (a correct trial succeeding a correct trial) under SOC and random sequence types. RT was then submitted to a 2 (Group) × 2 (Preceding Error) × 2 (Sequence Type) ANOVA with repeated measures on the last two factors. A significant Group × Preceding Error or Group × Preceding Error × Sequence Type interaction was identified as reflecting active and sham stimulation differences on post-error slowing.

Mauchly's test was used to test the sphericity assumption for repeated measures ANOVA. Where sphericity was violated, a Huynh–Feldt correction was applied to the *p*-value. Significant interactions were further analyzed using Fisher's LSD *post hoc* comparisons. For all analyses, a criterion of $p < 0.05$ was used to infer significant effects, interactions and differences.

RESULTS

Accuracy and RT performance during familiarization of the SRT task did not significantly differ between active and sham stimulation groups; $p = 0.12$ and $p = 0.64$, respectively. ACC performance was very high during experimental blocks (97%) and did not significantly differ between stimulation groups ($p = 0.57$), and there were no significant interactions between the Group factor and Sequence Type and Trial Type factors (*p*'s > 0.39).

For experimental block RT performance, a significant Sequence Type × Block interaction ($F[14,532] = 5.45$, $p < 0.0001$, $\eta_p^2 = 0.125$) provides support for sequence learning within the SRT task, see **Figure 2**. With the exception of Block 2 ($p = 0.19$), RT was significantly lower on SOC sequence trials than random trials (*p's* < 0.05). However, the Group × Block interaction

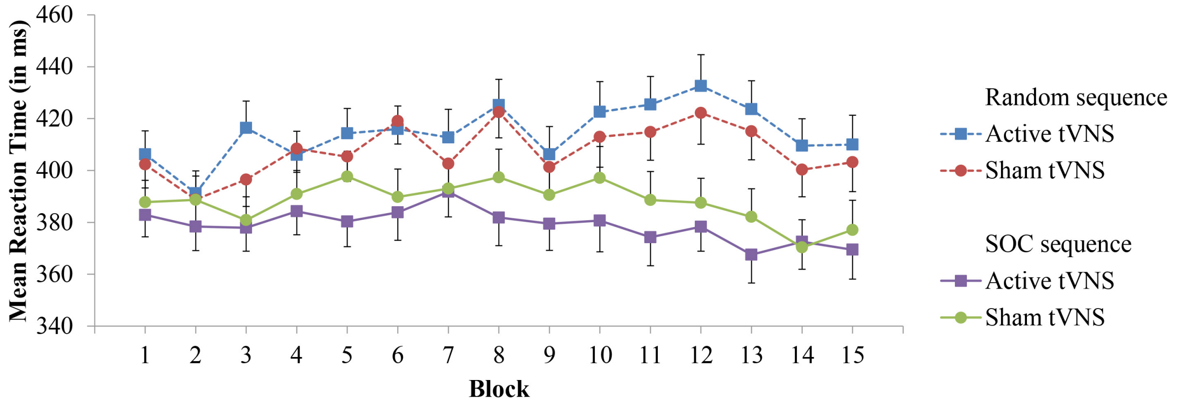

FIGURE 2 | Mean reaction time in the SRT task as a function of block, sequence type, and tVNS group. Error bars reflect standard error of the means.

(p = 0.89) was not significant. Important for the evaluation of sequence learning differences between stimulation groups, the Group × Sequence Type × Block interaction was not significant (p = 0.76). Further inspection of sequence learning based on assessment of post-error slowing did not reveal significant Group × Preceding Error (p = 0.27) or Group × Preceding Error × Sequence Type (p = 0.64) interactions, see **Table 1** for mean RTs. Thus, these results do not indicate that active tVNS stimulation enhanced sequence learning.

With respect to the evaluation of response selection enhancement, neither the Group effect (p = 0.93) or the Group × Sequence Type interaction (p = 0.07) for RT were significant. In terms of inhibition of return as an index of response selection efficacy, the stimulation groups did not significantly differ between non-reversal trials and reversal trials (p = 0.16). However, a significant Group × Sequence × Trial type interaction ($F[1,38] = 5.05$, $p < 0.05$, $\eta_p^2 = 0.117$) indicated that enhancement of response selection through suppression of inhibition of return depended on the nature of the sequence structure that the reversal trial was performed in, see **Figure 3** and **Table 1**. Specifically, under active stimulation and in SOC sequence trials, RT was not significantly different between non-reversal (M = 372, SE = 9 ms) and reversal trials (M = 386, SE = 11 ms; p = 0.10). In contrast, under sham stimulation, RT for SOC sequence trials was significantly longer for reversal trials (M = 406, SE = 11 ms) than non-reversal trials (M = 370, SE = 9 ms; $p < 0.0001$). For random trials, both active and sham stimulation groups demonstrated significantly longer

TABLE 1 | Mean reaction time in ms as a function of stimulation group and trial type in the SRT task.

	Stimulation group	
Trial type	**Sham**	**Active**
Random order trials (overall)	392 (8)	398 (8)
Reversal trials	426 (9)	434 (9)
Non-reversal trials	389 (8)	395 (8)
Post-correct trials	387 (8)	395 (8)
Post-error trials	513 (18)	504 (18)
SOC trials (overall)	373 (9)	373 (9)
Reversal trials	406 (11)	386 (11)
Non-reversal trials	370 (9)	372 (9)
Post-correct trials	369 (9)	371 (9)
Post-error trials	511 (19)	489 (19)

Standard error of the mean presented in parentheses. SOC, second order conditional sequenced trials.

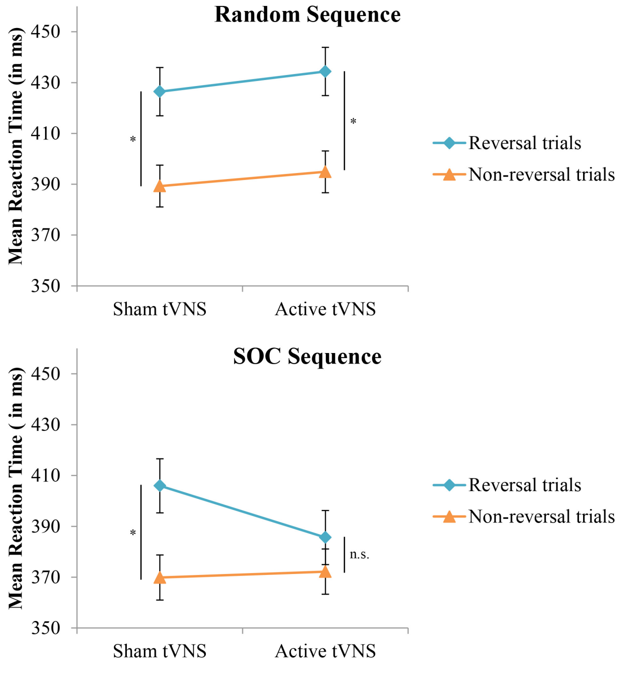

FIGURE 3 | Mean reaction time in the SRT task as a function of trial type, sequence type, and tVNS group. Error bars reflect standard error of the means. Whereas both groups demonstrate a typical increase in reaction time on reversal trials during random response sequences, this increase is eliminated in the active tVNS group on trials with an embedded (SOC) response sequence. *$p < 0.001$.

RT for reversal trials and non-reversal trials (both comparisons, $p < 0.001$). Nevertheless, under active stimulation, there were no significant differences between SOC sequence reversal trials and random sequence non-reversal trials ($p = 0.42$). In sum, these results indicate active tVNS eliminated inhibition of return during SOC sequenced response schedules.

DISCUSSION

The present study demonstrates that single-session tVNS improves response selection during sequential action. Whereas individuals tend to slow their responses when a response sequence contains an immediate reversal (e.g., 1-2-1 instead of 1-2-3) (Vaquero et al., 2006), this inhibition-of-return-like effect was eliminated under active tVNS while participants carried out an implicitly learned response sequence. The effect of tVNS was exclusive to response latency and did not extend to response errors, suggesting that the results are not attributable to a change in the speed-accuracy trade-off. This finding provides convergent evidence for the potential of tVNS to enhance action control in healthy adults.

In particular, this beneficial effect of tVNS on response selection is consistent with a wide range of studies demonstrating that increased GABA concentration facilitates action control (van Veen and Carter, 2006; Snyder et al., 2010; Boy et al., 2011; Munakata et al., 2011; de la Vega et al., 2014). Consistent with a winner-takes-all mechanism of response selection (Bar-Gad et al., 2003; Plenz, 2003), a higher GABA concentration promotes intracortical inhibition, leading to a suppression of incorrect response alternatives and thereby facilitating selection of the correct response (Munakata et al., 2011; de la Vega et al., 2014). It is conceivable, then, that a tVNS-induced increase in GABA is most beneficial when it is particularly challenging for the target response to successfully inhibit incorrect response alternatives.

This notion converges on the present results. In the SRT task the target response on reversal trials matches the response on trial N-2, which appears to be suppressed as evidenced by slower responses on reversal as compared to non-reversal trials (Vaquero et al., 2006). This possibly reflects the fact that on reversal trials it takes longer for the target response to successfully inhibit the incorrect response alternatives. In this case, a tVNS-induced enhancement of GABA could potentially aid in the inhibition of these response alternatives. The consequent facilitatory effect on selecting the target response accounts for the lack of RT slowing on reversal trials in SOC sequences.

The stimulation did not enhance or diminish implicit motor sequence learning. However, of note was the low rate of implicit learning in both groups. The task structure might have limited the opportunity to acquire the SOC sequence due to alternation of random and SOC response cycles within each block. Although this structure served to offer a more balanced inspection of performance on randomly sequenced versus SOC sequenced trials, the high prevalence of and frequent switching towards random response sequences might have interfered with participants' ability to acquire the SOC sequence by predisposing them to a stimulus-based rather than a plan-based action control style (c.f. Tubau et al., 2007). A reduced tendency for plan-based control might have then limited the potential for implicit learning to be modulated by tVNS. Therefore, we recommend the null-finding regarding tVNS and motor sequence learning to be examined in future studies that employ a more classic SRT task in which experimental blocks are strongly dominated by SOC cycles.

Notwithstanding the observed null-findings for sequence learning, the fact that tVNS selectively enhanced performance when response selection demands were high, is of potential theoretical interest and is reminiscent of a previous finding that tVNS enhanced inhibitory control only when working memory was also involved (Beste et al., 2016). In the present study tVNS selectively enhanced response selection on reversal trials during SOC cycles. From a neurobiological perspective, it is plausible that GABA's inhibitory effects on response selection have greatest behavioral impact, and are more sensitive to manipulation, during conditions of response conflict when several response alternatives are strongly activated and when it is particularly challenging for the target response to be selected, such as on reversal trials in the SRT task. This might also explain the lack of an effect of tVNS on the majority of SOC trials (i.e., non-reversal trials), as these trials might have led to insufficient competition between responses alternatives for a manipulation of GABA to be behaviorally detectable.

Before concluding, the present study gives rise to some theoretical questions that need to be addressed in follow-up studies: (i) Considering that the SRT task version used in this study had a one-to-one mapping of stimuli to responses, the results cannot disentangle whether tVNS affected stimulus-based versus response-based mechanisms (c.f. van Veen et al., 2001). That is, it is not clear whether tVNS on reversal trials facilitated in particular responding to the same stimulus as on trial $N-2$, or whether the same facilitation would be observed when not the stimulus but only the response was repeated. (ii) In a similar vein, repetition of the $N-2$ trial has been associated with the backward inhibition effect, where response slowing on trial N is attributed to inhibition of the task-set required on trial $N-2$ (Mayr and Keele, 2000). Considering that the present SRT task did not involve multiple task-sets, it remains to be determined whether the influence of tVNS on trial $N-2$ repetition is exclusive to response activation or extends to task-set activation as well. (iii) It is also uncertain whether tVNS affected specifically inhibition of return versus more general biases that promote an alternating pattern of responses (e.g., Cho et al., 2002; Jones et al., 2002). As such, it is necessary for future studies to consider these issues, starting for example with mapping responses to multiple stimuli in order to disambiguate these effects.

Furthermore, it is important to acknowledge that aside from GABA also the noradrenergic system can be affected by tVNS (Roosevelt et al., 2006; Raedt et al., 2011). A shortcoming of the present study is that its behavioral findings cannot unequivocally distinguish between effects on these different neurotransmitter systems. Although tVNS did not affect the components of SRT task performance linked with NA activity—i.e., sequence learning as supported by associative memory formation (Jacobs et al., 2015) and post-error slowing (Sellaro et al., 2015)—we cannot definitively conclude that NA did not contribute to our results. As such, future studies should provide clarity on this issue by for example including physiological markers of GABAergic and noradrenergic activity in an attempt to relate baseline differences and changes in these markers to tVNS-induced changes in SRT task performance.

To conclude, the present study extends the previous literature on tVNS and action control performance by showing that tVNS enhanced response selection processes during sequential action.

AUTHOR CONTRIBUTIONS

BJ, MI, and LC designed the study. AF ran the study. MI analyzed the data. BJ wrote the first draft of the manuscript. MI, AF, and LC edited the manuscript.

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REVIEW
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The Way We Do the Things We Do: How Cognitive Contexts Shape the Neural Dynamics of Motor Areas in Humans

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In spontaneously triggered movements the nature of the executed response has a prominent effect on the intensity and the dynamics of motor areas recruitment. Under time pressure, the time course of motor areas recruitment is necessarily shorter than that of spontaneously triggered movements because RTs may be extremely short. Moreover, different classes of RT tasks allow examining the nature and the dynamics of motor areas activation in different cognitive contexts. In the present article, we review experimental results obtained from high temporal resolution methods (mainly, but not exclusively EEG ones), during voluntary movements; these results indicate that the activity of motor areas not only depends on the nature of the executed movement but also on the cognitive context in which these movements have to be executed.

Keywords: primary motor areas, supplementary motor areas, CNV, preparation, reaction time (RT)

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INTRODUCTION

It is widely established that the nature of the recruited motor areas and the time course of their recruitment strongly depend on the nature of the movement to be performed (Krakauer and Ghez, 2000). This is well illustrated in humans by studies using the Bereitschaftspotential (BP). The BP, discovered, by Kornhuber and Deecke (1965), is a slow electroencephalographic (EEG) wave which precedes self-paced spontaneously triggered movements. It is composed of an early, mostly bilateral, component and a late lateralized one. These components are finally followed by a contralateral "motor potential" which develops over the primary motor area (M1) just before electromyogram (EMG) onset [Shibasaki and Hallett (2006) for a review]. For elementary (e.g., brisk finger movement) slow rate self-paced movements, there is a consensus for considering that the surface-recorded premovement components (early BP, late BP, and motor potential) are essentially generated by motor areas (Shibasaki and Hallett, 2006) and the influence on the BP of movement characteristics such as, for example, the nature of the effector (which finger is used, foot, shoulder, hip, knee, tongue, eyes, etc.), the force to be exerted, the speed, the accuracy, or the complexity of the response, etc. have been well documented [Lang (2003) and Shibasaki and Hallett (2006) for reviews; Kukleta et al., 2012].

It is also established that the nature of the movements executed to realize a given action depends on the cognitive context in which this action must be realized. For example, Rosenbaum and Jorgensen (1992) asked subjects to lift a rod in order to transfer it to a final given position.

The nature of the performed movement (hand orientation) depended on how comfortable the arm would be at the end of the transport following the lifting movement. Moreover, the choice of a hand grip also depended on the choices that had been used before. Haggard (1998) obtained similar results: the type of movement executed to grasp an object depended on whether this object should only be grasped or of it should be moved afterward.

Now, one can wonder whether, for a given movement, the cognitive context in which this movement is executed has any influence on the nature and the dynamics of the recruitment of motor areas (Mirabella et al., 2008). A key aspect of the cognitive context in which an action develops relates to the nature of the decision leading to the upcoming action. Intentional actions can be classified according to the nature of the decision to be performed before acting: the "... 'how' aspects of the act." (Kukleta et al., 2012, p. 65), its "what," its "when," and its "whether" (Brass and Haggard, 2008), or no decision. Therefore, in the following, we will examine the effects, on motor areas [and more specifically on primary motor (M1), dorsal premotor (PMd), and supplementary motor (SMA) areas] in humans of these decisional contexts in which an action develops and will conclude by showing that even more general cognitive states or attitudes regarding the actions to be performed may influence the dynamics of activation of the motor areas.

To access the dynamics of motor areas activation, one must resort to high temporal resolution brain imaging techniques and this is why, although metabolic (PET, fMRI) methods have provided highly valuable information on cortical motor control, we will not discuss much these results here, given their poor temporal resolution.

To give efficient access to most motor structures, MEG, although presenting excellent temporal resolution, presents a serious drawback: it is almost blind to radially oriented generators and, as a consequence, to the surface of the gyri. Once again, this has been clearly illustrated in BP recordings. The early, mostly bilateral, component of the BP is clearly visible on EEG recordings and it is demonstrated, on the basis of intracranial recordings that the supplementary motor area (SMA) is one of its main generators [Ikeda and Shibasaki (2003) and Sochůrková et al. (2006) for a review]. However, the onset of the magnetic counterpart of the BP occurs later and is mainly contralateral (e.g., Nagamine et al., 1996). The authors reasoned that, even if SMA is active in such situation, MEG is probably blind to it. First, if the SMAs are active bilaterally, then, intra-fissural activities generate tangential generators of opposite direction which should mainly cancel each other. Now, the part of the SMAs lying on the mesial part of the convexity, the gyral part of the primary motor areas and most of the premotor areas (PM), correspond to radially oriented generators to which MEG is poorly sensitive. Conversely, EEG is very sensitive to these generators and, as such, the early part of the BP can easily be recorded with this technique. This is certainly why tentative MEG-based generator reconstruction of movement-related potentials by Gerloff et al. (1998) failed to identify a generator in the SMAs and/or bilateral M1 or PM activity on the precentral gyrus (but see Erdler et al., 2000).

For these reasons, among the available high temporal resolution brain imaging techniques, we will mainly (but not exclusively) concentrate on EEG studies in the following. Because of volume conduction (Nuñez, 1981), overlapping effects may deteriorate the spatial resolution of EEG recordings and, secondarily, their temporal resolution (Law et al., 1993; Burle et al., 2015). However, as will be seen in the following, specific solutions may be used when necessary, to overcome this difficulty in the study of motor areas.

WHEN

Preparing When to Decide

It is possible to prepare according to the timing of task relevant events. Indeed, Requin et al. (1991) distinguished two, not mutually exclusive, types of preparation: "event" preparation and "time" preparation, time preparation does not correspond to deciding "when" to act but rather corresponds to prepare for "when" to decide. This preparation is classically studied by manipulating the duration of preparatory periods (PPs) of choice reaction time (RT) tasks.

Most PPs of RT paradigms involve a preparatory signal (PS) and an imperative signal (IS). During the delay between the PS and the IS, several preparatory operations take place, among which motor process can occur if a movement may be required.

Absolute accuracy of time estimation decreases proportionally to the increase of the duration to be estimated (Gibbon, 1977). Therefore, short PPs allow a better estimation of the occurrence of the IS than long PPs and, if administered in blocked designs, RTs are shorter after short than after longer PPs (Woodrow, 1914), provided that the PP is longer than 200 ms (otherwise, there is no time enough to get prepared: Bertelson, 1967). Note that this effect holds even when subjects have to make a choice after the IS.

The motor nature of time preparation is not warranted *a priori* since the effects of time preparation on performance have been demonstrated to hold even when subjects do not know in advance which response to execute after the IS. Moreover, Davranche et al. (2011), for example, showed that, in a detection task without any time pressure, time preparation does facilitate stimulus detection.

To examine the possible effect of time preparation on motor structures, Davranche et al. (2007) used transcranial magnetic stimulation to probe cortical and corticospinal excitability during the PP of a between-hand choice RT task: according to the nature of the IS (right or left from a fixation point), delivered at the end of the PP, subjects had to press a button with either the right or the left hand (respectively). They used a short and a long foreperiod. As expected, RTs were shorter after the short than after the long PP. Two indices were examined: the amplitude of the motor potential and the duration of the silent period which follows the motor potential (the silent period is the result of intracortical GABA-ergic inhibition).

The silent period decreased with increasing time until the end of the PP. Given that the silent period corresponds to cortical inhibition, its decrease reveals a release of intracortical inhibition (i.e., a net motor activation). This release of inhibition progressively increased during the PPs and was more pronounced for the short PP. For the short period, the motor potential decreased progressively until the end of the PP, suggesting that, when motor activation is maximal, increased cortico-spinal inhibition secures the development of cortical activation to prevent erroneous premature responding [but see also Duque and Ivry (2009) and Duque et al. (2010) for similar results].

Now, a follow-up study demonstrated the efficiency of this preparation on the reactivity of the motor structures: this preparation selectively speeded up corticospinal motor processes. Tandonnet et al. (2012) examined the time course of M1 excitability after the IS of short and long PPs where no prior knowledge regarding the responding hand was available. They showed that after the IS, the size of the motor evoked potential increased faster after a short than after a long PP, on M1 contralateral to the responding hand; such an effect was absent for ipsilateral M1. Moreover, the difference between contralateral and ipsilateral stimulation occurred earlier for the short PP.

In the same vein, Tandonnet et al. (2003) using Laplacian-transformed EEG data, examined the time course of the motor potential after short and long PPs. They showed that the time separating motor potential onset from EMG onset was shorter after a short than a long PP. This indicated that better time preparation (during short foreperiods) speeds up motor processes at primary motor cortex level.

Deciding When to Act

Bereitschaftspotential studies have shown that cognitive factors influence the BP and these observations might suggest that the cognitive context influences motor areas. However, this not warranted. Due to volume conduction effects (Nuñez, 1981), the mere analysis of scalp potentials does not allow drawing firm conclusions in this respect, unless it would be clearly established by other methods that the generators of premovement potentials are always confined to motor areas. This is not always the case (Kukleta et al., 2012); for example, spontaneously triggered grasping (Bozzacchi et al., 2012) movements or, more generally, spontaneously triggered movements implying interaction with an object, even when mimicked (Wheaton et al., 2005), generate early parietal pre-movement potentials [Di Russo et al. (2017) for a review].

Fortunately, as indicated earlier, for elementary (e.g., brisk finger movement) slow rate self-paced movements, there is evidence that the generators of the BP are essentially in motor areas (Shibasaki and Hallett, 2006): in this case, it is widely admitted that the early part of the BP begins in the SMAs, and, shortly after, spreads bilaterally into the PMds; finally, the late part of the BP develops in contralateral M1 and PMd.

Using simple spontaneously triggered voluntary movements, it is therefore possible to examine the influence of cognitive contexts (such as timing constraints), to conclude about their influence on these motor areas in internally triggered voluntary actions, as will be the case in the following.

Verleger et al. (2016) asked subjects to produce spontaneously triggered independent simple key-presses. In different experimental blocks of trials, different constraints were imposed regarding the minimum duration separating the upcoming action from the preceding one; no upper limit was set on this duration. Subjects received an error feed-back after a given produced key-press if it occurred too close in time from the preceding one. Verleger et al. (2016) showed that "... BPs did vary in accordance with the temporal constraints [put] on the intervals between movements ... ". (Verleger et al., 2016, p. 11).

To explore, may be more directly, the effects of timing constraints on motor structures, Baker et al. (2012) used a temporal reproduction task. Subjects were presented with pairs of tones separated by specific time intervals; afterward, they had to spontaneously reproduce the same interval between two brief button presses at their own choosing. Each button-press was therefore a spontaneously triggered self-paced action. Nevertheless, no timing requirement was imposed to the first action whereas timing control was explicitly required before the second one. It appeared that the BP preceding the second button press was much larger than that preceding the first one, suggesting that attention to elapsed time, "i.e. the process of orienting attention in time towards the moment of movement initiation" (Baker et al., 2012, p. 715), is one of the crucial factors in the elicitation of the BP and, therefore, the dynamics of activation of motor areas. This effect was obvious over the SMAs but absent over contralateral M1. This influence of temporal constraints on the BP, and therefore on motor structures, was consistent with several data sets indicating a prominent involvement of the SMAs in timing [Casini and Vidal (2011) and Coull et al. (2016) for short reviews] and by the fact that the SMA BOLD response correlates with the amount of attention paid to elapsing time (Coull et al., 2004).

Macar et al. (1999) obtained similar results and added supplementary information regarding the sensitivity of motor structures to the timing context. Subjects learned by trials and errors to produce, at the time of their own choosing, a target interval delimited by two brief button presses; they received after each trial a feed-back on their timing performance. As in the Baker et al. (2012) experiment, scalp potentials showed a greater BP after the second action of the sequence than after the first one, especially at midline fronto central electrode (**Figure 1**). Now, to attenuate spatial overlapping effects due to volume conduction (Nuñez, 1981), the authors resorted to the Laplacian-transformation of surface scalp potentials [see Kayser and Tenke (2015) for a tutorial review]. Acting as a high-pass filter, this transformation allows to better separate the activities issued from distinct cortical generators, not only in space but also in time (Law et al., 1993; Burle et al., 2015). Notably, this separation is efficient without any inference regarding the number, the orientation, or any other property of these underlying generators. Surface Laplacian revealed to be efficient in separating activities generated by sensorimotor areas from those generated by frontomesial structures, including the SMAs.

Once Laplacian-transformed, EEG data revealed qualitatively different patterns of activation before the first action and the second one. Whereas a very large BP was evidenced over the SMAs before the second action, no measurable activity was elicited before the first one (**Figure 1**). On the contrary, large BPs were evoked over contralateral and ipsilateral M1s before the first and before the second action. This indicates that, in the Macar et al.'s (1999) experiment, and probably

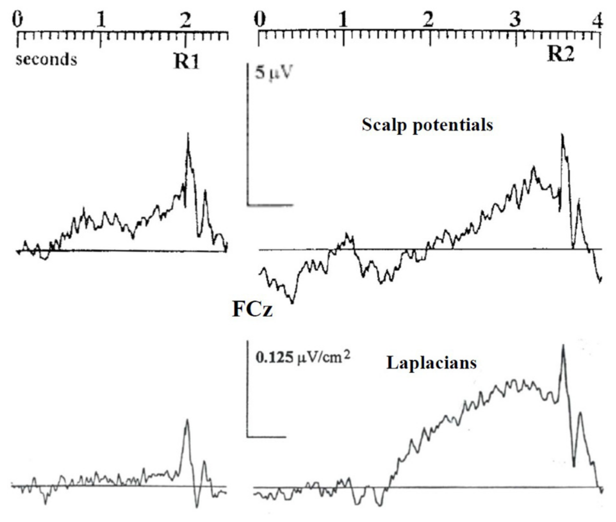

FIGURE 1 | The influence of timing control on the activities recorded over the SMAs. Adapted from Macar et al. (1999). Upper panel: response-locked scalp potentials (reference: right mastoid) recorded over the SMAs before the first (R1) and the second (R2) key presses of a spontaneously triggered interval delimited by two brief button presses (target interval: 2.5 s). Lower panel: same dataset after Laplacian transformation.

in Baker et al.'s (2012) one, the amplitude differences observed at the midline frontocentral sites on scalp potentials between the first and the second action can be explained by a strong participation of the SMAs to the BP before the second action and no contribution of the SMAs to the BP before the first action. The activity observed over the SMAs before the first action on scalp potentials was very likely volume conducted from bilateral M1 and/or PMd generators given that M1s and/or PMds were involved both before the first and the second action. One might argue that the Laplacian transformation does not solve the inverse problem, which is true. However, whatever the exact contribution of, say, the cingulate cortex areas, to the activities recorded right over the SMAs, the "flat" trace observed before the first action in Macar et al.'s (1999) data, indicate that at least the SMAs did not contribute to the BP and, therefore, to the activity of the motor areas, when triggering the first self-paced action of the sequence.

Of course, in this kind of situation, as stressed by Baker et al. (2012) or Macar et al. (1999), the status of the first press differs from that of the second press in that no specific timing constraint is required before the first action, whereas once this action has been triggered, the occurrence of the second one must be finely timed. It can therefore be concluded that the cognitive context regarding "when" to act has a strong influence on the dynamics of motor areas and, more specifically, of the SMAs.

WHAT

Although there have been clever attempts to test the influence of the "what" (e.g., Dirnberger et al., 2000) and "whether" (Brass and Haggard, 2007) components of intentional action, on the dynamics of motor structures using BP recordings, the contribution of non-motor structures to pre-movement activities (e.g., prefrontal areas:) is not unlikely (Dirnberger et al., 2000; Brass and Haggard, 2007). Moreover, there are more convenient situations to explore the "what" and the "whether," which have been used for more than one century. These correspond to RT situations.

This is why we will mainly concentrate on RT tasks, in the following, for evaluating the effects, on motor structures, of the cognitive context related to the "what" (and later on the "whether") component of response decision. In the following, we will argue that even for very simple voluntary movements such as, for instance, pressing a button, the dynamics of motor areas can depend on the cognitive context in which these very simple movements have to be executed after the response signal (RS). Contrary to voluntary internally triggered movements, such movements are externally triggered by the RS according to an arbitrary stimulus-to-response mapping rule (given by instructions). It is to be noted that, in general, these simple movements, although externally triggered, are not externally driven as would be the case for, say, tracking a moving target or seizing an object on a table, which control may reveal to be more automatic (bottom-up), once the subject is appropriately trained (Scott, 2016).

Preparing What to Decide

A very popular paradigm to manipulate subjects' knowledge regarding "what" has to be done is the precueing paradigm (Rosenbaum, 1983) and its variants. In this paradigm, the PS can deliver complete, partial, or no information regarding the characteristics of the movement (if any) required by the IS. More abstract information can also be delivered by the PS (for example, about the nature of the stimulus-to-response association). In these conditions, scalp EEG slow negative shifts are evoked during the preparatory interval. The ensemble of these shifts has been named contingent negative variation or CNV (Walter et al., 1964). Precues have a clear influence on the amplitude of the CNV. However, it has been recognized, very early, that the CNV is a complex activity involving several classes of generators, including motor and non-motor structures which, of course, because of volume conduction, often mix at scalp level. To overcome this difficulty the use of the lateralized readiness potential (LRP) has been proposed (e.g., Gratton et al., 1988). If a right-hand or a left-hand response are possible, the CNV may become larger over the hemisphere contralateral to the responding hand when prior knowledge (precue) regarding the responding hand is delivered by the PS (the lateralization occurs after the IS if no precue regarding the responding hand is available) (Kutas and Donchin, 1980). Therefore, the lateralized part of the CNV, during the PP, or the lateralized part of post-IS ERPs (called the LRP) have been assumed to correspond to motor channels activation, generated in contralateral M1 or at least contralateral motor structures (as it is the case for the lateralized part or the BP before elementary movements). Based on this reasoning, it has been concluded that examining the effects of information conveyed by precues on the LRP should allow examining precueing effects specifically on motor structures. However, although asymmetric activation of motor structures do generate LRPs, it has been shown that lateralized readiness activities during PPs may also be generated by non-motor processes generated by non-motor cortices (e.g., Verleger et al., 2000; Praamstra et al., 2005; Mathews et al., 2006; Praamstra and Kourtis, 2010). Therefore, because of volume conduction, motor and non-motor activities may mix at scalp level and may render precueing effects on the LRP difficult to interpret in terms of activation of the motor structures[1].

It is to be noted, as shortly indicated in the section "Introduction," that this "mixing" problem is not specific to LRP studies. Indeed, although EEG is a very suitable technique to study the time course of brain activities, volume conduction may result in overlapping effects in space which may cause, secondarily, a deterioration of EEG temporal resolution (Law et al., 1993; Burle et al., 2015); therefore, specific solutions must be implemented in EEG studies to cope, when necessary, with this difficulty. Sometimes it may be necessary to resort to intracranial recordings. For example, electrocorticography has proven efficient to clearly separate the activities from M1 and PMd in humans (Mattia et al., 2012) while intracerebral recordings (local field potentials) have proven efficient to clearly separate the activities of SMA proper from those of pre-SMA (Bonini et al., 2014). Fortunately, as already indicated, it is not always necessary to resort to intracranial recording in humans to improve the spatial and, as a consequence, the temporal resolution of electrophysiological recordings in humans: it is possible to separate quite efficiently the activities issued from left, right, or medial motor structures using the Laplacian transformation [e.g., Vidal et al. (2003) for an illustration], and, when using a realistic model of each subject's head, it may even provide an "... estimate of the electrical potentials that would be recorded near the cortical surface" (Gevins et al., 1995). In the following, all the reported EEG-based precueing experiments used the Laplacian transformation to examine the effect of different precues on motor (and non-motor) areas. In all cases, precues modified RTs, as could be expected from the relevant literature.

Force and Direction

MacKay and Bonnet (1990) examined the effect of prior information ("what") regarding the force (weak or strong) and the direction (flexion or extension) of an elbow movement, during a 1.5 s PP. The authors showed that prior knowledge about force or direction increased sensorimotor areas activities during the PP, but not the activities of mediofrontal motor areas, including the SMAs (recorded at central midline site). The effect of directional precue on M1 activity was predicted based on a previous stretch-reflex experiment conducted by Bonnet (1983), as will be developed now.

Although the short-latency stretch reflex has a purely spinal origin, long latency stretch responses (LLSR) are, now, admitted to involve oligosynaptic transcortical long loop responses which efferent pathway originates in the motor cortices [Matthews (1991) for a review]. Bonnet (1983) studied the effect of prior knowledge regarding the direction of a wrist movement, on the amplitude of the stretch reflex. Subjects had to perform either a wrist flexion or a wrist extension with their right hand. In some trials, a stretch was applied to the flexor muscles and this stretch could be applied at different moments of the 1 s PP. When the PS indicated in advance that the movement required by the IS would be a flexion, the late component of the LLSR of the flexor muscles increased; when the PS indicated an extension, the same late component decreased. Moreover, these differential effects progressively increased with time during the PP and were maximal just before the IS. Given that the efferent pathway of the LLSR originates in the motor cortices, advance information regarding the nature of the muscles involved in the response generated a progressive increase of excitability of the cortical neurons controlling the acting muscles, or a progressive decrease of excitability of the cortical neurons controlling the muscles antagonists to the required response; this activation/inhibition pattern of the required/non-required responses was reproduced later (Bonnet et al., 1991). Of course, this activation/inhibition pattern might represent a special case, due to the mutually exclusive nature of the activation of antagonist muscles in flexion/extension movements (see below for discussion). Nevertheless, it remains that the effect of prior knowledge regarding the nature (flexion/extension) of the upcoming movement has a strong influence on M1s activity, and this influence is functionally relevant to the task since it was found to be larger in fast (short RT) performers than in slow performers (Bonnet, 1983).

Duration of a Short Motor Sequence

Vidal et al. (1995) studied the time course of preparatory activities over contralateral primary motor areas, contralateral parietal areas, and mediofrontal areas including the SMAs, as a function of prior knowledge regarding the duration (short: 700 ms or long 2500 ms) of an interval delimited by two brief button presses. In other word, the choice was between a short or a long motor sequence. In the early part of the PP, the precues evoked no effect over contralateral M1s, whereas this same precues had a strong and sustained influence over the SMAs. The reverse occurred at the end of the PP: as time elapsed during the PP, the sensitivity of mediofrontal activities vanished. In the same time, activities recorded over contralateral M1s became sensitive to the precues. This exchange in activation across areas suggests that advance preparation began in the mediofrontal motor areas including the SMAs and that information regarding this preparation was transferred to contralateral M1 in the last phase of the PP.

It is interesting to note that over the contralateral parietal areas, contrary the effects observed over motor areas, the precues did not evoked any effect at any time during the 2 s PP.

Relative and Overall Durations of a Short Motor Sequence

Leuthold and Jentzsch (2011) extended these results. In a RT task, subjects had to produce one among four possible sequences of two consecutive key presses. The produced sequence could be either an overall short (500 ms) or an overall long (800 ms)

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[1] Moreover, most often, non-lateralized information regarding the activation of mediofrontal motor structures is lost.

sequence and in each sequence, the duration of the first key press either had to correspond to one-third of the second one or had to last three time more than the second one. The IS was preceded by a PS which could either deliver advance information on overall duration (500 or 800 ms), on relative duration (1:3 or 3:1) or both. The PS could also provide no prior information. The right or the left hand were used in different blocks of trials. A very large activation was observed from the beginning of the PP over the SMA (**Figure 2**) when full advance information was available (overall duration and ratio between first and second press). The comparison between early mediofrontal and M1s activation was not of interest for the purpose of the study and, therefore, was not explicitly reported by the authors; however, from **Figure 2**, it seems that medial sensitivity to the full precue developed very early over the SMAs while it seemed to develop later over the left M1 (whatever the responding hand). Moreover, the activity recorded over the left motor areas was sensitive to partial advance information (overall duration or ratio). Finally, it is interesting to note, as stressed by the authors, that contralateral lateralization was evidenced only after full information. This suggests that prior knowledge regarding the "what" may or may not be conveyed to motor structures, depending on the availability of other complementary information. This suggests the existence of a hierarchy in the motor implementation of prior information regarding the properties of upcoming responses, i.e., motor areas cannot get prepared to certain response characteristics unless prior knowledge regarding other ones is available.

Complexity, in Temporal Order, of a Short Motor Sequence

Leuthold and Schröter (2011) studied the effect of prior information regarding motor sequences that differed in structural complexity but not in length or number (and nature) of involved effectors. When hand and sequence were precued, additional prior knowledge about the structural complexity of the upcoming sequence unequivocally influenced mediofrontal motor structures but leaved M1s insensitive. M1 sensitivity to structural complexity could be evidenced later, after the IS, just before response execution. This sequential sensitivity, between mediofrontal areas and M1s, to sequence complexity, for temporal order, is somewhat similar to the sequential sensitivity to response duration, between mediofrontal areas upstream and primary motor areas downstream (Vidal et al., 1995). These sets of results also suggest that, for temporal order and response duration, there is a functional hierarchy in the implementation of these response characteristics between mediofrontal motor areas, upstream and primary motor areas, downstream.

A comment is in order here. From what precedes (regarding the effects of prior information on motor areas) it is an empirical fact that advance (partial or complete) information regarding specific features of incoming movements does influence the dynamics of motor areas when they get prepared for responding; however, this does not necessary means that these features are coded as such by motor structures. In other words, this does not mean that response parameters or other types of movement characteristics (such as for example the detailed pattern of muscle contractions required to achieve the movement) are represented at the level of motor areas. Certain experimental results are compatible with the view that response parameters and/or kinetic movement properties are coded by motor cortices (e.g., Riehle and Requin, 1989; Kalaska, 2009; Milekovic et al., 2015), while other ones (e.g., Shenoy et al., 2013; Kao et al., 2015) suggest that the evolution of neural activity ". . . should be best captured not in terms of movement parameter evolution, but in terms of the dynamical rules by which the current state causes the next state" (Shenoy et al., 2013, p. 340).

Given that the brain has probably more than one string to its bow, it is not impossible that the response to this important matter may depend on the nature of the control exerted to trigger and/or execute the ongoing movement: bottom up or top down [see Scott (2016) for a clear distinction between these two classes of motor control]. Now, whatever the issue of this controversy (which, nevertheless, is out of the scope of the present article), the sensitivity of motor areas to prior information regarding specific response features allows concluding that the dynamics of these areas is influenced by prior knowledge, that is, by the cognitive context in which these movements are to be executed. Moreover, the fact that motor areas cannot get prepared to certain response characteristics unless prior knowledge regarding other ones is available (Leuthold and Jentzsch, 2011) indicates that motor areas cannot be influenced by just any information regarding upcoming actions. This might put certain constraints regarding the way movements are controlled by motor structures.

Deciding What to Do

During the short time scale (about 500 ms or less) of RT, post-stimulus and pre-response ERPs tend to overlap, due to the joint effects of (1) their temporal proximity and (2) volume conduction (Kutas and Donchin, 1980). As mentioned earlier, to isolate motor components from this ERPs mixture, the use of the LRP has been proposed. We have already presented some difficulties encountered with the interpretation of this measure as a "purely motor" index. Besides these difficulties, another problem has been identified since the very beginning by Gratton et al. (1988, p. 339): the LRP cannot "... distinguish cases in which one response is activated from cases in which the other response is inhibited . . .". What was a theoretical statement at that time turned out to be empirically verified in RT conditions.

Vidal et al. (2003) asked subjects to perform a between-hand choice RT task. They studied Laplacian-transformed ERPs activities over motor areas. These ERPs were time locked to EMG onset (**Figure 3**). Over M1s contralateral to the responding hand, a transient negativity developed before and culminated shortly after EMG onset. Over M1s ipsilateral to the responding hand a transient positive deflection began shortly before and lasted until shortly after EMG onset [but see also Amengual et al. (2014) or van de Laar et al. (2012)]. Several pieces of evidence indicate that the negativity corresponds to contralateral M1 activation while the positivity corresponds to ipsilateral M1 inhibition [see Burle et al. (2004) for a detailed discussion]. Before this activation/inhibition pattern, another component could be evidenced over the SMAs (**Figure 3**). This component began, peaked and resolved before the beginning,

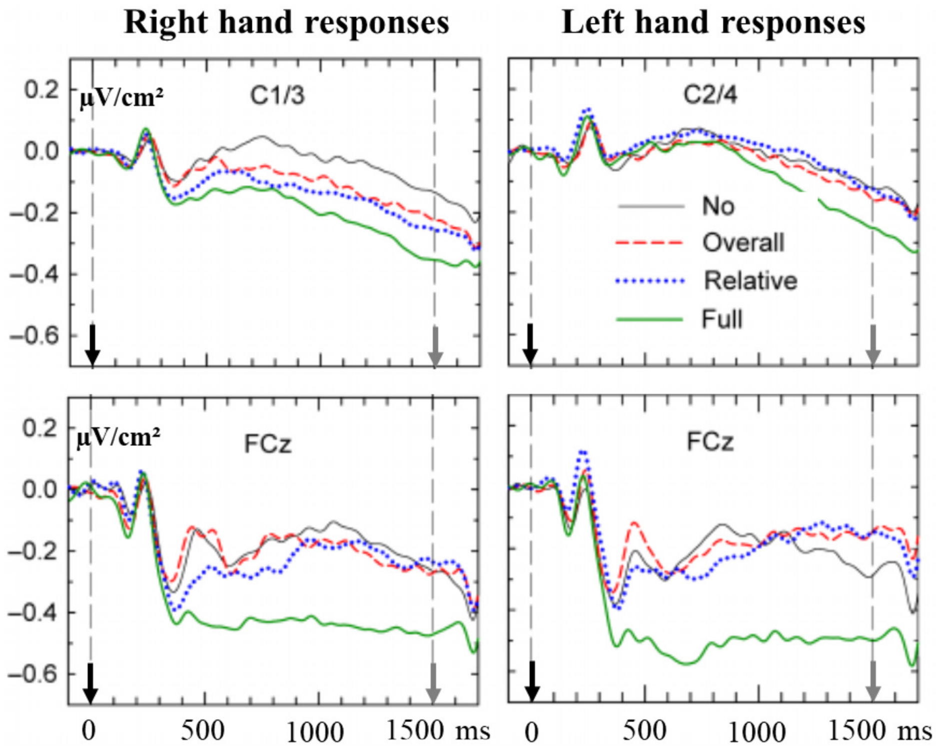

FIGURE 2 | Preparatory effects recorded over the SMAs (lower panel) and M1s (upper panel) before a right hand (left panel), or a left hand (right panel) response, depending on the nature of a precue: No prior information solid black line, information about "relative duration" dotted blue line, information about "overall duration" dashed red line, and full information solid green line (see text for more details). Adapted from Leuthold and Jentzsch (2011). - The upper left panel corresponds to recordings over left M1 (C1/C3) before a right-hand response. - The upper right panel corresponds to recordings over right M1 (C2/C4) before a left-hand response. - The lower left and right panels correspond to recordings over the SMAs (FCz) before a right- or a left-hand response, respectively. On each panel, the black arrow indicates the occurrence of the PS (0 of time) while the gray arrow indicates the occurrence of the response signal (at 1500 ms).

the peak, and the resolution of M1 activation, respectively. It was called N-40 because it culminates about 40 ms before EMG onset [but see also Mansfield et al. (2012) who discovered independently this same component and named it N-120 by reference to response-locked data instead of EMG locked]. Therefore, when a decision regarding what to do must be taken under time pressure, both M1s are involved (although very differently) as well as the mediofrontal motor structures (recording electrodes placed over the premotor cortices did not evidence any specific components before EMG onset). Note that these components are perfectly mixed on scalp potentials recordings and cannot be identified unless separation methods (here Laplacian transformation) are applied [see Burle et al. (2015, figure 7) for a demonstration].

Tentative source localization identified the generator of the N-40 within the SMAs (Carbonnell et al., 2013). Inverse problem solutions must always be interpreted cautiously; however, these localizations used two independent inversion methods, both pointing to a quite superficial generator, consistent with the fact that Laplacian-transformed data hardly pick up deep sources activities. Therefore, it seems rather safe to admit that the generator or, at least, the main generator of the N-40 is a superficial one lying in the SMAs. Although the Laplacian transformation dramatically improves the spatial (and temporal) separation of distinct generators, this improvement is not sufficient, however, to distinguish between the subdivisions of the SMAs, namely pre-SMA and SMA-proper (Luppino et al., 1991; Matsuzaka et al., 1992) and the inversion methods did not allow either to separate the activities of these two subdivisions. However, Ramdani et al. (2018) showed that the amplitude of the N-40 was reduced by acute dopamine depletion, provoked by diet-induced depletion in the precursors of dopamine synthesis (McTavish et al., 1999), namely tyrosine and phenyl-alanine. On the other hand, neither Larson et al. (2015) nor Ramdani et al. (2018) found any reduction of the error negativity (Falkenstein et al., 1991; Gehring et al., 1993), a response-related ERP for which amplitude is modulated by performance (it is usually large on errors and small on correct trials; Vidal et al., 2000). Now, being established by intracerebral recordings in humans that the generator of the error negativity or at least its main generator, lies in the SMA proper but not in the pre-SMA (Bonini et al., 2014), one can conclude that SMA proper activity is not noticeably impaired by acute dopamine depletion. Therefore, the dissociation between the N-40 and the error negativity as regards their sensitivity to dopamine depletion, suggests that the generator of the N-40 (or at least its main generator) lies in pre-SMA but not in SMA-proper.

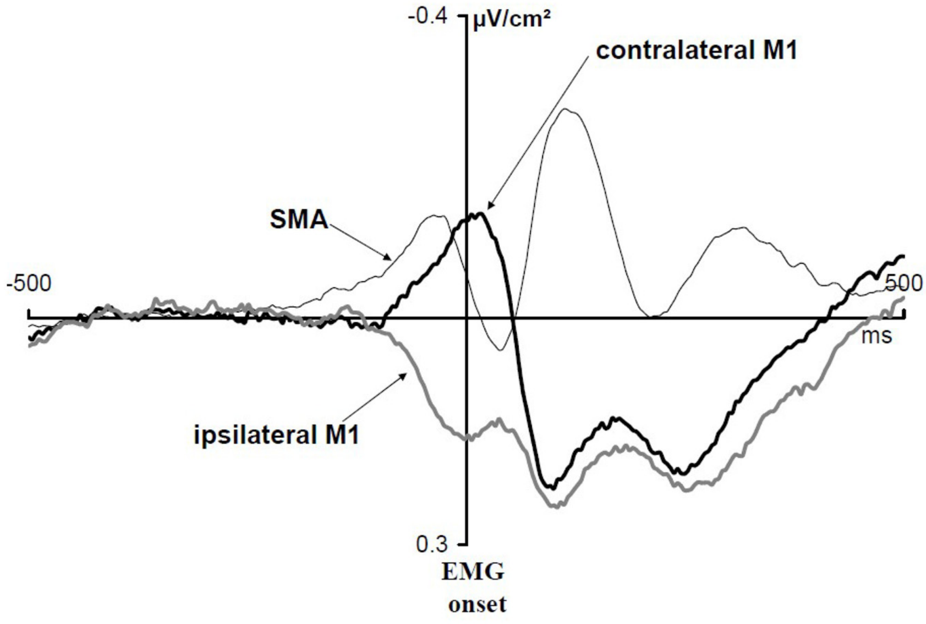

FIGURE 3 | EMG-locked ERPs recorded over M1s and SMAs in a between-hand choice RT task. Adapted from Vidal et al. (2003). Activation of contralateral M1s (black thick line), inhibition of ipsilateral M1s (gray thick line), and N-40 (black thin line). Laplacian-transformed data.

Two main differences show up between spontaneously triggered movements or preparatory process, on the one hand, and externally triggered movements to be chosen under time pressure, on the other hand. The first one is obvious: even though there is an additional decision to be taken regarding "what" in choice conditions, the time course of motor areas activations develops in much shorter time ranges: no more than 300–400 ms before EMG onset. The second one is motor inhibition. To our knowledge, in spontaneously triggered movements, no inhibition of the non-involved primary motor cortex has been described. For example, in the Dirnberger et al.'s (2000) study, participants, on each trial, had either to alternate or to spontaneously choose which hand should spontaneously be moved. No sign of inhibition at M1 level was evidenced, although the extra activation recorded over the SMA in the choice condition was interpreted by the authors as a need for inhibition.

Of course, during a PP, Bonnet (1983) evidenced an activation/inhibition pattern between flexors and extensors at M1 level, via transcortical long-loop reflexes. However, this may have resulted from some sort of reciprocal inhibition between agonistic and antagonistic muscle commands, which are mutually exclusive, if flexion or extension is required. In the present case, each hand is not "naturally" antagonistic of the other one. Instructions only, render them mutually exclusive.

We will see now that ipsilateral M1 inhibition is not the mere by-product of a variant of (hard-wired) reciprocal inhibition between right and left M1s, but that it is driven by the cognitive context of the task.

In some situations, the decision process must also take into account not simply "what" to do but also the likelihood of each possible response. Meckler et al. (2010) compared a standard between-hand choice RT task to a "biased" one. In the biased task, one of the two possible responses was frequent (80%) and the other one was rare (20%). In cognitive terms, one response was expected, while the other one was unexpected (expectancy was manipulated between-blocks). In the standard task (50% right 50% left) no specific expectation could be drawn from the situation.

As could be anticipated, no effect of expectancy was observed over contralateral M1. Indeed, there is good evidence from corticograms recorded in monkeys as well as in humans that the motor potential (contralateral negativity) represents the activation of M1 contralateral to the responding hand [see Vidal et al. (2003) or Burle et al. (2004) for a discussion on this point].

On the contrary, response expectancy had a clear effect on ipsilateral inhibition, i.e., on inhibition of M1 involved in the not to be given response. It was very small (yet present) when subjects produced the expected response (hence inhibited the unexpected one), very large when subjects produced the unexpected response (hence inhibited the expected one), and just in between when no specific expectation could be drawn (i.e., standard choice condition). We concluded that ipsilateral inhibition is a context-dependent component representing a pro-active control of errors, that is, a mechanism aimed at preventing the risk of committing an error. Consistent with this interpretation, was the fact that, in the unexpected condition (where ipsilateral inhibition was the strongest), there was a negative correlation between the size of this component and the error rate: subjects who presented the strongest inhibitions were those who presented the smaller error rates.

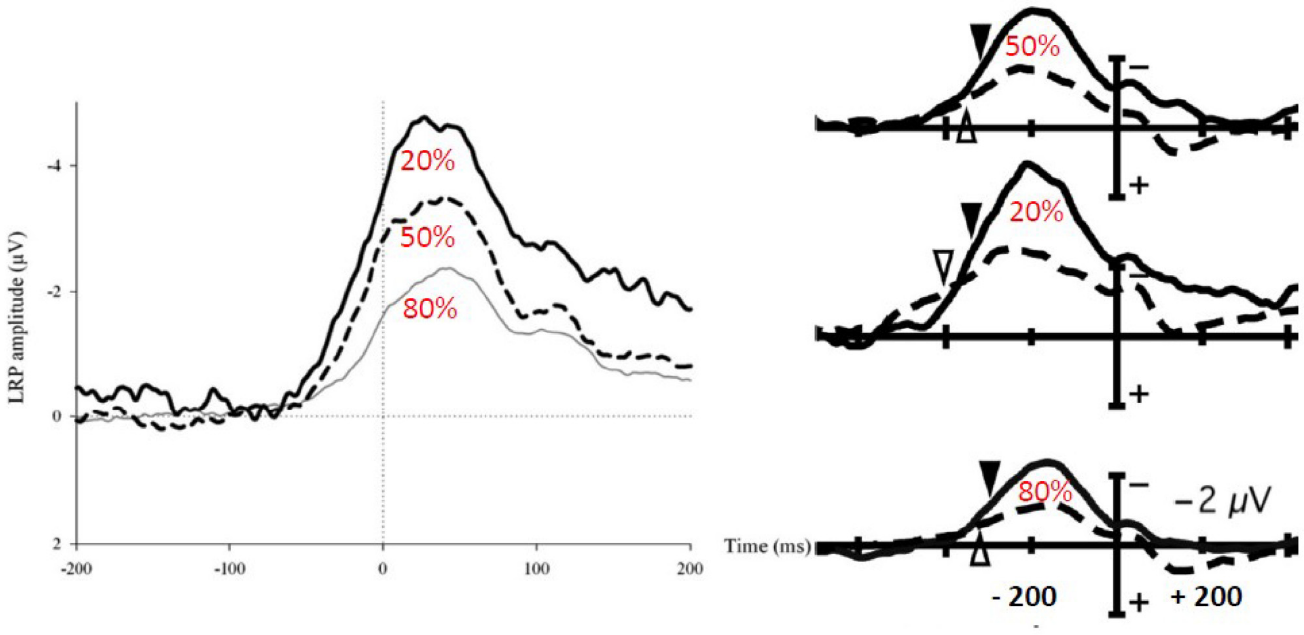

FIGURE 4 | Effects of a probability bias on EMG locked LRPs. The LRP corresponds to the difference between activities recorded over M1 contralateral an ipsilateral to the response. Left panel [adapted from Vidal et al. (2015)]: EMG-locked LRPs computed from the data reported in Meckler et al. (2010) in a between-hand choice RT task. Each trace corresponds to expected responses (80% thin line), no-expectation responses (50% dashed line), and unexpected responses (20% bold line). Right panel [adapted from Luck et al. (2009)]: response-locked LRPs from Luck et al. (2009) in healthy controls (solid lines) and schizophrenic patients (dashed lines). Lower traces correspond to expected responses (80%), middle traces correspond to unexpected response (20%), and upper traces correspond to no-expectation responses (50%). The latency differences between left and right panel are due to EMG locking and response locking on the left and right panels, respectively.

Back to the problem identified by Gratton et al. (1988) regarding the use of the LRP and the possible confound between contralateral activation and ipsilateral inhibition, the results of Meckler et al. (2010) demonstrate that this theoretical concern turned into a concrete difficulty.

Luck et al. (2009), also compared the effects of expectancy on motor ERPs (also with 50/50 and 80/20 probabilities in different blocks of trials) but they did so using the LRP in healthy control subjects and schizophrenic patients. **Figure 4** (right panel) shows that the LRP increases from expected to unexpected responses, the no expectation condition being in between. The authors interpreted their results in terms of motor activation "… when a given stimulus category is expected, the appropriate response can be prepared before stimulus onset and less stimulus-triggered response activation (and hence less LRP) may be needed once the stimulus has been presented …" (p. 7). Scalp potential LRP-transformed data from Meckler et al. (2010) were calculated by Vidal et al. (2015), and it appears from **Figure 4** (left panel) that they obtained exactly the same time course and patterns of activity as those reported by Luck et al. (2009). Therefore, contrary to the interpretation given by Luck et al. (2009), the LRP decrease with response expectancy was not due to decreased activation of the required response. On the contrary, this decrease was due to decreased inhibition of the non-required response.

Schizophrenic patients in Luck et al. (2009) showed decreased LRPs when compared with healthy subjects in all conditions (**Figure 4**, right panel). It is not possible to draw any functional or physiological interpretation from this observation because this effect could be due to decreased activation, decreased inhibition, or both. "Simple" effects of conditions on the LRP correspond, in fact, to interactions between sites (contralateral/ipsilateral) and experimental conditions. Therefore, no firm conclusions can be drawn regarding the causes of these interactions.

Manipulating the probability of a response modulates incorrect response inhibition. A question remains as to when this modulation is set. Indeed, in the studies quoted above, the participants knew at the beginning of each block the probability bias. They could have hence set *a priori* an asymmetric inhibition coefficient, explaining the observed modulation. Burle et al. (2016) evaluated whether this modulation is set *a priori* or is modulated online as a function of the context. Instead of manipulating the probability of individual responses, they manipulated the probability of compatible and incompatible trials (30% vs. 70%), in a Simon task [Simon (1990) for a review]. In the rare-incompatible condition, participants tend to activate the response ipsilateral to the stimulus. When an incompatible trial occurs, the risk of an error is hence very high. On such trials, inhibition was larger on incompatible than in compatible trials (**Figure 5**). On the contrary, in the frequent-incompatible condition, in which the risk of committing an error was low, no effect of compatibility was observed on ipsilateral inhibition.

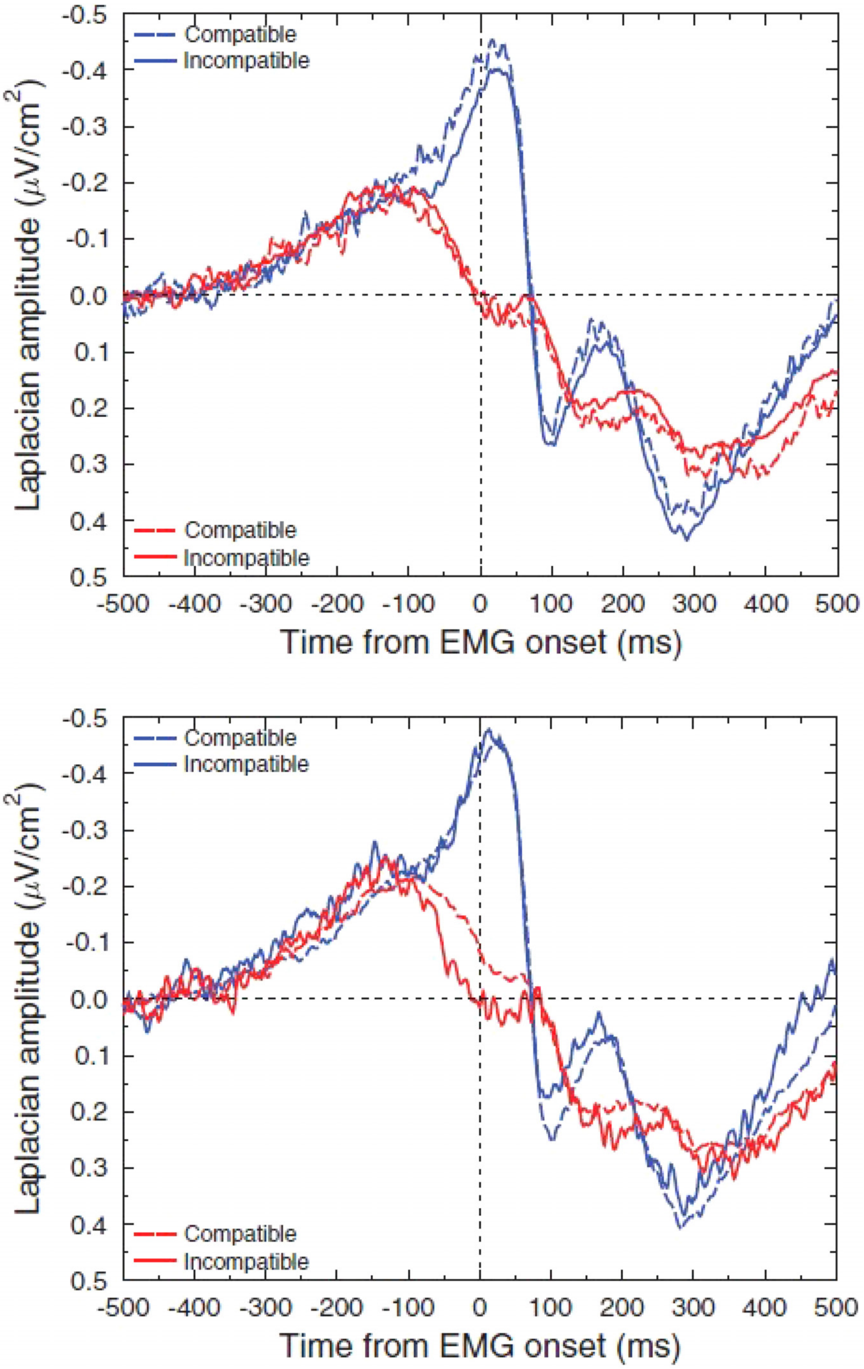

FIGURE 5 | Effect of the probability of compatible and incompatible trials on ipsilateral inhibition. Adapted from Burle et al. (2016). Upper panel: activation (M1 contralateral to the responding hand: blue lines)/inhibition (M1 ipsilateral to the responding hand: red lines) pattern in compatible (dashed lines) and incompatible (solid lines) trials when incompatible trials are highly probable. Lower panel: activation (M1 contralateral to the responding hand: blue lines)/inhibition (M1 ipsilateral to the responding hand: red lines) pattern in compatible (dashed lines) and incompatible (solid lines) trials when compatible trials are highly probable.

It must be stressed that in this experiment, all responses (right and left) and stimulus positions were equiprobable. Hence, the level of required inhibition had necessarily to be set after the IS, since compatibility could vary from one trial to another. In other words, high expectancy regarding compatibility did not result in a constant ipsilateral stronger inhibition for all the trials but in fast stimulus-triggered trial-by-trial adjustments of inhibition to congruency. This demonstrates the high versatility of these knowledge-dependent (i.e., cognitive-pendent) motor effects.

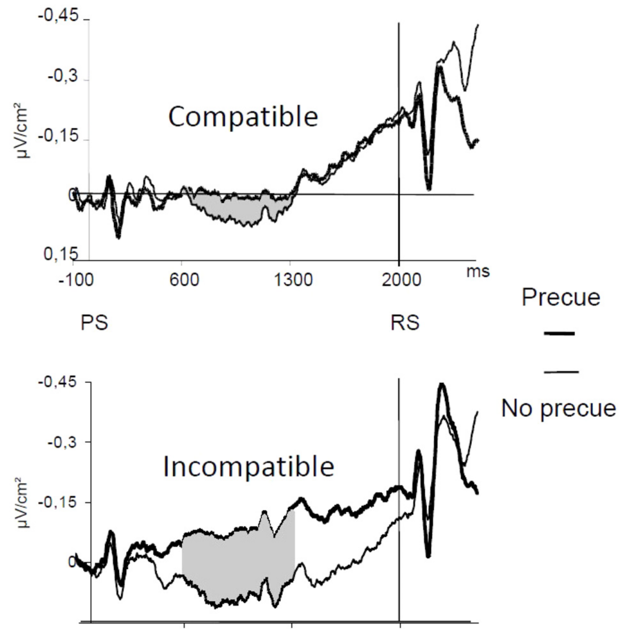

FIGURE 6 | Effect of stimulus response compatibility on the sensitivity of the CNV to advance information. Adapted from Carbonnell et al. (2002). CNVs recorded over the SMAs (FCz) as a function of precueing: bold lines: hand precued, thin lines hand uncued. Upper panel: compatible mapping. Lower panel: incompatible mapping. PS, preparatory signal; RS, response signal.

DECIDING: "HOW," "WHETHER," OR NOT DECIDING AT ALL

How

In several RT task situations, the stimulus-to-response (S–R) mapping is arbitrary and necessitates applying a rule. This rule specifies *how* to transform a given stimulus into an appropriate response. The mapping rule can be quite easy or difficult to apply, easiness being judged by its effect on RTs and error rates. This is on this aspect of the "how" (to transform a given stimulus into an appropriate response) that will focus now.

Carbonnell et al. (2002) asked subjects to press a right or a left button according to the IS: a word centrally presented on a screen. The words could be either "droite" or "gauche" (right or left in French). Two seconds earlier, the PS could either be the same word as the IS or the word "neutre" (neutral in French). This last PS conveyed no prior information regarding the responding hand. Two different groups of subjects had to apply two different S–R mapping rules. The easy rule consisted in pressing the right button in response to the word "right" and the left button to the word "left." This condition was said "compatible." The uneasy rule was opposite: right response to the word "left" and left response to the word "right." This condition was said incompatible.

When no precue was available (PS: "neutral") RTs were longer for the incompatible group than for the compatible group. When a precue was available no RT differences were observed between the two groups. This latter result is not unexpected since it is assumed that when precued, the S–R mapping (or response selection operation) is completed during the PP.

When the responding hand was precued, no effect of the precue could be evidenced above the primary motor areas during the PP, neither in the compatible, nor in the incompatible group. A different picture showed up over the mediofrontal motor areas. Activity was slightly (yet non-significantly) larger in the precue than in the no-precue condition for the compatible group. On the contrary, at the same recording site, a very strong and long-lasting effect of the precue was observed for the incompatible group (**Figure 6**). Therefore, the nature of the transformation of a given stimulus into a given response has a strong influence on mediofrontal areas (including the SMAs), but let primary motor areas insensitive, suggesting that SMAs are specifically involved in response selection, acting upstream to M1s, which would be more concerned by execution processes. One might argue that not only do response selection processes can take place during the PP, but also response programming, which is true. However, in the present case, the movements to be performed were identical; as such, the programming operations needed to prepare them was not different between groups. Therefore, the interaction observed between group (compatible/incompatible) and precueing (precued/uncued) factors could be attributed to nothing but the nature of the S–R mapping rule to be applied, i.e., solving the "how" problem.

Whether

The prototypical paradigm in which the "whether" component of response decision is best explored in RT tasks is the Go Nogo task. In these tasks, only one response is possible and, according the nature of the IS, subjects have to choose whether or not they will respond. At variance with Brass and Haggard (2008) assumption, it has been proposed that deciding between executing a response or withholding it involves the same (Nieuwenhuis et al., 2003; Gomez et al., 2007) or, at least similar (Verleger et al., 2006) types of motor decision as deciding to execute one among several responses.

Vidal et al. (2011) examined the pattern of activation of SMAs and M1s in a between-hand choice RT task and a Go Nogo task, performed in different blocks of trials. Their results are in line with Brass and Haggard (2008) assumption. Deciding "what" or deciding "whether" involve qualitatively different processes. Considering that there was no risk of committing an error, no ipsilateral inhibition was expected and, indeed, there was no sign of ipsilateral inhibition in the Go Nogo task, contrary to the choice condition. More important, contrary to the choice task, there was no N-40 in the Go Nogo condition (**Figure 7**). This shows that the SMAs were not involved in the decision required in the Go Nogo task and suggests that the N-40 is a physiological sign of choice (and/or motor programming) between alternative movements.

But what about activation? In the Go Nogo task, activation was significantly shorter (more phasic) than in the choice condition and, indeed, the time separating EMG onset from the mechanical response was longer in the choice than in the Go Nogo task. Therefore, in the comparison between "whether" and "what," the build-up of the motor command is also affected, and this results

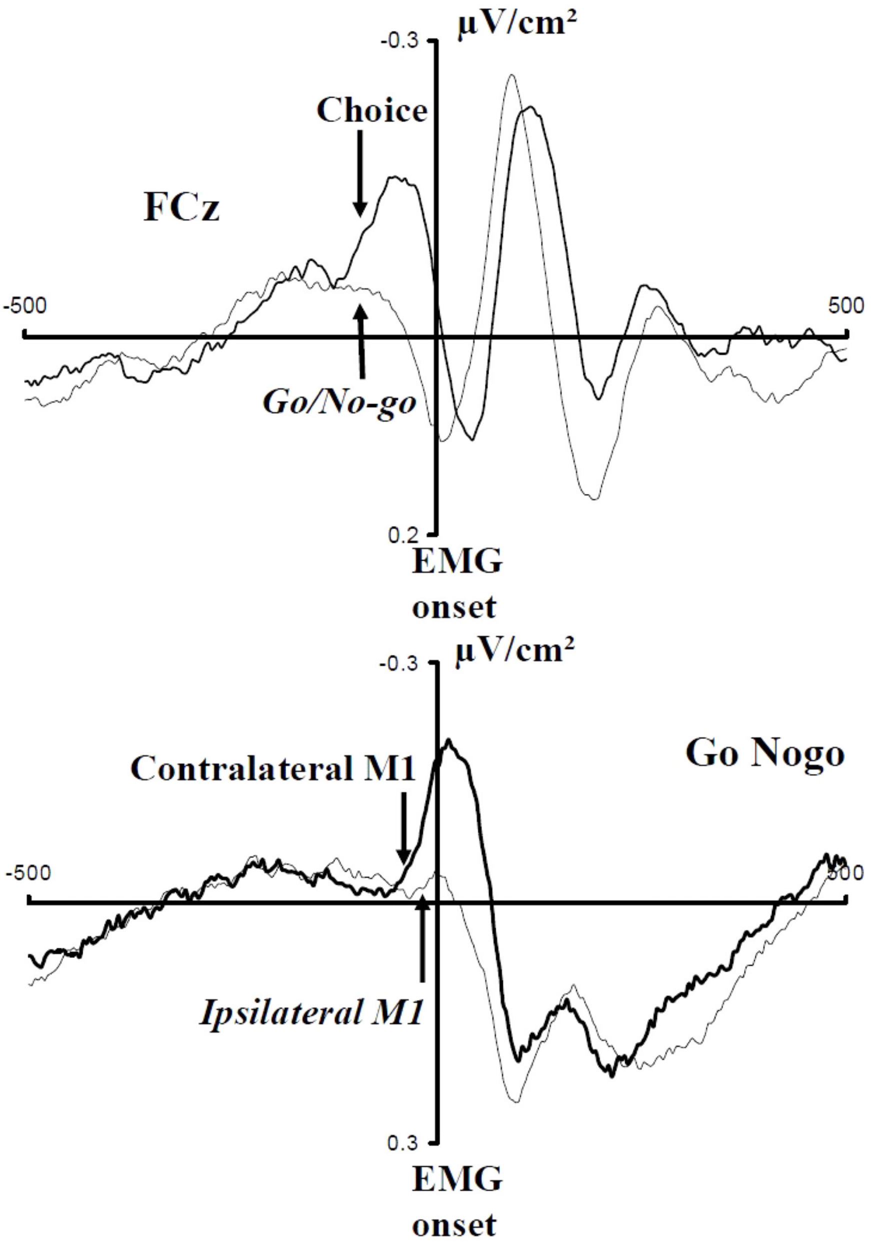

FIGURE 7 | Effect of the nature of the decision to be performed (Choice vs. Go-Nogo). Adapted from Vidal et al. (2011). Upper panel: activities recorded over the SMAs in Choice (bold line) and Go Nogo (thin line) tasks; note the absence of a N-40 in the Go Nogo task and its presence in the choice task. Lower panel: activities recorded over contralateral (bold lines) and ipsilateral (thin lines) M1 in a Go Nogo task; note the absence of inhibition before EMG onset.

in different execution times. This is in line with observations reported by Ulrich et al. (1999) who showed that Go Nogo tasks yield more forceful responses than choice RT tasks.

In other words, even the motor command can be affected by the decisional context in which this command must be issued and executed.

Another interesting situation can be informative about the "whether" element of response decision: the Stop Signal paradigm (e.g., Logan and Cowan, 1984). While in the Go Nogo tasks the IS can require to withhold a prepared response, in the Stop task, the IS always indicate a response. However, in a certain proportion of trials, the IS is followed by another signal (the so-called "stop" signal) requiring withholding the response indicated by the IS. RTs of correctly executed responses have been shown to be influenced by the possible presence of these stop signals: RTs are longer on go trials of a stop task compared to (classical) go-only tasks (e.g., Mirabella et al., 2006). However, this contextual increase in RT does not necessarily mean that motor processes or motor structures are concerned. Mirabella et al. (2008) went a step further and examined the execution of hand-reaching movements in a stop and a non-stop context in humans. They observed again that RTs of correct go responses of a stop task were longer than RTs of a go-only task. More important, they evidenced an increase in the movement time, i.e., the time separating movement onset from target reaching. It is very likely that movement time corresponds to the involvement of motor structure during execution, and/or completing "... of the motor plan during the execution of the reach" (Mirabella et al., 2008, p. 1007). It is to be noted that contrary to Go Nogo tasks where only one go response is possible, a choice is required in the go trials of a stop task, as it is the case in a (classical) go-only task. Therefore, the differences in RT and/or movement time evidenced by Mirabella et al. (2008) cannot be attributed to a difference in the number of possible responses. As a consequence, these results indirectly show that knowledge about the possible occurrence of a stop signal after the IS (i.e., cognitive context) has a strong influence on (at least) motor areas functions on go trials (Mirabella et al., 2008).

Besides motor areas, subcortical structures certainly take part to contextual effect and, interestingly, it has been shown that the subthalamic nucleus is causally involved in stop-related context-dependent effect (Mirabella et al., 2013); however, this is clearly out of the scope of the present review and we will not develop further the implication of motor-competent subcortical structures in contextual effects.

Not Deciding at All

In certain conditions there is no decision at all to be taken during the RT period, regarding the upcoming response. These situations regarding decisional processes can be found in simple RT tasks. Burle et al. (2004) presented data obtained in a simple RT task (figure 7 on p. 159 of Burle et al., 2004). As can be expected from what precedes, no inhibition was evidenced over ipsilateral M1 and no N-40 was evidenced over the SMAs.

Now, Carbonnell et al. (2004) used a precueing paradigm in which the PS either precued which response (right or left) should be executed after the IS or did not precue the responding hand. Precue and no-precue trials were presented in pseudo random order. Therefore, at the occurrence of the IS, subjects had to decide which response should be executed in the no-precue condition while in the precue condition, no choice was necessary if we admit that decision took place during the 2 s PP. In other words, one may consider that precue trials functionally correspond to a simple RT task while no-precue trials functionally correspond to a choice RT task.

According to these assumptions, one should expect ipsilateral inhibition preceded by a N-40 in the no-precue condition and neither ipsilateral inhibition nor N-40 in the precue condition. The no precue-condition conforms to these predictions but this is not the case for the precue condition. In the precue condition, a very small but significant inhibition developed over ipsilateral M1 and a small, short-lasting but significant, N-40 also developed over the SMAs. Of course, there was a very large difference between these inhibitions and N-40s, between the precue and no precue conditions. Nevertheless, contrary to what happened in the blocked simple RT task or in the blocked Go Nogo task, N-40 and ipsilateral inhibition had not completely vanished. We reasoned that this could, at least in part, be due to the fact that precue and no-precue trials were mixed in the same blocks of trials. It is possible that in the precue condition, even though no choice was necessary after the IS, the contralateral response still belonged to the repertoire of the possible responses and, as such, required a small amount of, "by security" decision and inhibition. In other words, in the precue trials there would persist a kind of "cognitive remanence" of the S–R mapping requirements to be applied in no-precue trials.

But what about activation? There was no reliable difference between choice (no precue) and simple (precue) conditions over M1 contralateral to the response. Given what has been obtained in the Choice vs. Go Nogo comparison, this may appear surprising. Nevertheless, this, again is in line with the observations reported by Ulrich et al. (1999), who showed that although Go Nogo tasks yield more forceful responses than choice tasks, the force developed in choice tasks does not differ from the force developed in the simple tasks. This later point is consistent with the fact that the EMG bursts (from which the exerted force results) were identical in precue and no-precue conditions in Carbonnell et al.'s (2004) experiment.

The antecedence of sensitivity of SMAs to certain precues during PPs, compared to M1s, the antecedence of SMAs and PMds activation in spontaneously triggered movements or in RT tasks, compared to M1s and finally the disappearance of SMAs activation when no choice is required in RT tasks, suggest the existence of a hierarchy between motor areas, M1 being downstream. But this question is far from being definitely settled, and this view has been strongly challenged [see for example, Cisek and Kalaska (2010) or Mirabella (2014) for a distributed conception of motor decisions].

Moreover, although this article focuses on the sensitivity of motor areas (M1, SMA, and PMd) to cognitive context, we do not mean in any way that these are the only structures to be influenced by this context or that they are the only structures concerned with the decisional context (as indicated before): for example, parietal (e.g., Wheaton et al., 2005), or prefrontal areas (e.g., Brass and Haggard, 2008) may be concerned, as well as subcortical structures (e.g., Mirabella et al., 2013).

MORE GENERAL COGNITIVE ATTITUDE *VIS-À-VIS* THE UPCOMING ACTION

Motivation

In an early study, McAdam and Seales (1969) manipulated the level of motivation of subjects performing simple spontaneously triggered movements through monetary reward. In the motivated condition, the BP was larger than in the non-motivated condition.

However, one cannot exclude that motivational effects may be confounded with attentional ones. For example, in this experiment, subjects were told that a reward would be delivered for each "correct" button press, signaled by an auditory tone. However, as indicated by the authors "These instructions were

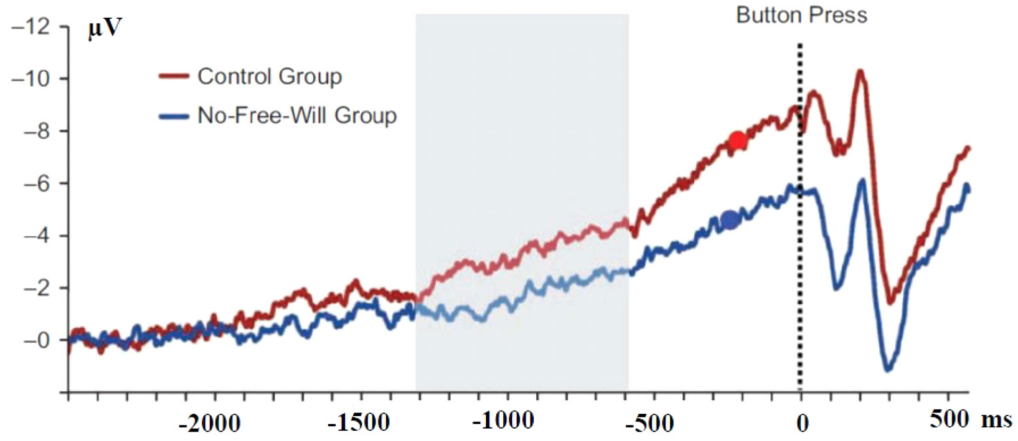

FIGURE 8 | Effect of belief in free-will on the amplitude of the BP. Adapted from Rigoni et al. (2011). Response-locked movement-related activities in control subjects (red line) and subjects who red a text inducing disbelief in free-will (blue line). The red and blue dots indicate the time of decision in control and No-Free-Will groups, respectively. Differences became significant during the period indicate in gray.

kept vague and subjects were allowed to form their own hypotheses about what might be 'correct' response. . . " (McAdam and Seales, 1969, p. 74). As a consequence, an alternative interpretation in terms of attention cannot be excluded: subjects might have allocated more attention to their response in the reward condition than in the standard one (without good or bad response and no reward), in order to guess which movement characteristic might be followed by a "correct" (reward) signal.

Nevertheless, the motivational context did affect the activity of motor areas, as revealed by the BP preceding these simple spontaneously triggered movements, either directly or indirectly through motivation-induced attentional involvement.

Attention

If subjects producing short sequences of unilateral spontaneously triggered simple movements are required to perform a concurrent task, the BP is reduced if the concurrent task requires a high attentional load (Baker et al., 2011). This decrease cannot be attributed to a general reduction of cortical activity, since decrease was maximal over central areas for the early BP, and specific to central and ipsilateral sites for the late BP; no effect of attentional load was evidenced at contralateral sites. Although it is always risky to draw strong inferences from surface potential data (Nuñez, 1981; Kayser and Tenke, 2015; Vidal et al., 2015), it is likely that these effects were attributable to a decrease in SMA activity, in line with fMRI data indicating an increase of movement-related SMA BOLD response when subject pay attention to their intention to move (Lau et al., 2004).

Going a step further, Rigoni et al. (2013) attempted to precise the dynamics of cortical activation in the task used by Lau et al. (2004): a variant of Libet et al. (1983) paradigm. Subjects simply pressed a key at the time of their own choosing while watching a rotating clock hand. They were instructed either to pay attention to their intention to move by reporting the moment (position of the clock hand) when they had the intention to act (W condition) or to pay attention to their action by reporting the moment when they began moving (M condition). To attenuate spatial and temporal overlapping effects due to volume conduction, the authors resorted to the Laplacian-transformation. Over the SMAs, the BP was much larger in the W than in the M condition and this effect showed up very early. An opposite pattern was observed over M1 contralateral to the response: the late part, and the late part only, of premovement activities was larger in the M than in the W condition.

First, this confirmed that the increase of SMA BOLD activity reported by Lau et al. (2004) in the W condition concerns premovement activity, consistent with the tight focus observed over the SMAs for the early BP in Rigoni et al.'s (2013) data. Moreover, these data evidenced a dissociation between SMA and M1 activities as a function of attentional conditions. Finally, it must be stressed that these differences showed up under precise EMG control with no EMG differences between W and M conditions. Therefore, it was evidenced that the dynamics of motor areas (even M1) strongly depend on the cognitive state of the subjects, although the executed movements and their motor commands were identical.

Intentionality

Since the first article of Libet et al. (1983), showing that BP onset precedes the conscious decision to move, there has been a long-lasting, yet unresolved, debate regarding the functional significance of this observation. However, whatever the final outcome of this controversy, it has been demonstrated that instructions regarding the decision influence the BP dynamics. Keller and Heckhausen (1990) compared the BPs preceding involuntarily and voluntarily triggered movements. Involuntary movements consisted in irrelevant slight movements of the finger hand or wrist, performed automatically while subjects were involved in a counting task (counting backward from

3521 in steps of 3). Voluntary movements were obtained in a replication of Libet et al. (1983) paradigm. The voluntary movements evoked larger BPs. Now, voluntary movements were accompanied by larger EMG activity; it is well established that there is a monotonic relationship between the size of the EMG burst and the produced force (Bigland and Lippold, 1954; Bigland-Ritchie, 1981). Given that increased movement force is associated with larger BPs (Kutas and Donchin, 1974) this effect might have corresponded to a by-product of movement force. However, this interpretation is unlikely because the effect of intentionality was confined to midline frontocentral electrodes, indicating either that the involved generators were recruited differentially for involuntary and voluntary movements, or even that midfrontal generators were inactive before involuntary movements.

Up to now, elementary cognitive states such as decisional context, attention motivation, or intentionality have been shown to influence the dynamics of the recruitment of motor areas before movements. More complex cognitive states such as personal belief may also have a strong influence. Rigoni et al. (2011) asked two groups of subjects to read two different texts, one of which had been shown to induce disbelief in free will, the other one being neutral to this respect.

Afterward, using the Libet et al. (1983) paradigm, subjects had to produce self-paced simple movements and report the moment when they decided to act. The "disbelief group" showed reduced BP amplitudes as early as one second before the reported time of intention to act (**Figure 8**). Moreover, early (but not late) BP amplitudes (assumed to be generated by medio-frontal structures) correlated negatively with subjects personal free will disbelief scores. Interestingly, disbelief had no influence on the reported time of intention to act.

How can such elaborated cognitive context such as beliefs influence the dynamics of motor structures, remains an open question. One might speculate, for instance, that these effects are achieved via less motivational and/or attentional involvement. In any event, whatever the final answer to this question, it remains that ". . . beliefs about free will can change brain processes related to a very basic motor level . . ." (Rigoni et al., 2011, p. 617).

To conclude, it appears clearly that the way we do does not solely depend on what we do. It also depends on our knowledge regarding the circumstances in which we must do. More specifically, motor structures and motor processes are permeable to cognitive operations; motor processes are very sensitive to the influence of cognitive operations and might, as well, contribute to elementary aspects of cognition. Finally, motor structures being a final pathway of several cognitive operations, they can be studied not only for themselves, but also to probe the nature of the upstream cognitive operations that finally recruit them.

AUTHOR CONTRIBUTIONS

All the authors participated to the redaction of this article.

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Accuracy of Motor Error Predictions for Different Sensory Signals

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Detecting and evaluating errors in action execution is essential for learning. Through complex interactions of the inverse and the forward model, the human motor system can predict and subsequently adjust ongoing or subsequent actions. Inputs to such a prediction are efferent and afferent signals from various sources. The aim of the current study was to examine the impact of visual as well as a combination of efferent and proprioceptive input signals to error prediction in a complex motor task. Predicting motor errors has been shown to be correlated with a neural signal known as the error-related negativity (Ne/ERN). Here, we tested how the Ne/ERN amplitude was modulated by the availability of different sensory signals in a semi-virtual throwing task where the action outcome (hit or miss of the target) was temporally delayed relative to movement execution allowing participants to form predictions about the outcome prior to the availability of knowledge of results. 19 participants practiced the task and electroencephalogram was recorded in two test conditions. In the *Visual* condition, participants received only visual input by passively observing the throwing movement. In the *EffProp* condition, participants actively executed the task while visual information about the real and the virtual effector was occluded. Hence, only efferent and proprioceptive signals were available. Results show a significant modulation of the Ne/ERN in the *Visual* condition while no effect could be observed in the *EffProp* condition. In addition, amplitudes of the feedback-related negativity in response to the actual outcome feedback were found to be inversely related to the Ne/ERN amplitudes. Our findings indicate that error prediction is modulated by the availability of input signals to the forward model. The observed amplitudes were found to be attenuated in comparison to previous studies, in which all efferent and sensory inputs were present. Furthermore, we assume that visual signals are weighted higher than proprioceptive signals, at least in goal-oriented tasks with visual targets.

Keywords: EEG, error negativity, feedback-related negativity, error prediction, reinforcement learning, forward model

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INTRODUCTION

Previous research suggests that prediction represents a general framework underlying many perceptual and motor processes (Yuille and Kersten, 2006; Friston and Kiebel, 2009; Bubic et al., 2010; Bar, 2011; Clark, 2013). Predictive motor control is closely connected to the concept of internal models. It is currently thought that the motor system uses two forms of internal models:

inverse models and forward models (Jordan and Rumelhart, 1992; Miall and Wolpert, 1996; Wolpert and Flanagan, 2001; Shadmehr et al., 2010). Inverse models relate intended action goals to the motor commands to achieve those goals and thus generate motor commands sent to the effectors to produce the intended sensory consequences. Forward models represent the inverse direction of causality relating the motor commands to the resultant sensory consequences and thus predict the future state of the sensorimotor system. These predictions can serve a multitude of functions, such as compensating for delays and noise in neural signal transduction, distinction between self and others, attenuation of self-produced sensory reafferences, or facilitating executive functions such as response inhibition (Mirabella, 2014). In this study, we seek to explore predictive mechanisms underlying performance monitoring and error perception in the course of motor learning.

In the context of motor learning, humans constantly need to process information from the environment and from internal sources to improve and maintain performance. In order to improve the performance in a motor task and learn from previous errors, we have to be able to detect that the intended action goal has not been achieved and subsequently attribute this failure to a cause (Holroyd and Coles, 2002). Predictions generated by an internal forward model can support error attribution. If errors were predicted by the forward model during action execution, these errors would most likely be due to internal causes (e.g., inappropriately selected motor commands). On the other hand, if the intended action goal was not achieved and no error was predicted by the forward model throughout the movement, errors should be attributed to external perturbations (e.g., the wind has changed the trajectory of the ball during a free kick in soccer) and should not trigger subsequent adjustments to the motor commands as long as the perturbations are unsystematic. Another advantage of error prediction pertains to the learning of sensorimotor skills that are characterized by a temporal separation of action execution and the perception of action outcome. Based on the observation that delays in the availability of feedback about the outcome of an action attenuate sensorimotor learning (Kitazawa et al., 1995; Kitazawa and Yin, 2002; Brudner et al., 2016; Schween and Hegele, 2017), predicting errors before they actually occur could support learning, as the error signal would be closer in time to movement execution. Thus, forward model predictions can offer valuable information to adequately adapt movements during motor learning.

The importance of forward model predictions in learning and their development are highlighted by both computational models (Jordan and Rumelhart, 1992; Wolpert et al., 1998; Haruno et al., 2001) and empirical studies (Flanagan et al., 2003; Tseng et al., 2007; Shadmehr et al., 2010). Neurophysiological approaches, more specifically the analysis of event-related potentials (ERPs) in the electroencephalogram (EEG), provide more detailed insights into the time course of error processing and prediction. Two of the most prominent ERPs in the EEG with respect to error processing are the error-related negativity (Ne/ERN; Falkenstein et al., 1991b; Gehring et al., 1993) and the feedback-related negativity (FRN; Miltner et al., 1997). The sources of both potentials are primarily located in the medial prefrontal cortex including the anterior cingulate cortex (ACC; Location Ne/ERN: Dehaene et al., 1994; Mathalon et al., 2003; Holroyd et al., 2004; Debener et al., 2005; Location FRN: Luu et al., 2003). Furthermore, both potentials are present in situations in which erroneous movements or incorrect motor responses to a stimulus result in a failure of achieving the desired movement outcome. However, it is important to clearly distinguish between Ne/ERN and FRN as they reflect error processing at different time points throughout an action. The FRN can be observed after feedback about the action outcome is available, i.e., it reflects a REACTION to this outcome feedback. In contrast, the Ne/ERN is manifested shortly after movement onset and, importantly, prior to feedback about action outcome. In these cases, the Ne/ERN reflects a PREDICTION of an event in the future (i.e., an upcoming error). The onset times of the Ne/ERN can vary, depending on the type of motor task, from 80 to 100 ms after movement onset in choice-reaction time tasks (Falkenstein et al., 1991a; Gehring et al., 1993) to 200–350 ms in motor tasks composed of multiple submovements (Anguera et al., 2009; Maurer et al., 2015; Joch et al., 2017). However, as long as the Ne/ERN is related to the action outcome and emerges prior to external feedback about action outcome, it seems reasonable to consider the Ne/ERN as a correlate of predictive error processing, while the FRN in response to outcome feedback is a correlate of postdictive error processing. In this article, we will focus on the question whether the availability of different sensory signals modulates predictive error perception.

The functional significance of the Ne/ERN has been discussed in light of post-response conflict monitoring (Yeung et al., 2004), reinforcement learning (Holroyd and Coles, 2002), and surprise because of the non-occurrence of predicted events (Alexander and Brown, 2011). Regardless of whatever explanation might hold, all of these functions require prediction in the absence of external outcome feedback. Only with prediction about an outcome, it is possible to process information about a deviation to this expected outcome, to detect an error or to evaluate a conflict about the correct outcome. Since the Ne/ERN emerges prior to the availability of external outcome feedback, it is reasonable to assume that the Ne/ERN arises from the output $\hat{o}$ of a predictive model P (e.g., an internal forward model) on the basis of several input signals I and their respective weights w $[P(I_1 \cdot w_1 \cdots I_n \cdot w_n) = \hat{o}]$. The Ne/ERN can be interpreted as a correlate of the comparison between predicted outcome and intended outcome indicating an upcoming error. Input signals to the predictive model might be provided by efferent information (e.g., via efference copy) and by afferent information about the environment, the movement execution, and the movement outcome (e.g., via visual or proprioceptive signals).

Feedback about the final outcome of an action is not the only source of error information available. In a throwing task we see and feel our hand moving and we see the thrown object flying toward the target clearly before we observe the final result [hit or miss]. Previously, we defined continuous (visual) information about the immediate movement effect (the flying ball), which is available prior to outcome feedback (hit or miss), as action effect monitoring (Maurer et al., 2015). In a recent study, Joch et al. (2017) showed that error prediction is possible in the absence of action effect monitoring: a Ne/ERN signal was observed in a target-oriented ball-throwing task even when information about the ball trajectory toward the target was not shown. Yet, the Ne/ERN amplitude was noticeably smaller compared to the control condition where effect monitoring was possible (Maurer et al., 2015). The attenuation of the Ne/ERN can be interpreted as an increase in uncertainty about $\hat{o}$ when restricting input information to *P*.

The aim of the present study was to estimate the contribution of other afferent and efferent signals to error prediction as quantified by the amplitude of the Ne/ERN. We used the same semi-virtual ball throwing task (Skittles) as described in Maurer et al. (2015) and Joch et al. (2017) and removed (a) visual information about movement execution as well as action effect monitoring in one condition and (b) proprioceptive and efferent signals related to movement execution in another condition. As a result, we expected a further decrease of the Ne/ERN amplitude as an expression of increasing prediction uncertainty due to a reduced number of input signals to the predictive model. Since the additional removal of input signals could diminish the effects to the extent that the signal becomes smaller than the noise in the EEG signal, we sought to validate our results by comparing effects on the Ne/ERN with effects on the FRN with the rationale being as follows: based on the notion of the Ne/ERN being the first neural indicator of a motor error (Holroyd and Coles, 2002; Stahl, 2010), cases when an error of the movement outcome occurs and can be predicted based on internal information, should render external outcome information [i.e., knowledge of results (KRs) feedback] less relevant for the motor system. In other words, if the error was already predicted by the internal prediction model (i.e., higher Ne/ERN amplitude), the motor system should not be "surprised" to perceive error feedback (resulting in a lower FRN amplitude). This complementary behavior of Ne/ERN and FRN has been shown in several studies (e.g., Holroyd and Coles, 2002; Pietschmann et al., 2008). Thus, we will take advantage of this reciprocal behavior of Ne/ERN and FRN to better understand the absence of a significant fronto-central negativity in either condition.

MATERIALS AND METHODS

Participants

Participants of the current EEG study were recruited from the student population of the Justus Liebig University Giessen. The sample consisted of 19 participants (four males) with an average age of 21.7 years (*SD* = 4.2 years). Participants received course credit and had the chance to win up to 30 € by participating in the experiment, which was conducted in accordance with the ethical standards laid down in the Declaration of Helsinki. The protocol was approved by the Ethical Review Board of the Justus Liebig University Giessen.

The Semi-Virtual Throwing Task

Participants practiced a semi-virtual version of a British pub game called *Skittles*. In the real game, a ball is attached to the top of a post by a string. The player throws the ball in order to hit one or multiple target skittles on the opposite side of the post. In the semi-virtual adaptation of Skittles, this setup is displayed on a computer monitor (size: 15-inch, format: 3:4; model: AOC 919Va2, screen resolution: 1024 × 768 Pixel) from a bird's-eye view. On the computer screen, participants could see a green BALL (radius on display = 2.5 mm) which had to be thrown around a blue center POST (radius on display = 12.5 mm) to hit a red TARGET object (radius on display = 2.5 mm). The ball's trajectory was determined by the simulated physics of the task (Müller and Sternad, 2004) and described an elliptic path around the post. In the model, the relevant objects were defined as follows: center POST (radius = 0.25 m; position: x = 0.0 m, y = 0.0 m), TARGET (radius = 0.05 m; position: x = 0.35 m, y = 1.0 m), BALL (radius = 0.05 m).

To throw the ball, participants used a metal lever (see **Figure 1**). They sat on a stool and rested their arm on a foam pad attached to the lever. The lever could be rotated within the horizontal plane around a vertical rotation axis located approximately under the participant's elbow joint. The distance between the participants' eyes and the computer screen was 1 m. A contact sensor was placed at the tip of the lever so that when participants placed their index finger on the sensor, the virtual ball was picked up and visually attached to a virtual equivalent of the lever (length: 0.4 m, position of the fixed end: x = 0.0 m, y = −1.5 m). Then, they rotated the lever clockwise and released the ball at any time during the movement by lifting their finger off the contact sensor. Because fast and rhythmic executions of subsequent trials could be a confounding factor of the results, we introduced a constant foreperiod before a Go-Signal appeared in the screen instructing the participants not to initiate their movement before its onset (see **Figure 1**, Start Signal). In detail, at the start of each trial, participants had to move the tip of the lever into a red circle positioned to the left of the fixed end of the lever (corresponding with a 0° lever position in the physical model). When the tip of the virtual lever reached the red circle, it immediately turned yellow and, subsequently, green when the lever was held at least 1 s within that circle. The green circle was used as a cue that the subjects were now free to move at any time. Note that participants did not start the throwing movement as a reaction to the green signal; it merely signaled that they were allowed to commence the movement at any time after the start circle had turned green.

The actual trajectory and thus the final outcome of the throwing movement was defined by angle of the lever and velocity of the BALL at the moment of its release. The feedback given during and after a trial depended on the experimental phase and condition. For more details about the experimental conditions see section "Study Design and Experimental Conditions". Task performance was quantified by measuring the number of hits in relation to the total number of executed trials (i.e., hit rate).

The general task instruction was given in a standardized way at the beginning of the study, whereas condition specific instructions were provided directly before a specific condition started. To keep the participants motivated throughout the whole experiment, the individuals with the three highest target hit rates were rewarded with 30 € for the first, 20 € for the second and 10 € for the third place.

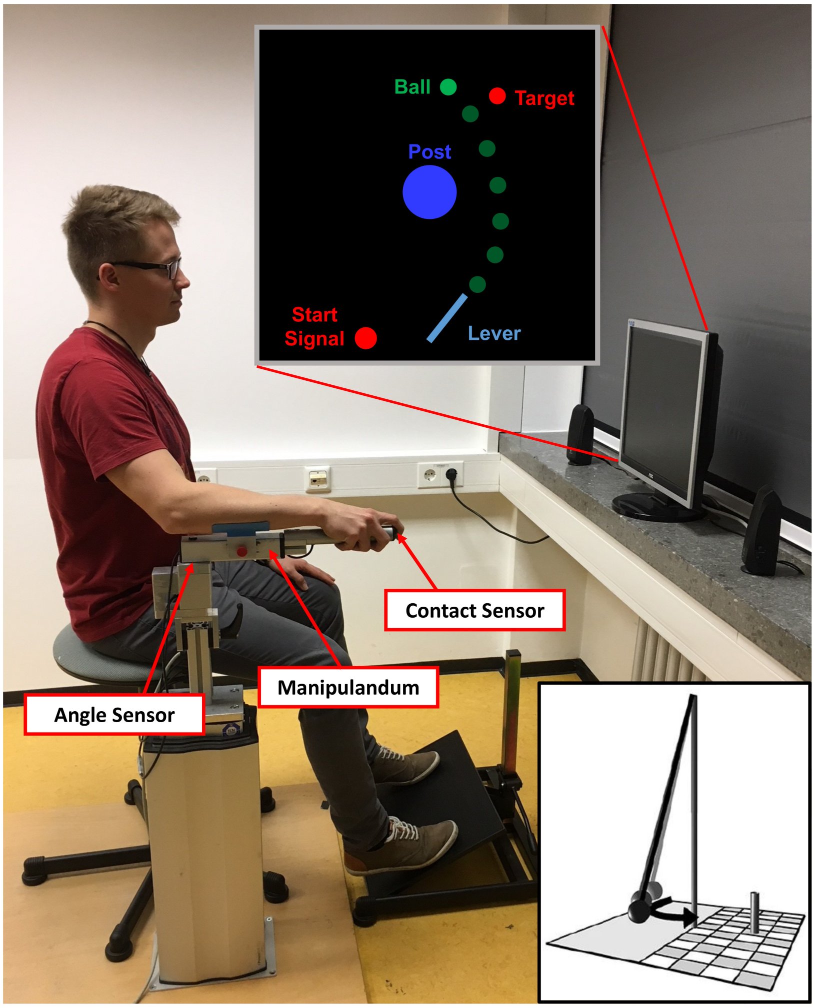

FIGURE 1 | Setup of the virtual adaptation of the Skittles task. The participant uses the manipulandum to throw the green ball with a horizontal rotational movement. The ball travels with an elliptical trajectory around the central post and toward the target. The distance between the manipulandum and the computer screen was one meter. The depicted participant gave written informed consent for the publication of this picture. The little insert depicts a symbolic illustration of the real version of Skittles.

Study Design and Experimental Conditions

The study consisted of six sessions on six separate days. The first four sessions were used as practice/training sessions and the last two were experimental sessions, in which the motor task had to be executed under different conditions by the participants while EEG was measured. The duration of the practice sessions was approximately 30 min each and the EEG sessions had a duration of 1.5–2 h each. In order to improve the performance in the motor task (i.e., improve the hit rate), 400 trials had to be executed at every practice session (1600 practice trials in total). In addition, each EEG session consisted of 430 trials (see **Figure 2**).

Practice Phase (Sessions 1–4)

Since displaying the ball's trajectory toward the target influences the neural prediction process (Joch et al., 2017), it was incrementally reduced during the practice sessions. For the first 200 trials of session 1, the ball trajectory was displayed starting immediately after the release of the ball from the virtual lever. In addition to this immediate dynamic feedback, a static depiction of the entire ball trajectory as well as a feedback about the action outcome were displayed on the screen 850 ms after ball release. In detail, the static feedback consisted of simultaneously depicted ball positions at temporally equidistant moments of ball flight along the trajectory of the actual trial (see **Figure 1**). Regarding outcome feedback, a collision sound was played for the hit trials, the target object was knocked out of its position, and the German word for "hit" ("Treffer") was displayed in green on the computer screen. In case of an error, participants received the feedback "Unfortunately a miss" ("Leider vorbei") written in red. Outcome feedback information was delayed by 850 ms because this was the average time it took the ball to reach the vicinity of the target object (calculated based on preliminary data). The static trajectory and the outcome feedback was presented throughout

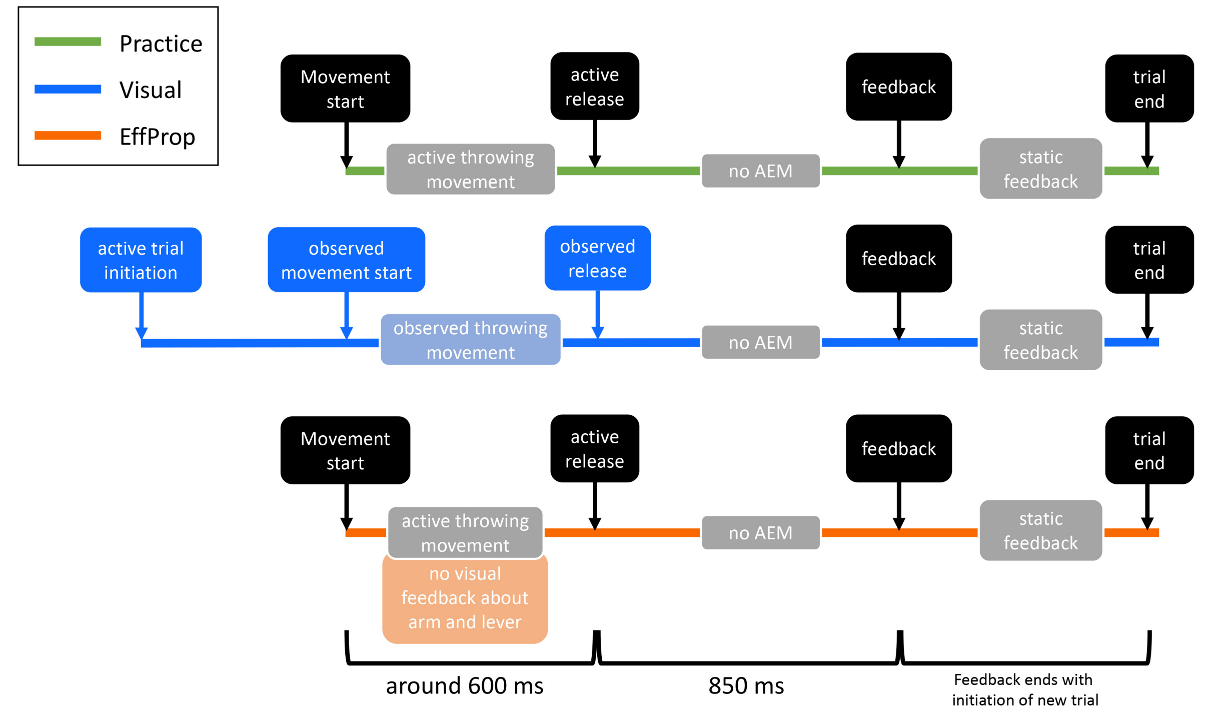

FIGURE 2 | Illustration of the differences between practice and the two experimental conditions (*Visual, EffProp*). Shown are, one below the other, the temporal events of one trial in each condition. Similar action event are depicted in black. The lighter colored boxes represent information sources for error processing (AEM = action effect monitoring). Differences are marked with the corresponding color (green = practice, blue = *Visual* condition, orange = *EffProp* condition).

all four practice sessions. In contrast, the dynamic display of the ball flight was decreased by 33% every 100 trials over the second part of day 1. On day 2, participants started with 66% dynamic ball flight display, which was again decreased every 100 trials by 33%. As a result, they executed the last 200 trials of day 2 with 0% dynamic ball flight information. In the 0% condition, the ball was masked at the moment of ball release and participants exclusively received the static feedback and the result-feedback after 850 ms. Practice sessions 3 and 4 as well as the experimental sessions were conducted with 0% ball flight trajectory.

Visual (Session 5)

In session 5, participants passively observed trials on the computer screen. Hence, in this session, error prediction could solely be based on the visual input signals that were available until the observed ball release. For motivational reasons and to keep participants from forgetting the skill, the observation trials (*O*) were interspersed by normal execution trials (*E*), where the ball had to be actively thrown in order to hit the target analog to the practice sessions. In the observation blocks, subjects started an observation trial by directing the manipulandum and thus the virtual lever toward the starting position (red circular area) located at a 90° angle of the virtual lever. The observation trial started as soon as participants lifted the index finger off the contact sensor within the starting position. Participants saw the throwing movement of the virtual lever until the release of the ball but not the ball flying toward the target. After 850 ms, they received result-feedback in form of the static ball trajectory (analog to the practice session). The presented trials were taken from the participant's practice phase (without their knowledge) and chosen so that the total number of observed trials were composed of 50% hits and 50% misses. Session 5 started with 20 execution trials to re-familiarize participants with the task. Afterward, observation trials and execution trials were alternatively conducted in blocks of 20 trials (*O*) and 10 trials (*E*), respectively. This block-wise condition switching was conducted until 280 observation trials had been recorded (i.e., the observation session ended with block *O*).

EffProp (Session 6)

On the sixth and last session of the study, participants completed the task without visual display of the movement. We removed any visual information about the effectors and the lever. In detail, manipulandum and throwing arm of the participant were covered by a horizontal board. The virtual lever on the computer screen was masked as soon as participants started their throwing movement. We determined the movement start by means of the angular velocity of the lever. Whenever the angle velocity exceeded 50°/s after being in the starting position, the movement was classified as started. Altogether, the participants had to execute 430 throws on the last day. There was a drop out of two participants in the *EffProp* condition due to technical changes.

EEG Data Acquisition and Preprocessing

Acquisition of EEG data started on day 5. Furthermore, an electrooculogram (EOG) was conducted to measure eye movements (e.g., blinks). EOG electrodes were placed above and below the right eye and on the external canthi of both eyes. For the recordings, we used a 16 channel AC/DC amplifier with Ag/AgCl active scalp electrodes (V-Amp, Brain Products GmbH, Gilching, Germany). The position of the electrode was set according to the international 10–20 system (Klem et al., 1999). The actual positioning was done using the actiCAP electrode cap by Brain Products. Specifically, we used the electrodes F3, Fz, F4, FCz, C3, Cz, C4, P3, Pz, P4 and placed the ground electrode on the Fpz position. For signal reference, we used two electrodes, one online and one offline reference. The online reference electrode was placed on the left mastoid. The offline reference electrode was placed on the right mastoid. This electrode was used for offline re-referencing, hence, an average of both reference electrodes was used for further analyses. Electrodes impedances were held below 15 kΩ. The data was recorded using a 500 Hz acquisition frequency.

After data acquisition, EEG and EOG data were preprocessed offline using the Brain Vision Analyzer 2.1. software. First, the signals were filtered using a Butterworth filter with a low cut-off frequency of 0.2 Hz and a high cut-off of 30 Hz. To correct for ocular artifacts, we applied the ocular correction algorithm of the Analyzer 2.1 software, which is based on the Infomax Independent Component Analysis (ICA; Makeig et al., 1996, 1997). To calculate the ICA components, only EEG activity around blinks was fed into the ICA algorithm. Blinks were detected using the mean slope algorithm by Gratton et al. (1983). After visual inspection of the components, the component(s) explaining more than 30% of the eye movements were then removed from all other EEG activity.

After EOG correction, the signal was segmented. The size of the segments was different for the two experimental conditions. In the *Visual* condition, each segment began 600 ms before the observation trial was initiated by the participant. The end of the segment was set 2800 ms after the start of the segment. Hence, each segment included the following events: trial start, virtual ball release, and outcome feedback presentation. In condition *EffProp*, the segment started 600 ms before the subject released the ball in the throwing motion and it ended 2200 ms after the segment's start. Each segment was manually controlled for remaining artifacts.

Skittles Data Preparation

The electrophysiological potentials of interest, the Ne/ERN and FRN, typically emerge when an incorrect response to a stimulus is executed. Therefore, target hits and target misses had to be separated for further analyses. To do so, the minimal distance between the center of the thrown ball and the center of the target was measured yielding a distance (*d*) value. In the underlying physical model, ball and target both had a radius of 5 cm. Hence, trials with a *d* value greater than 10 cm were classified as misses. Trials in which the center post was hit were excluded from the analysis. Because close hits/misses could blur the neural signatures of hits and errors, we classified only trials with $d \leq 7$ cm as hits and trials with $d \geq 12$ cm as errors. In addition, hit rates for every session were calculated to measure the performance in the Skittles task. Task performance is assumed to be related to the quality of the internal forward model of the task (Jordan and Rumelhart, 1992).

Statistical Analysis

For the statistical analyses, we used Mathworks MATLAB R2016a. To be able to statistically analyze the electrophysiological data, we conducted a mean amplitude analysis of the FCz segments that resulted from the data pre-processing. For this, a baseline corrected difference curve for every participant's average hit and error curve was calculated. For baseline correction, we used the time interval between ball release and the effect window for the Ne/ERN (see below) as the baseline interval (i.e., 0–200 ms). The data of the difference curves were then averaged over *a priori* set effect windows (EffW) for the Ne/ERN (200–350 ms after ball release; EffW_{ERN}) and the FRN (150–350 ms after feedback; EffW_{FRN}) to yield a mean amplitude for EffW_{ERN} and EffW_{FRN} for each participant. Averages of the mean amplitudes can be found in **Table 1** (Δ*MeanAmpl.*). Note that the EffW_{ERN} in the *Visual* condition was set to 200–350 ms after the *observed* ball release (as opposed to the active ball release in the practice sessions and in *EffProp*). The resulting mean amplitudes were tested with a one-sample t-test using a test value of zero. To confirm the results from classical inference statistics, we used a Bayesian inference approach to calculate Bayes factors (*BF*) that can be interpreted as the amount of evidence for the null-hypothesis before versus after seeing the data (Verdinelli and Wasserman, 1995). The computation of the Bayes factors was done in JASP 0.8.2.0 and separately for both effect windows and both conditions. The size of the *BF*s are interpreted according to Raftery (1995).

To describe the ERPs in more detail, peak amplitudes were calculated for every participant within both effect windows. The peak amplitude was defined as the minimum activation (since Ne/ERN and FRN are negative potentials) in the corresponding effect window. The peak amplitudes of the participants were then averaged to yield average peak amplitudes (Δ*PeakAmpl.* in **Table 1**). Note that Δ*PeakAmpl.* can differ from the peak of the difference curves shown in the electrophysiological result figures because there the difference curves represent the difference between grand average curves of hits and misses respectively (averaged over all participants' mean curves).

RESULTS

Behavioral Results

Participants practiced the Skittles task for four sessions on four separate days (400 trials per session) before EEG recordings were conducted in sessions 5 and 6. During the practice sessions, participants were able to improve task performance (quantified by the hit rate) from 64.6% (*SD* = 11.4%) in session 1 to 77.9% (*SD* = 15.6%) in session 4 [see **Figure 3**; $F(3,88) = 3.657$; $p = 0.01$].

TABLE 1 | Overview of electrophysiological results.

	Visual		*EffProp*	
	EffW_{ERN}	EffW_{FRN}	EffW_{ERN}	EffW_{FRN}
ΔMeanAmpl.	$-0.6\ \mu V$	$-3.4\ \mu V$	$0.05\ \mu V$	$-5.6\ \mu V$
ΔPeakAmpl.	$-1.8\ \mu V$	$-7.9\ \mu V$	$-1.6\ \mu V$	$-10.7\ \mu V$
p	0.01	<0.001	0.55	<0.001
Effect size d	0.57	1.49	0.03	1.15
BF_{10}	5.3	1063	0.21	170

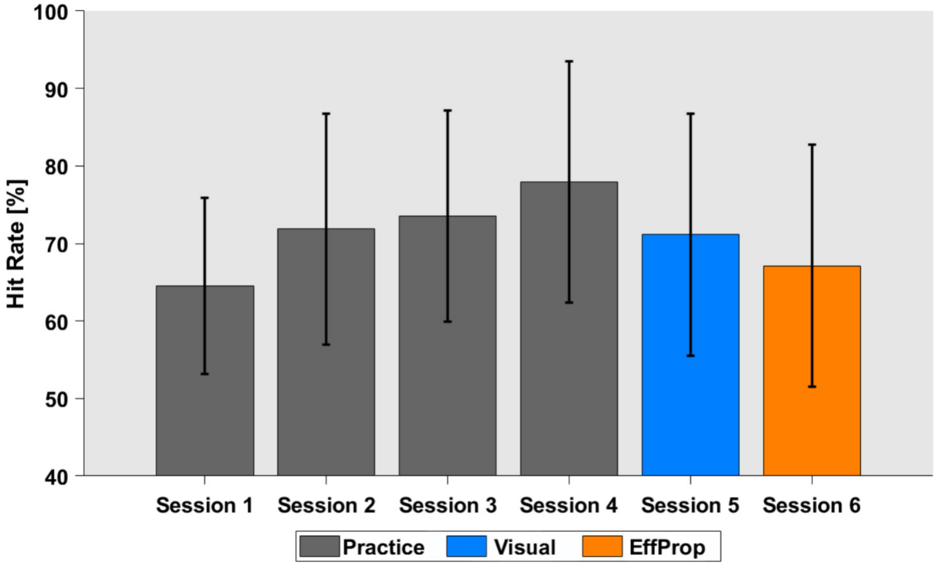

FIGURE 3 | Task performance in hit rates over the four practice sessions (gray), the *Visual* (blue), and the *EffProp* condition (orange). Error bars represent standard deviations.

The hit rate for the execution trials that alternated with the observation trials in the *Visual* condition was 71.1% ($SD = 15.3\%$). The average hit rate slightly dropped in the last (*EffProp*) session to a hit rate of 67.1% ($SD = 18.8\%$). However, this difference was not significant [$t(16) = 1.18$; $p = 0.25$].

Electrophysiological Results

Condition: Visual

In the *Visual* condition, participants did not actively throw the ball toward the target but passively observed trials on the computer monitor. This way, the prediction model had access to visual signals of the lever movement while efferent as well as proprioceptive signals were unavailable.

We found a significant effect within the Ne/ERN effect window [$t(17) = -2.4$; $p = 0.01$; $d = 0.57$] determined by the mean amplitudes ($\Delta MeanAmpl._{\text{ERN}} = -0.6\ \mu V$; $CI_{95\%} = [-1.18\ \mu V, -0.08\ \mu V]$) of the difference curves (misses minus hit trials; see **Figure 4**, left). This result is supported by a Bayesian inference approach yielding a Bayes Factor of $BF_{10} = 5.3$ (corresponding to a positive evidence after Raftery, 1995). Furthermore, the ERP is characterized by a difference signal peak amplitude ($\Delta PeakAmpl._{\text{ERN}}$) of $-1.8\ \mu V$.

In reaction to negative result-feedback, we observed a highly significant negative deflection ($\Delta MeanAmpl._{\text{FRN}} = -3.4\ \mu V$; $CI_{95\%} = [-4.55\ \mu V, -2.28\ \mu V]$) within the FRN effect window [$t(17) = -6.3$; $p < 0.001$; $d = 1.49$; $BF_{10} = 1063$] (i.e., very strong evidence; **Figure 5**, left). The measured peak amplitude was $\Delta PeakAmpl._{\text{FRN}} = -7.9\ \mu V$.

Condition: EffProp

In the condition *EffProp*, participants had to actively throw the ball, but no visual information about movement execution and ball flight was available (i.e., the internal prediction model had access to proprioceptive and the efference copy signals, but not to visual signals). We found an average mean amplitude of $\Delta MeanAmpl._{\text{ERN}} = 0.05\ \mu V$ ($CI_{95\%} = [-0.80\ \mu V, 0.90\ \mu V]$). There was no significant effect in the mean amplitudes of the difference curves within the preset Ne/ERN effect window [$t(16) = 0.13$; $p = 0.55$; $d = 0.03$; **Figure 4**, right]. In line with this result, the Bayesian analysis revealed more evidence for the null hypotheses in the data than for the alternative hypothesis ($BF_{10} = 0.21$). Furthermore, the measured peak amplitude of the difference curve within EffW_{ERN} was $\Delta PeakAmpl._{\text{ERN}} = -1.6\ \mu V$.

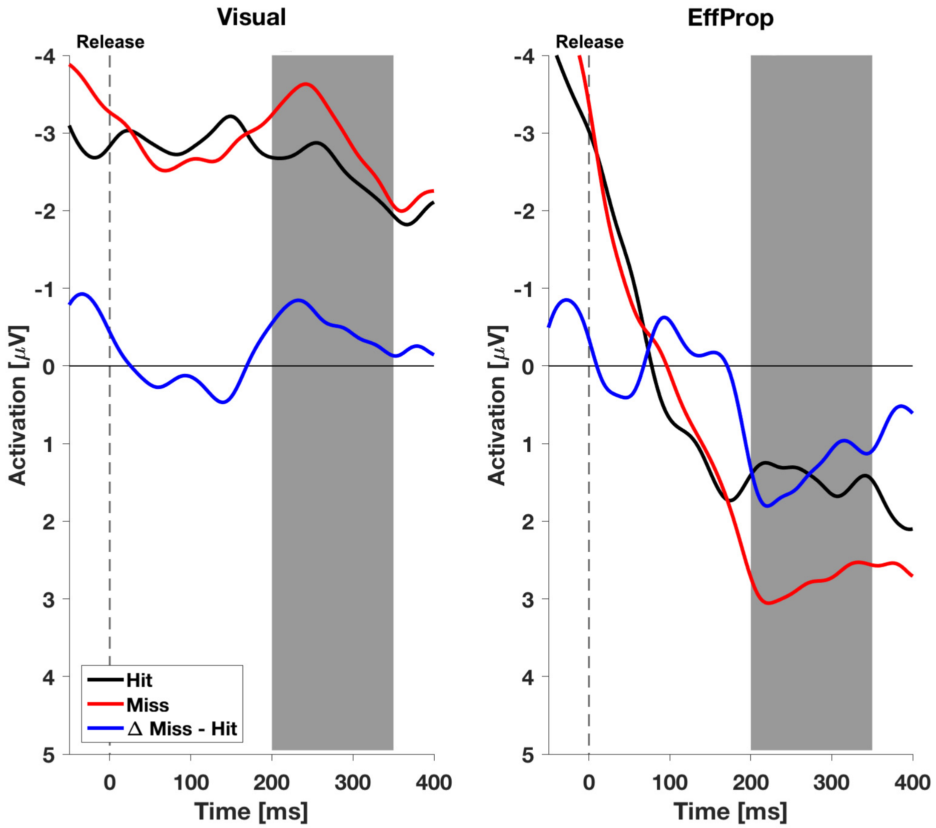

FIGURE 4 | Electroencephalogram signals in the effect window EffW_{ERN}, 200–350 ms after ball release for both experimental conditions (*Visual* and *EffProp*). Ball release is indicated with the broken line. As feedback was shown 850 ms after ball release, the gray shaded interval represents the time window for error prediction.

Participants reacted with a sharp negative deflection to negative result-feedback ($\Delta MeanAmpl._{\text{FRN}} = -5.6\ \mu\text{V}$; $CI_{95\%} = [-8.12\ \mu\text{V}, -3.10\ \mu\text{V}]$) within the preset effect window EffW_{FRN} [$t(16) = -4.73$; $p < 0.001$; $d = 1.15$; $BF_{10} = 170$] (i.e., very strong evidence; **Figure 5**, right). The observed potential had a peak amplitude of $\Delta PeakAmpl._{\text{FRN}} = -10.7\ \mu\text{V}$. An overview of the measured values in both conditions can be found in **Table 1**. Figures of the grand averages of all recorded electrodes can be found in **Supplementary Figures S1–S4**.

Visual vs. EffProp

In addition to the intra condition testing, we tested if there were differences between the mean values for the *Visual* and *EffProp* conditions (see also **Figure 6**). Comparing the mean amplitude values of *Visual* and *EffProp* in the effect window for the error prediction (EffW_{ERN}), we found a difference of 0.65 μV. However, the significance level was slightly missed [$t(33) = -1.44$; $p = 0.08$; $d = 0.25$]. In the Bayesian analysis, updating the prior distribution with the data revealed slightly more evidence for the alternative hypothesis (difference in mean amplitudes between *Visual* and *EffProp*) than for the null hypothesis [$BF_{10} = 1.99$ (i.e., weak evidence); *median effect* = 0.38].

With respect to the result-feedback reaction (EffW_{FRN}), we found significantly larger mean ERP amplitudes (i.e., stronger negative deflections) in the *EffProp* condition compared to the *Visual* condition [$t(33) = 1.77$; $p = 0.047$; $d = 0.31$; see also **Figure 5**]. This observation is supported by the conducted Bayesian analysis [$BF_{10} = 2.77$ (i.e., weak evidence); *median effect* = 0.43].

DISCUSSION

In this study, we focused on the availability of different sensory signals to the internal forward model that generates a prediction of a terminal movement outcome. So far, there is not much experimental research on the dependencies of the internal forward model on sensory signals from vision, proprioception, and audition or the efference copy as an efferent signal. In a recent study, we showed that action effect monitoring (i.e., observing the effect of the executed movement as it unfolds over time) was not an essential input for the prediction model (Joch et al., 2017). However, the absence of action effect monitoring led to a diminished amplitude of an ERP related to error prediction. In the present study, we further aimed to test the impact of visual and proprioceptive signals about the movement on prediction- and feedback-related ERPs. To do so, participants practiced a semi-virtual throwing task for four sessions (1600 trials total). The task in session 5 was to visually observe throwing movements

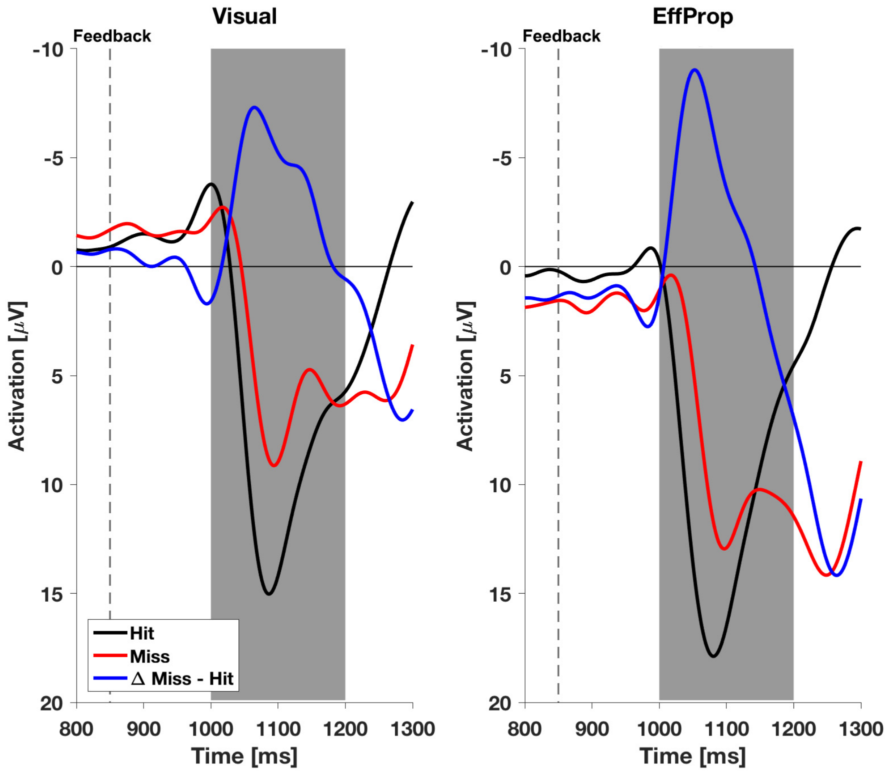

FIGURE 5 | Electroencephalogram signals with respect to feedback in both experimental conditions (*Visual* and *EffProp*). The broken line represents the time terminal result feedback was provided. The gray shaded interval represents the time window for error postdiction.

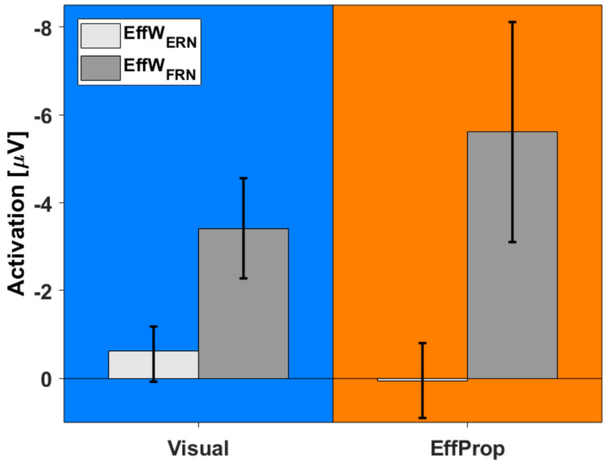

FIGURE 6 | Comparison between activations found in *Visual* (blue) and *EffProp* (orange) with regard to the mean amplitude of the differences curves (signals measured in error trials minus signals measured in hit trials). Error bars represent 95% confidence intervals.

(i.e., *visual* condition; no proprioceptive signals and no efference copy were available as inputs for the prediction model). In the sixth and last session, participants executed the motor task without any visual display of the effectors (i.e., condition *EffProp;* virtual lever and real arm of the participant were occluded). That way, the prediction model received no movement-related visual signals.

Performance and Behavioral Results

Participants improved their task performance (quantified by the target hit rate in %) over the practice session from 65% to approximately 78%. Accounting for theoretical considerations by Jordan and Rumelhart (1992) and empirical findings from Maurer et al. (2015) and Joch et al. (2017), we assume that this performance increase reflects the development of an internal forward model during practice so that predicting the movement outcome was possible during the experimental conditions. Task performance dropped in session 5 (*Visual* condition) and decreased slightly further in session 6 (*EffProp* condition). However, hit rates during the experimental sessions were still similar to the hit rates described in previous studies using the Skittles task (Maurer et al., 2015; Joch et al., 2017). To ensure that the slight decreases did not arise from changes in throwing strategy (which could have an influence on the neural signals), we checked *post hoc* whether ball kinematics had changed from practice phase to the *EffProp* condition. For this, we plotted the trajectories of all trials executed in the last practice session and in the *EffProp* condition for each participant. We then manually checked for different throwing strategies. **Figure 7** exemplarily shows two participants. We could

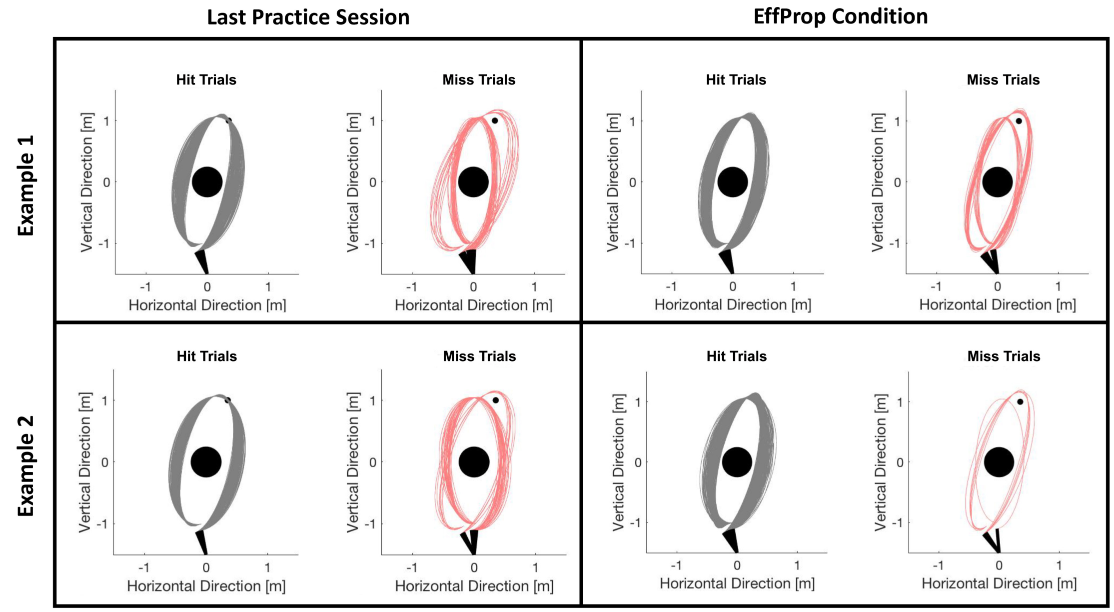

FIGURE 7 | Comparison of ball flight trajectories of trials from session 4 (last practice session) and session 6 (*EffProp*) for two exemplary participants. The trials are separated in hit (gray) and error (red) trials. There was no change in strategies from session 4 to session 6.

not find any strategy changes during *EffProp* in any of the participants.

Electrophysiological Results – More Accurate Error Prediction With Visual Inputs

We quantified the accuracy of error prediction in two ways. First, by means of the Ne/ERN amplitude (i.e., high amplitude stands for high prediction accuracy and vice versa) and, second, using the complementary behavior between the Ne/ERN and FRN amplitudes (see section "Introduction").

Ne/ERN Amplitude

We found a larger Ne/ERN mean amplitude (larger means more negative) in the *Visual* condition than in the *EffProp* condition. Hence, the reliability of the forward model predicting the throwing error seemed to be higher in the observation condition (neither efferent, nor proprioceptive input to the prediction model) compared to the execution condition without any visual input to the prediction model. The diminished effects of the Ne/ERN can be explained in terms of flexible strategies for sensory integration during motor planning (Sober and Sabes, 2005) suggesting a strong connection between the task's target properties and the input requirements of the internal prediction model. Since the target in the Skittles task can be categorized as a visual target, it is possible that visual signals are essential during movement planning. Thus, restricting the heavily weighted visual signals in the *EffProp* condition might have led to high uncertainty of the outcome prediction and thus a miniscule amplitude of the Ne/ERN. On the other hand, in the *Visual* condition, where visual feedback was available but proprioceptive and efferent signals could not serve as inputs to the prediction model, the Ne/ERN indicated a more accurate error prediction. The smaller Ne/ERN in the *EffProp* condition could alternatively be explained by prediction error accounts (Holroyd and Coles, 2002; Alexander and Brown, 2011), which predict lower Ne/ERN amplitudes in conditions with more frequent errors and hence smaller prediction errors. With the present data we cannot finally rule out this possibility since the hit rate in the *EffProp* condition was in tendency (but not significantly) smaller than in the *Visual* condition. The reduced performance could either manifest in a lower error likelihood having an impact on error evaluation or in a poorer quality of the forward model corrupting error prediction. However, the performance difference of only 4% supports our belief that error likelihood should not noticeably deviate between conditions. Consequently, we assume that the prediction model in our goal-oriented throwing task relies more on visual signals.

Furthermore, the amplitude of the Ne/ERN in the *Visual* condition was smaller relative to conditions where visual and proprioceptive signals had been available (e.g., Joch et al., 2017). This is in line with studies investigating the so called "observation Ne/ERN" (e.g., Van Schie et al., 2004; Bates et al., 2005) that reported decreases in the Ne/ERN amplitude when participants observed the actions of another person.

FRN Amplitude and Ne/ERN – FRN Complementarity

Participants received a result-feedback in each trial of the practice and test sessions, informing them about target hit or miss 850 ms after ball release. In both, the *Visual* and *EffProp* conditions, we found a highly significant negative deflection within the effect window of 150–350 ms after the onset of outcome feedback. The amplitude of this FRN in the *EffProp* condition was, however, significantly more negative than in the *Visual* condition. Combining the observed neural responses related to error prediction (Ne/ERN) and outcome feedback (FRN), we find a complementary behavior of these two neural markers. In case of only limited sensory signals (efferent and proprioceptive signals or visual signals alone) being available to the system, the prediction model was not able to accurately predict the movement outcome and, thus, the corresponding neural correlate (Ne/ERN) was less pronounced (compared to the FRN) or absent. Subsequently, when the outcome feedback became available, presentation of an error gave rise to a strong FRN amplitude. This finding is in line with the observations of Weismüller and Bellebaum (2016) who suggest an association between the amplitude of the FRN and error awareness or error expectancy, respectively. Thus, since an error is less expected with a less accurate error prediction in the *EffProp* condition, the FRN is stronger after error occurrence. In the *Visual* condition, we observed the opposite behavior. The prediction model had access to visual signals during movement execution and was able to predict the movement outcome more accurately as in the *EffProp* condition, resulting in a stronger negative deflection of the Ne/ERN. Since the system was consequently aware of a possible upcoming error, the neural response to the result-feedback was less pronounced relative to the *EffProp* condition. Overall, the findings of Ne/ERN amplitude and FRN amplitude support the assumption that visual inputs are more important for error prediction in a goal-oriented throwing task.

Limitations and Differences to Other Studies

The onset of the Ne/ERN potentials in our motor task is later than in studies using for example choice-reaction-time (CRT) tasks (e.g., Nieuwenhuis et al., 2004). This is not surprising since the throwing movements in the Skittles task are much more complex than button-presses in CRT tasks involving at least two joints (i.e., shoulder and elbow joint), whose sensory signals have to be evaluated and integrated together with visual signals to complement mere efferent information and yield a reliable estimation of the movement outcome. In our view, the longer onset latencies are a result of the longer processing time needed for the integration of these different information sources. Support for this interpretation comes from a study of Godefroid et al. (2016) who also found the Ne/ERN to be influenced by the number of sensory channels (Ne/ERN amplitude was modified by visual feedback in a Go/No-Go task, in addition to efferent information).

Furthermore, all of the observed mean amplitudes in $\mathrm{EffW}_{\mathrm{ERN}}$ were smaller than the amplitudes within the same effect window and with same task as reported by Maurer et al. (2015) and Joch et al. (2017). However, these differences are in line with theoretical considerations as the quantity of input signals to the forward model was higher in the other two studies. In the study of Maurer and colleagues, the prediction model had access to a complete set of afferent and efferent input signals (efferent, visual, and proprioceptive signals of the movement as well as action effect monitoring). Joch and colleagues eliminated the action effect monitoring but kept all other afferent and efferent inputs of the movement. Thus, we assume that the mean amplitude of the Ne/ERN should attenuate with a decreasing prediction accuracy induced by restricted sensory input signals.

Another possible limitation of the present study arises from the fixed order of experimental sessions (session 5: *Vision*; session 6: *EffProp*). This procedure was chosen to provide a maximum of practice trials before executing the *EffProp* condition, which we expected to be the most difficult condition. Hence, task disengagement or fatigue could have led to poorer performance monitoring accompanied by a smaller Ne/ERN amplitude. However, the preserved and even larger amplitude of the FRN speak against this assumption.

CONCLUSION

Altogether, the results of this study suggest that, at least in a goal-oriented throwing task like Skittles, visual signals about the movement are essential inputs to the internal prediction model. The prediction of an outcome error seems possible on the basis of visual signals alone. Conversely, restricting these signals might lead to a poorer prediction performance and less pronounced neural responses. However, the weighting of sensory signals could change, according to Sober and Sabes (2005), if a proprioceptive target is used in favor of proprioceptive signals, which could be an objective for a follow-up study. In situations where relevant inputs from sensory signals are not available for the model, prediction accuracy decreases and with it the occurrence (e.g., amplitude) of the Ne/ERN. Our findings are based on the effects of the two different experimental conditions (restricting visual signals vs. restricting efferent and proprioceptive signals) on the Ne/ERN and on the FRN. The two signals showed complementary behavior, which suggests that both brain potentials are related to the same motor error.

AUTHOR CONTRIBUTIONS

MJ and LKM conducted experiments, analyzed data, and drafted manuscript. MJ prepared figures. All authors interpreted results of experiments, edited, revised, and approved final version of manuscript and were involved in the conception and design of the study.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2018.01376/full#supplementary-material

FIGURE S1 | Grand Average EEG curves of all electrodes (black = hits, red = errors, blue = difference curve) −100 ms–400 ms around release for the *EffProp* condition. The green area marks the EffW_{ERN}.

FIGURE S2 | Grand Average EEG curves of all electrodes (black = hits, red = errors, blue = difference curve) −100 ms–400 ms around release for the *Visual* condition. The green area marks the EffW_{ERN}.

FIGURE S3 | Grand Average EEG curves of all electrodes (black = hits, red = errors, blue = difference curve) −100 ms–500 ms around feedback for the *EffProp* condition. The pink area marks the EffW_{FRN}.

FIGURE S4 | Grand Average EEG curves of all electrodes (black = hits, red = errors, blue = difference curve) −100 ms–500 ms around feedback for the *Visual* condition. The pink area marks the EffW_{FRN}.

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Long-Distance Runners and Sprinters Show Different Performance Monitoring – An Event-Related Potential Study

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Previous findings have reported that track and field athletes may monitor and utilize internal information, including anxiety level, suggesting that the ability to inwardly monitor one's own functioning and utilize anxiety are required to achieve superior performance. Performance monitoring has been investigated using two event-related potential components; the error (-related) negativity (Ne/ERN) and error positivity (Pe). It is unknown whether performance monitoring differs among various types of athletes. It has also been reported that Ne/ERN amplitude is increased in individuals who are more anxious and the prevalence and effect of anxiety also differs among various types of athletes. In this study, we recorded both Ne/ERN and Pe from long-distance runners (n = 24) and sprinters (n = 24) while they were performing a spatial Stroop task under motivation and no motivation conditions. We also collected scores on the Sport Competitive Anxiety Test (SCAT). Mean error rate on incongruent trials was lower in the motivation condition than in the no motivation condition. There was neither group effect, nor condition effect found in Ne/ERN amplitude. However, for the long-distance runners, Pe amplitude was larger in the motivation condition than in the no motivation condition. We also investigated the relationships between Ne/ERNs and individual differences in performance anxiety using the SCAT. A multiple linear regression analysis in the motivation condition revealed an interaction between type of runner and SCAT scores, indicating that long-distance runners with higher SCAT scores showed larger Ne/ERN amplitudes whereas the sprinters with high SCAT scores tended to exhibit smaller Ne/ERN amplitudes. Our findings provide further evidence that performance monitoring differs across various types of athletes.

Keywords: performance monitoring, error-related negativity, error positivity, Sport Competitive Anxiety Test, long-distance runner, sprinter

INTRODUCTION

It is well-known that the physical properties of muscles differ among various types of elite athletes. When comparing the muscles of sprinters and long-distance runners, distinct differences can be observed. In sprinters large numbers of fast-twitch muscle fibers are required to accelerate in a transient period, whereas for long-distance runners a greater number of slow-twitch muscle fibers are required to maintain their own pace during a relatively long-lasting race (Costill et al., 1976). Through long-term training, athletes learn to acquire not only specific physical functions related to performance characteristics; they also develop specific cognitive functions critical to maximize performance (Ripoll and Latiri, 1997; Nakamoto and Mori, 2012). Although previous studies have reported differences in muscle functions (Abe et al., 2000) as well as physiological functions (Itoh and Ohkuwa, 1990) between sprinters and long-distance runners, it remains unclear whether cognitive functions also differ between these two types of runners.

Previous findings support the notion that track and field athletes monitor and utilize internal information, including pace, fatigue and race image, during a competition (Morgan and Pollock, 1977; Mallett and Hanrahan, 1997). Morgan and Pollock (1977) found that elite marathoners were more aware of, and were better at monitoring their own level of fatigue compared to poorer marathoners. In addition, Mallett and Hanrahan (1997) found that elite sprinters carefully self-monitored their own performance, but were much less aware of their competitors. These findings suggest that the ability to inwardly monitor one's own functioning is a necessary condition to achieve superior performance.

Performance monitoring, as currently conceptualized (Ullsperger and von Cramon, 2001) may be an essential cognitive function for improvement of motor skills (for a review see, Masaki and Sommer, 2012). Performance monitoring is associated with incorporation and examination of internal information and detecting errors between an actual ongoing movement and a desired movement. Performance monitoring has most often been investigated using two event-related potential (ERP) components. The first is the error negativity (Ne, Falkenstein et al., 1990) also referred to as the error-related negativity (ERN, Gehring et al., 1990) (referred to hereafter as the Ne/ERN). The second is the error positivity (Pe, Falkenstein et al., 1991). The Ne/ERN emerges over the frontocentral region approximately 70 ms after an erroneous response (Falkenstein et al., 1991), is thought to be generated by the anterior cingulate cortex (ACC) (Dehaene et al., 1994) and hence is maximal at FCz; whereas the Pe emerges over centroparietal regions approximately 200 to 500 ms after conscious error detection (Overbeek et al., 2005) and is maximal over Cz or Pz. Earlier studies have asserted that the Ne/ERN represents response conflict (Yeung et al., 2004) or error detection (Gehring et al., 1993). On the other hand, the Pe has been interpreted to reflect error evaluation and/or error awareness (Nieuwenhuis et al., 2001).

Recent studies have reported a relationship between aerobic capacity and performance monitoring processes. For example, Themanson and Hillman (2006) found that in individuals with high aerobic capacity the Ne/ERN amplitude was smaller but the Pe amplitude was larger than in those with low aerobic capacity. Because, it has been reported that aerobic capacity is higher in long-distance runners than in sprinters (e.g., Niemelä et al., 1980; Kusy and Zieliñski, 2015), it is presumed that the ERN amplitude should be smaller and the Pe amplitude should be larger in the long-distance runners compared to sprinters.

In this study, a spatial Stroop task was used to induce stimulus–response interference and thus response errors (Masaki and Segalowitz, 2004). We focused on error trials, and compared amplitudes of both the Ne/ERN and Pe between sprinters and long-distance runners who were members of a university track and field club.

It has also been noted that traits associated with emotion, such as anxiety, may influence performance, especially in long-distance runners. A field study examining long-distance runners reported that anxiety and motivation changed their pacing strategy in 1,600 m time trial races such that the lap time for the first 400 m was faster in the enhanced anxiety condition than in the reduced anxiety condition (Lane et al., 2016). Thus, it is likely that long-distance runners utilize anxiety and motivation to determine their pacing during this race. On the other hand, sprinters did not change their performance in a sprint task even in a highly anxious situation (Rathschlag and Memmert, 2015). According to these findings, we can presume that the relationship between anxiety and performance monitoring should differ between long-distance runners and sprinters.

Supporting a conceptualized notion that the ACC is involved in affective-emotional processes, it has also been reported that performance monitoring is influenced by anxiety and motivation (Bush et al., 2000). Hajcak et al. (2005) reported larger Ne/ERNs in a high incentive condition than in a low incentive condition, and concluded that the increases in Ne/ERN amplitude reflected the motivational significance of error. In addition, larger Ne/ERNs were also observed for individuals high in trait anxiety (Olvet and Hajcak, 2009a). These studies assumed that Ne/ERN amplitude is determined by the interaction between the motivational significance of the error and individual differences in trait anxiety (Proudfit et al., 2013). We hypothesized that the relationship between Ne/ERN amplitude and anxiety should differ between sprinters and long-distance runners, reflecting differences in how anxiety may affect their performance (Lane et al., 2016).

Previous studies asserted that the Pe reflects subjective error evaluation following error detection (Falkenstein et al., 2000). Endrass et al. (2010) reported a larger Pe in a monetary punishment condition compared to a control condition where there was no monetary penalty for errors. They suggested that Pe amplitude might reflect motivational evaluation of errors that was enhanced with monetary punishment. These findings appear to indicate that the Pe may represent subjective evaluation of errors. According to previous findings (Endrass et al., 2010), both the Ne/ERN and the Pe should be larger in high motivation conditions than in low motivation conditions.

Thus, we also wanted to investigate if the relationship between competitive anxiety and performance monitoring varies based on the type of athlete (i.e., long-distance runners vs. sprinters). We measured competitive anxiety from long-distance runners and sprinters, using the Sport Competitive Anxiety Test (SCAT; Martens, 1977). As can be seen above, it is highly possible that interactions among performance monitoring and individual differences in anxiety may be observed across different types of exercise (Thiel et al., 2012; Rathschlag and Memmert, 2015). If long-distance runners utilize anxiety to maintain their running pace during races (Thiel et al., 2012), the Ne/ERN amplitude for the long-distance runners should be larger for individuals higher in competitive anxiety than for those lower in competitive anxiety. On the other hand, sprinters performance is unrelated to anxiety (Rathschlag and Memmert, 2015); therefore, the Ne/ERN amplitude for the sprinters should not be associated with competitive anxiety. Thus, the relationship between the degree of competitive anxiety experienced in sports and performance monitoring might differ between the sprinters and long-distance runners. Specifically, we only expect a relationship between the Ne/ERN amplitude and anxiety for the long-distance runners.

MATERIALS AND METHODS

Participants

Fifty-three participants (*Mage* ± *SEM* = 20.4 ± 0.2 years) were recruited from Waseda University's Faculty of Sport Sciences. Five participants were excluded because they had fewer than six errors (Olvet and Hajcak, 2009b). We tested long-distance runners (n = 24) and sprinters (n = 24) who were members of a university track and field club. Participants had normal or corrected-to-normal vision and were paid 2,400 yen (about 28 U.S. dollars) for their participation. All participants gave written informed consent prior to the experiments. This study was approved by the Waseda University Ethics Committee.

Questionnaire

Participants were administered the SCAT (Martens, 1977). The SCAT is a 15-item measure that assesses competitive trait anxiety. **Table 1** shows the SCAT scores in each group.

Procedure

The participants rested both forearms and palms comfortably on a table to minimize any movements unrelated to their responses. We adopted a stimulus–response compatibility task, classified as a spatial Stroop task (Masaki and Segalowitz, 2004). A white fixation cross (0.7° × 0.7°) on a black background was continuously presented in the center of a computer monitor, placed 1 m in front of the participant. A white arrow (visual angle: 0.7° × 0.4°) pointing either up or down was shown above or below the fixation cross with an eccentricity of 0.8° visual angle (between center of fixation and arrow). Arrow direction (pointing up or down) and location (above or below fixation) were combined orthogonally, with each combination occurring equally often across participants. Trials where arrow direction agreed with arrow location (e.g., above fixation; pointing upward) were defined as congruent; trials where this was not the case (e.g., below fixation, pointing upward) were defined as incongruent.

TABLE 1 | SCAT scores (scores, SEM) in each group.

	SCAT
Sprinters	21.50 (0.77)
Long-distance runners	20.25 (0.79)

Each trial began with a central fixation cross, shown for 300 ms; then, an arrow stimulus appeared either above or below the fixation for 150 ms. The arrow was followed by a blank screen for 1100 ms until the next fixation cross. Thus, the duration of each trial was 1400 ms. Participants were asked to respond both quickly and accurately with a brisk finger extension according to the pointing direction of the arrow (i.e., up or down), but not to its location. If participants did not respond within 600 ms, the feedback "Too Late!" was presented for 500 ms. Omitted responses were not regarded as errors, but excluded from analyses.

Responses were recorded with two microswitches mounted 150 mm apart in the mid-sagittal line. The microswitches were operated with small cantilevers that required an upward displacement for switch closure. A plastic plate (30 mm × 20 mm × 1 mm) was attached to the end of the cantilever key, providing leverage. Participants placed their middle fingers on the end of the plastic plate. The displacement of the key by lifting the finger resulted in switch closure and this was used as our definition of an overt response onset. We compared two conditions. In the motivation condition, each correct response was rewarded with a small amount of money (10 yen; about 12 cents), while participants lost 10 yen for each incorrect response. After the experiment, participants were told that their total could not become negative (i.e., below zero) in the motivation condition. Participants were given feedback about their current balance only at the end of each block – no feedback was given after individual trials. In the no motivation condition, participants would neither lose nor earn money and were not given any feedback regarding their performance.

In each condition participants performed four blocks of 72 trials each (288 trials in total). This resulted in a total of 72 trials for each combination of arrow direction and arrow location. Prior to the experiment participants practiced the task for 72 trials without any reward/punishment. The order of the two conditions and hand-to-key assignments were counter-balanced across participants.

EEG Recording

The EEG was recorded from 128 sites with Ag/AgCl electrodes. Horizontal electrooculograms (hEOG) were recorded from the left and right outer canthi, and vertical electrooculograms (vEOG) from above and below the left eye. These were recorded with DC and 100 Hz low-passed filters, using the Biosemi Active Two system (Biosemi, Inc.). All physiological signals were digitized at 2048 Hz.

Data Analysis

RT was measured as the interval between stimulus onset and microswitch closure. The error analysis reported here focused on incongruent trials (see section "Procedure") because congruent trials resulted in were very few errors.

All ERPs were averaged, response-synchronized, using Brain Vision Analyzer. The EEG was re-calculated to an average common reference, and band-pass filtered 0.1–30 Hz (roll off 12 dB). Ocular artifacts were corrected using the procedure developed by Gratton et al. (1983). We excluded from averaging all trials in which response time was below 100 ms and where EEG voltages exceeded a threshold of 100 μV during the recording epoch. Percentage of exclusion from averaging was 0.3% in the motivation condition, and 0.4% in the no motivation condition, respectively.

A baseline of −400 to −300 ms prior to response was used. Ne/ERN amplitudes were scored at FCz as peak-to-peak amplitude by subtracting the most positive peak amplitude preceding the Ne/ERN from the negative peak amplitude of the Ne/ERN (Endrass et al., 2010). The negative peaks were determined within the time window of 100 ms following response onset. The positive peaks were determined within the time window of 100 ms preceding response onset. The Pe was measured at Cz as the mean amplitude in error trials between 200 and 350 ms after response onset.

Mean RTs and error rates were subjected to mixed three-way ANOVAs with repeated factors of Stimulus–Response congruency (congruent/incongruent), and Condition (motivation/no motivation) with Group (sprinters/long-distance runners) as a between group factor. Peak-to-peak Ne/ERN amplitudes (measured at FCz) and mean Pe amplitudes (measured at Cz) were subjected to a mixed two-way ANOVA with repeated factors of Condition with Group as a between factor. These sites for analysis were chosen based on previous research (e.g., Boksem et al., 2006) and examination of the topographic maps to determine where the effect was localized (see **Figure 2**). A Bonferroni correction was applied to *post hoc* comparisons. To investigate the effect of group on the relationship between SCAT scores and ERPs, we conducted a multiple linear regression analysis with SCAT scores, group, and the interaction SCAT scores × group separately for each condition. Cohen's effect sizes were calculated to ensure the reliability of obtained results, adopting values of 0.02, 0.15, and 0.35 indicating small, medium, and large effect sizes, respectively (Cohen, 1992). To estimate how much a multiple linear regression analysis was sufficiently powered to detect significant difference, we conducted a power analysis using G*Power 3 (Faul et al., 2007) and obtained power values 0.08, 0.33, and 0.67 for small, medium, and large effect sizes, respectively.

RESULTS

Behavioral Data

Reaction Time

Figure 1A shows the RTs. A three-way ANOVA for RTs revealed a three-way interaction among congruency, condition, and group [$F(1,46) = 8.45$, $p = 0.006$, $\eta_p^2 = 0.16$]. An additional two-way ANOVA restricted to incongruent trials revealed an interaction between condition and group [$F(1,46) = 4.55$, $p = 0.04$, $\eta_p^2 = 0.09$]. Simple effects analyses showed that sprinters tended to show shorter RT in the motivation condition than in the no motivation condition ($p = 0.06$). For congruent trials, no interaction between condition and group was found ($F < 1$).

A two-way ANOVA on RT with repeated measures of congruency and condition conducted only for sprinters showed an interaction between congruency and condition [$F(1,23) = 8.30$, $p = 0.008$, $\eta_p^2 = 0.27$]. Simple effects analyses showed that RTs on incongruent trials tended to be shorter in the motivation condition than in the no motivation condition ($p = 0.09$). The same two-way ANOVA conducted only for long-distance runners showed neither a main effect of condition ($F < 1$) nor an interaction ($F < 1$). RT of long-distance runners was significantly longer in the incongruent trials than in the congruent trials [$F(1,23) = 470.72$, $p < 0.001$, $\eta_p^2 = 0.95$]. In the no motivation condition, a mixed two-way ANOVA with a repeated measure of congruency revealed no interaction between congruency and group ($F < 1$). RT was significantly longer in the incongruent trials than in the congruent trials [$F(1,46) = 862.20$, $p < 0.001$, $\eta_p^2 = 0.95$]. In the motivation condition, a two-way ANOVA showed no interaction between congruency and group ($F < 1$). RT was significantly longer in the incongruent trials than in the congruent trials [$F(1,46) = 887.84$, $p < 0.001$, $\eta_p^2 = 0.95$].

Error Rate

Figure 1B shows error rates. A three-way ANOVA subjected to the error rate confirmed a significant interaction between condition and congruency [$F(1,46) = 4.78$, $p = 0.03$, $\eta_p^2 = 0.17$]. Simple effects analyses showed that error rate on incongruent

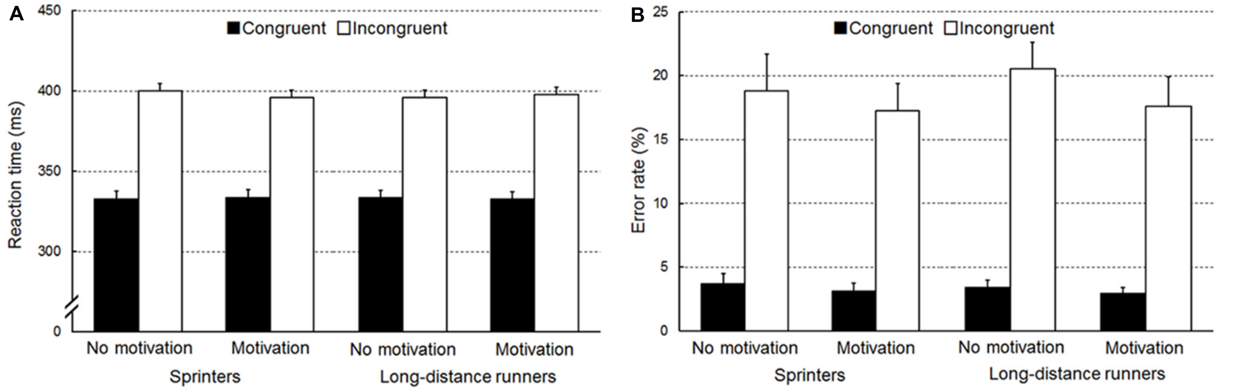

FIGURE 1 | (A) Reaction time [ms, standard error of the mean (SEM)] and **(B)** the error rate (%, SEM) are presented separately for sprinters and long-distance runners.

trials was lower in the motivation condition than in the no motivation condition ($p = 0.02$). For congruent trials, there was no difference between the two conditions ($p = 0.54$). Neither a group effect nor an interaction was found (*Fs* < 1).

Response-Locked ERP

Ne/ERN

Figure 2 depicts the response-locked ERP waveforms at Fz, FCz, Cz, and Pz. The frontocentrally distributed Ne/ERNs emerged about 50 ms after erroneous responses in both the motivation and the no motivation condition and were maximal at FCz. Mean amplitudes of the Ne/ERN for the long-distance runners in the motivation and the no motivation condition were −10.0 μV (*SEM* = 0.83), and −10.4 μV (*SEM* = 0.85), respectively. Mean amplitudes of the Ne/ERN for the sprinters in the motivation and the no motivation condition were −9.4 μV (*SEM* = 0.93), and −9.8 μV (*SEM* = 0.77), respectively. A two-way ANOVA with factors of condition and group showed no difference in ERN amplitudes between the two conditions ($F < 1$). Neither a group effect nor an interaction was found (*Fs* < 1).

Pe

Figure 2 also shows Pe waveforms that emerged approximately 250 ms after erroneous responses and were maximal at Cz. Mean amplitudes of the Pe for the long-distance runners in the motivation and the no motivation condition were 5.8 μV (*SEM* = 0.68), and 4.2 μV (*SEM* = 0.63), respectively. Mean amplitudes of the Pe for the sprinters in the motivation and the no motivation condition were 4.6 μV (*SEM* = 0.74), and 4.6 μV (*SEM* = 0.80), respectively. A two-way ANOVA with factors of condition and group revealed a significant interaction between condition and group [$F(1,46) = 4.06$, $p = 0.05$, $\eta_p^2 = 0.08$]. Simple effects analyses revealed that the long-distance runners showed a larger Pe in the motivation condition than in the no motivation

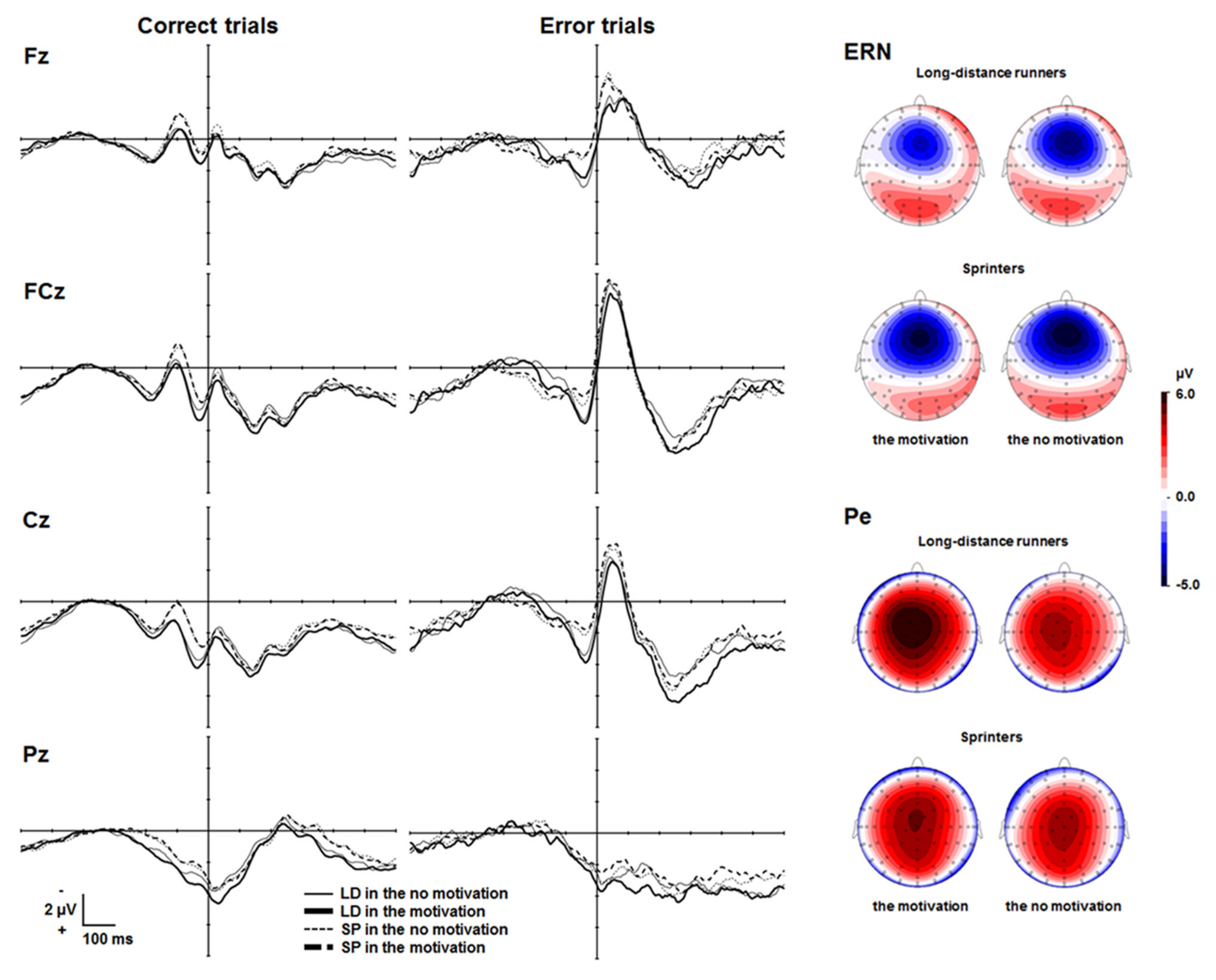

FIGURE 2 | Response-locked grand averaged waveforms on error and correct trials at Fz, FCz, Cz, and Pz. Topographies (only for illustrative purpose) represent brain activities during the time windows ranging from 25 to 75 ms for the Ne/ERN and ranging from 200 to 350 ms for the Pe, respectively. LD, long-distance runners; SP, sprinters. Response-locked grand averaged waveforms on correct trials are shown only for illustrative purposes.

condition (p = 0.01), although the sprinters did not show any significant difference in Pe amplitudes between two conditions (p = 0.91). In addition, Pes did not differ between sprinters and long-distance runners in the no motivation condition (p = 0.70) or the motivation condition (p = 0.22).

Multiple Linear Regression Analyses

To investigate the effect of group on the relationship between SCAT scores and the Ne/ERN amplitudes, we conducted a multiple linear regression analysis with SCAT scores, group, and the interaction of SCAT scores × group as predictors separately for each condition. In the no motivation condition (**Figure 3A**), no interaction between SCAT scores and group was found ($\beta = 0.27$, $t = 1.29$, $p = 0.21$); however, in the motivation condition (**Figure 3B**), a significant interaction between SCAT scores and group was obtained ($\beta = 0.53$, $t = 2.73$, $p = 0.01$). Simple effects analyses showed that the long-distance runners with higher SCAT scores showed larger Ne/ERN amplitudes ($\beta = -0.40$, $t = -2.05$, $p = 0.046$). However, the sprinters with higher SCAT scores tended to exhibit smaller Ne/ERN amplitudes ($\beta = 0.37$, $t = 1.82$, $p = 0.08$).

The same analyses were conducted on Pe amplitudes but revealed no interaction between SCAT scores and the group in the either condition (motivation condition, $\beta = -0.29$, $t = -1.39$, $p = 0.17$; no motivation condition, $\beta = -0.34$, $t = -1.67$, $p = 0.10$).

DISCUSSION

We investigated if the differences in performance characteristics between sprinters and long-distance runners were associated with ERP indices of performance monitoring. Regardless of the type of runner, error rate was significantly lower in the motivation condition than in the no motivation condition. Because both speed and accuracy were emphasized and RT did not differ between conditions, this result is unlikely due to a spead-accuracy trade off. The lower error rate indicates that participants attempted to gain reward and avoid punishment in the motivation condition. This is consistent with previous reports that enhanced significance of an error decreased the error rate in a motivational situation (Hajcak et al., 2005; Maruo et al., 2016). Contrary to the behavioral results, the Ne/ERN did not differ between the motivation and the no motivation conditions, even though previous studies have reported larger Ne/ERNs associated with monetary reward and punishment (Hajcak et al., 2005). In addition, Ne/ERN amplitudes did not differ between sprinters and long-distance runners. Previous studies reported that smaller Ne/ERNs are associated with higher aerobic capacity (Themanson and Hillman, 2006; Pontifex et al., 2011). Our findings were not consistent with these previous studies. However, it is difficult to interpret our results according to these findings, because we did not directly measure aerobic capacity nor cerebellar gray matter volumes. Our results may also have been affected by a ceiling effect. Athletes in both types of running events have likely achieved a very rigorous error-detection system that was aqcuirred through multiple years of practice and competition and this may have contributed to a similar activation of the ACC in both groups.

To investigate the relationship between competitive anxiety and enhanced performance monitoring with monetary reward, we calculated correlations between SCAT scores and Ne/ERN amplitudes in the motivation condition. For the long-distance

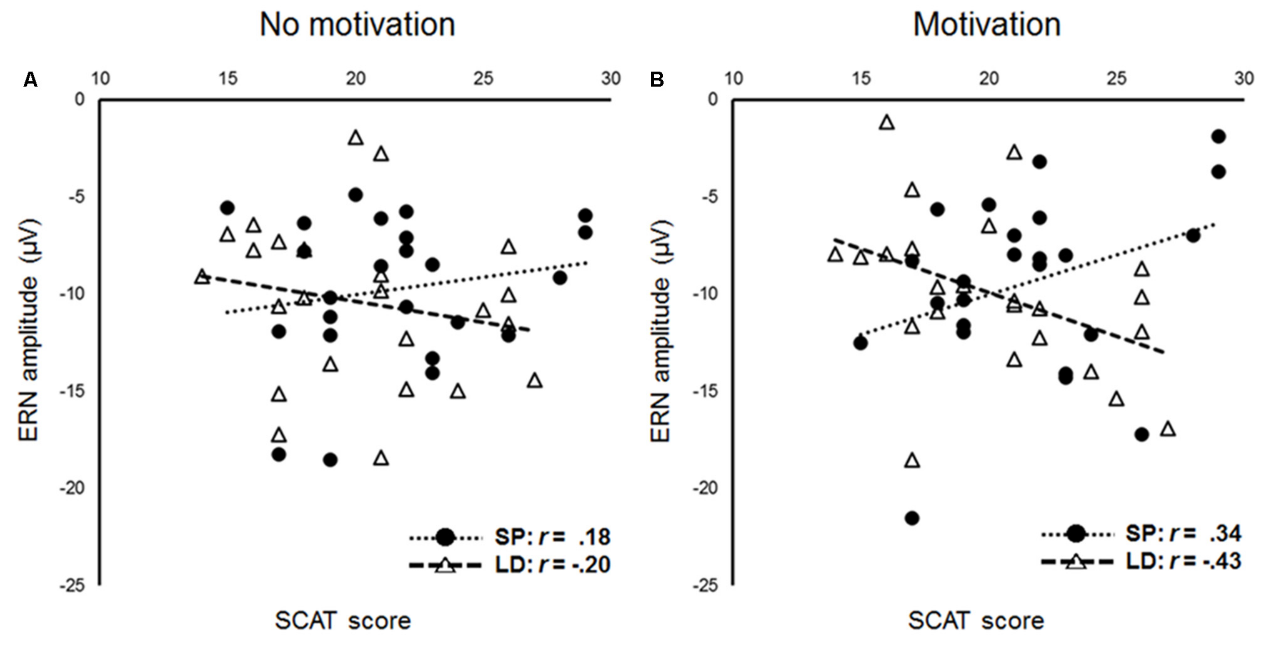

FIGURE 3 | Scatter plots showing the relationships and correlations between scores on the SCAT and amplitudes of error-related negativity (ERN) [**A**, no motivation condition, **B**, motivation condition, circle: sprinters (SP), triangle: long-distance runners (LD)].

runners, individuals who had higher SCAT scores exhibited larger Ne/ERN amplitudes in the motivation condition in accordance with previous studies (Olvet and Hajcak, 2009a). However, sprinters with higher SCAT scores tended to exhibit smaller Ne/ERNs in the motivation condition. As we expected, the relationship between SCAT and Ne/ERN in the motivation condition differed between these two types of runners (i.e., sprint vs. long-distance). To our knowledge, this is the first demonstration of an effect of exercise type on the relationship between Ne/ERN and anxiety. Competitive anxiety may predict larger Ne/ERN amplitudes in the long-distance runners but not in the sprinters.

Many studies have confirmed that the Ne/ERN is associated with anxiety and negative affect (Olvet and Hajcak, 2009a; Aarts and Pourtois, 2010; Proudfit et al., 2013). For example, Aarts and Pourtois (2010) found larger Ne/ERNs for high-anxious than for low-anxious participants. Hajcak et al. (2004) also found a larger Ne/ERN in a high negative-affect group than in a low negative-affect group. According to these findings, a high anxiety trait is generally associated with a larger Ne/ERN. Our Ne/ERN results for the long-distance runnners are consistent with these previous findings. In this context, the results of the long-distance runners are expected and understandable.

Therefore, a weak relationship with higher anxiety being associated with smaller Ne/ERN for the sprinters might be a special case. Rathschlag and Memmert (2015) investigated whether or not self-generated emotion could enhance the performance of sprinters. Although induced anxiety did not influence running time in a 40 m sprint task compared to the emotionally neutral condition, induced happiness improved the running time. They also found that in the anxiety condition sprint time did not correlate with either trait or state anxiety as measured by the State-Trait Anxiety Inventory (STAI; Spielberger et al., 1970). Thus, the sprinters appeared to achieve performance skills relatively independent of trait anxiety. It is possible that the error detection system of sprinters is not noticeably influenced by competitive anxiety and they are not as concerned about a risk of error commission.

Long-distance runners, but not sprinters, showed a larger Pe amplitude in the motivation condition than in the no motivation condition. This result is consistent with previous findings. Endrass et al. (2010) found larger Pe amplitudes when they manipulated extrinsic motivation with monetary punishment, reflecting enhancement of subjective error evaluation. Maruo et al. (2016) also showed that the Pe increased in amplitude with either monetary reward or punishment. Thus, it is reasonable to conclude that long-distance runners experienced enhanced conscious error-evaluation with increased extrinsic motivation. By contrast, the Pe amplitude in sprinters was not increased in the motivation condition. The interaction between exercise types and the motivation condition suggests that long-distance runners and sprinters may show different motivational evaluations of errors (Endrass et al., 2010). Although Themanson and Hillman (2006) reported that the Pe amplitude was larger in individuals with high aerobic capacity than in those with low aerobic capacity, the Pe amplitude did not significantly differ between sprinters and long-distance runners.

It should be noted that our study has some limitations. First, we did not test non-athletes as a control group. Comparing track-and-field athletes with a group of non-athletes may have helped further clarify differences among long-distance runners, sprinters, and non-athletes. Second, if we had directly measured aerobic capacity from participants we could have reconfirmed the differences in aerobic capacity between long-distance runners and sprinters previously reported by others (Niemelä et al., 1980; Kusy and Zieliñski, 2015). Third, we did not find any significant correlations between SCAT scores and Pe amplitudes. In accordance with a previous finding (Proudfit et al., 2013), this result suggests that the error evaluation process might not be influenced by anxiety.

In sum, we found that Pes in the long-distance runners are modulated by the affective-motivational significance of errors, suggesting that long-distance runners may thoroughly evaluate their own errors in a motivational situation. We also found that in the motivation condition the long-distance runners with higher competitive anxiety showed larger Ne/ERNs, whereas the sprinters with higher competitive anxiety tended to exhibit smaller Ne/ERNs. These results suggest a particularity associated with long-distance runners in terms of their reaction to errors. Taken together, our findings may provide further evidence that the relationship between performance monitoring and individual differences in anxiety may differ across various types of sports.

In order to maximize the effectiveness of athlete's training and subsequent performance in competition it is important for coaches and athletes to understand all aspects of their performance, both physically, and cognitively. Our results suggest that different types of athletes may differ cognitively and utilize performance monitoring in different ways. If sprinters and long-distance runner not only have significant differences in muscle structure but also brain structure/performance this may be an important consideration in terms of how athletes train. Further research in this area will be required to enhance our understanding of the cognitive differences among various types of athletes in order to optimize each individual performance.

ETHICS STATEMENT

This study was carried out in accordance with the recommendations of human research of guidelines, the Ethics Review Committee on Research with Human Subjects of Waseda University with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the Ethics Review Committee on Research with Human Subjects of Waseda University.

AUTHOR CONTRIBUTIONS

YM and HM: designed the experiment and analyzed data. YM: performed the experiment. YM, TM, and HM: interpreted the data and wrote the paper. All authors made direct contribution to the work and approved it for publication.

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Influences of Synchronized Metronome Training on Soccer Players' Timing Ability, Performance Accuracy, and Lower-Limb Kinematics

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Planning and performance of all complex movement requires timing, integration, and coordination between sensory-perception and motor production to be successful. Despite this, there is limited research into "if" and "how" timing training may influence movement performance in athletes. The aim of the present study was to investigate the effect of synchronized metronome training (SMT) on sensorimotor timing ability, and in view of that, if improved timing may be transferred to lower-limb movement planning, precision performance, and kinematics. The sample consisted of 24 female elite- and semi-elite soccer players, randomly assigned to receive SMT and a control group. The SMT group received 12 sessions of Interactive Metronome® (IM) training over 4 weeks. At pre- and post-test, timing-precision was assessed through hand and feet movement synchronization with rhythmic sound; and leg-movements performance accuracy, duration, and kinematics were recorded during embodied high cognitive-load stepping task (6 trials×20 s) by use of a optoelectronic motion capture system. Pre- to post-test comparisons showed significant timing improvements as an effect of the IM training. Significant pre- to post-test improvements on the stepping task performance were seen in an increasing number of accurate foot taps during the stepping task sequence and by shorter duration for the SMT-group only. No evident pre- to post-test effects of SMT on the kinematic parameters investigated were found. These findings signify that the guided attention and working-memory functioning may be positively affected by SMT training; thereby, resulting in better motor planning, performance, and movement precision. Still, independent of group and test-occasion, significant correlations were found between the participants' outcome performance differences and the kinematic parameters. It was found that a decreasing 3D movement distance and less segmented movements correlating negatively, and increasing velocity (speed) positively, with accuracy and performance duration, respectively. These findings are likely associated with inter-individual variations in the nature of higher-order cognitive processing capacity due to the highly cognitive demanding stepping task.

Keywords: timing-training, sensorimotor, kinematics, soccer, cognitive-load

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INTRODUCTION

Synchronized sensorimotor timing skills are important for all daily actions, not least vital for athletic performance, where the smallest mistake in movement can be costly, and only a few milliseconds can make the difference between triumph and failure. Undeniably, timing is especially essential in fast-changing and complex situations and stimuli; as in soccer games. The players have just a few tenths of a second to anticipate where the ball will land, how to position their bodies, decide their next move and speed, be aware of the team-member's and opponent's positions and (possible) moves, and decide at what angle and force to direct their next return. These actions are all about timing, planning, sensory-motor synchronizations, coordination and control. The question then is if it possible to train the timing ability? There are convincing numbers of scientific studies that have confirmed positive effects of synchronized metronome training (SMT) for improvements of timing and performance, although surprisingly few includes athletes. In this study we will investigate the possible transfer effects of timing training on soccer player's lower-limb performances.

The Interactive Metronome® (IM) training program is a specific method of SMT. IM is a unique training tool that challenges sensory and motor systems simultaneously as the individual synchronizes movements with a steady auditory rhythm. Millisecond feedback for mental/interval timing is provided following each movement to help the individual refine and better their sensory-motor timing ability. Several lines of research have shown evidence that after IM training one can see improvements in numerous sensorimotor and cognitive performances (Interactive Metronome® [Equipment], 2012; McGrew, 2013). It is suggested that IM training promotes synchronization within the neural network for more coordinated movement through a series of progressive exercises. Thus, in line with research finding that listening to rhythmic sound activates the centers of the brain involved in coordinated motor planning and sequencing (Bengtsson et al., 2009), and influences internal timing for coordinated movement (Jantzen et al., 2007). Additionally, that action both enriches and complicates the interpretation of sensory inputs and that sensorimotor event may also be transmitted from motor to sensory areas (Merchant and Yarrow, 2016).

The aim of the SMT is to reduce one's mean asynchrony, or in other words, improve one's timing and rhythmic ability. When SMT achieves reduction in asynchrony, it results in improved sensorimotor synchronization (SMS). SMS is most often thought about in regards to music and dance, where one's ability to coordinate perception and action to a beat are necessary (Repp, 2005; Repp and Su, 2013). However, with the increasing popularity of SMT programs such as IM training alongside the growth of neuroimaging studies, there is a growing area of research that suggests that SMS induces transfer effects that are potentially much wider than just for musicians and dancers. For instance, neuroimaging studies (e.g., fMRI) provides support for the idea that SMT can improve spatial-temporal networks within the brain (Chen et al., 2008; Bengtsson et al., 2009), and thereby, inducing changes in motion performance. Intriguing relationships have also been observed between SMS ("beat synchronization"), variability and neural processing of speech in preschoolers (Woodruff Carr et al., 2014). Positron emission tomography (PET) brain investigations have shown that functional cortico-cerebellar circuits sub-serve differential aspects of rhythmic synchronization regarding rhythmic motor control and rhythmic pattern tracking (Thaut et al., 2009). Additionally, relationships between multimodal timing based integrations, brain intrinsic oscillatory gamma activity and reading skills in adolescents have been shown (Woodruff Carr et al., 2017); these findings suggest that beat synchronization and auditory processing may rely on overlapping neural resources that facilitate temporal precision.

The functionality of the brain's spatiotemporal network, that is to say the brains internal timing mechanisms is inextricably linked with not only motor performance, but even to executive functions (e.g., Stemmer, 1996; Rossini and Pauri, 2000; Diamond, 2003; Mauk and Buonomano, 2004; Nelson et al., 2013). This relationship between timing, motor performance and executive functions, can most obviously be seen in children diagnosed with developmental coordination disorder (DCD). Children with DCD are described as having difficulty with motor planning and control, timing, maintaining attention, and working memory (American Psychiatric Association, 2013). Furthermore, studies of individuals with cerebellum damage have shown that these individuals often suffer problems in executive functions such as learning and memory (Bellebaum and Daum, 2007; Koziol et al., 2012). These studies provide a sound argument, from an evolutionary perspective, for understanding why these two brain areas would be linked. These neural relationships contribute to the explanation of the positive results that SMT has had on children with attention deficit hyperactivity disorder (ADHD) and reading disorders (Shaffer et al., 2001; Taub et al., 2007), as both disorders involve deficits in executive functioning, and in which traditional interventions target executive functioning. Rosenblum and Regev (2013) have described that timing deficits in children with DCD are found to be manifested by their timing performance of the IM tasks, as well as in the temporal measures of their handwriting performance. It has been suggested that SMT has an effect on choice discrimination, which is also a feature of executive functioning (Diamond, 2003).

Taking into consideration the theoretical knowledge and understanding of neural pathways between timing, rhythmicity, and motor planning and control in the brain, it has been proposed that training participants' timing and rhythmicity can lead to improved motor planning and performance by strengthening these neural pathways (Libkuman et al., 2002; Sommer and Rönnqvist, 2009; Beckelhimer et al., 2011; Chen et al., 2012; Johansson et al., 2012, 2014). A brief review of scientific articles where SMT was used as an intervention has shown support for this. For instance, Shaffer et al. (2001) found that SMT training led to improvements in attention regulation and motor control in both children with special needs and children with ADHD. Beckelhimer et al. (2011) showed improved upper-limb functionality in two participants who had suffered stroke, and Johansson et al. (2012, 2014) saw improved upper-limb movement in two different case studies of children with a different severity of cerebral palsy. An extensive number of clinical studies have also shown that fixed-tempo by the use of Rhythmic Auditory Stimulation (RAS) improves different aspects of gait timing (e.g., Thaut et al., 1996; Hove et al., 2012), and have described the effectiveness of RAS and its promising therapeutic role of improving different aspects of gait performance in patients affected by Parkinson's disease (e.g., Thaut and Abiru, 2010; Murgia et al., 2015, 2018; Pau et al., 2016; Dalla Bella et al., 2017; Bailey et al., 2018). It's suggested that RAS would facilitate the activity of the internal clock, thus dys-functioning in patients with Parkinson's disease (PD), and thereby help in regulating the fluidity of muscular activation, improving coordination, and facilitating the execution of automatic movements, such as walking in PD (Murgia et al., 2018).

In the field of sport science, although existing scientific research is limited, many professional and amateur sport teams have used the IM training method, and reported that their athletes have improved on skills assessments as well as on educational assessments (Interactive Metronome® performance training, 2001; Notre Dame and the Interactive Metronome, 2011; Massad, n.d.). For example, Massad has described how the IM training program has been used and praised by top PGA tour golfers, American football team *Notre Dame*, and NBA team *Miami Dolphins*. In line with these findings, both general rhythm training and tennis specific rhythm training have been described to have an effect on both rhythmic competences as well as on tennis performance in tennis players (Sogut et al., 2012). Although there are many reports from different sports teams and coaches that the IM training program is effective, there are still a limited number of scientific research publications on the relationship between SMT and athletic performance. From the available empirical research, Libkuman et al. (2002) and Sommer and Rönnqvist (2009) have shown that SMT by means of IM training improved golf shot accuracy and reduced the outcome variability. Additionally, Sommer et al. (2014) found that the effect of SMT may not only improve golf shot accuracy, it may also influence the underlying coordinative structures and the temporal synchronicity of the upper-limb movements during the golf-swing performance. Additionally, in a recent study by Kim et al. (2018), the IM training program was implemented to investigate the associations between brain connectivity (during resting state functional MRI) and golf putting performance. The study outcomes showed that IM training reduced the variability of timing between back swing and ball impact in a two-meter putt. In addition, IM training was found to increase brain connectivity from the cerebellum to the frontal cortex. These findings suggest that optimization of motor timing can promote improved motor learning and putting performance in professional golfers (Kim et al., 2018). A recent study from the authors own lab has investigated the effect of IM training in female soccer players performance on cross-pass kick accuracy, and the associated brain response by fMRI while the players were watching videos with soccer-specific actions (Sommer et al., 2018). The results from this study provided both behavioral and neurophysiological evidence that timing training positively influences soccer skill (cross-pass accuracy) and thereby strengthens the action-perception coupling by means of enhanced SMS abilities. Furthermore, it was found that SMT affects the underlying brain responses by means of evident reduced activation within the cerebellar lobule VI activity (Sommer et al., 2018); the brain areas originate to be important for temporal planning, movement coordination, action recognition, and higher cognition functioning (see Keren-Happuch et al., 2014, for a meta-analysis).

At large, the current scientific literature provides evident support for positive outcomes after SMT in a variety of populations, performances, and functions. The present findings of how IM training seemingly effect brain activity within regions facilitating the action perception coupling, as well as induced positive effects on sport performance could be vital for enhancing timing training techniques for athletes. Still, there is a need for further scientific investigation in order to better understand the underlying mechanisms that lead to better motor performance and cognitive functioning, after SMT in athletes. In the present study our aim was to determine whether IM training would add value to traditional soccer training, and if so, if it would induce positive effects on the soccer players planning ability, performance, and in the organization of kinematic properties of leg movements.

Even if the existing literature and theories supports the mediating effect of timing and rhythmicity in regards to one's attention, cognitive functioning, and motor control, it is uncertain how these mechanisms work together. Accordingly, the present study aimed to contribute to the literature through using an experimental design to investigate the possible effect of the expected timing improvement on lower-limb performance and kinematics, after 4 weeks of IM training. The relationships between timing, motor performance, and executive functions, are central to the design of the present study. Therefore, the stepping task applied in the present study was specifically designed, not only to be relevant to soccer players, but also to require the use of on-line multi-processing such as, inhibition, updating, and shifting. Thereby, creating a state of high cognitive load (simulating the executive chain of decision makings), similar to a real soccer situation. Inhibition, updating, and shifting are three of the most studied constructs within cognitive psychology, and according to Miyake and Friedman (2012) are required to complete complex tasks. Cognitive load and executive functions are related because they rely on working memory to process information (Johannsen et al., 2013).

Based on previous research findings, we expected that the soccer players who undertook the SMT program would improve their timing ability from pre- to post-test, and as a result, perform more accurate and faster lower-limb movements on the specifically designed stepping task. Additionally, we assumed that SMT may lead to changes in the kinematic properties, possibly by means of a less spatio-temporal segmented (smoother) and more time effective movement trajectories (increasing velocity and shorter movement distance), as to be seen in the 3D kinematics recorded of the soccer players whilst preformed the dual motor-cognitive demanding stepping task.

MATERIALS AND METHODS

Participants

Twenty-four female sub-elite and elite outfield soccer players, who played for teams based in Umeå, Sweden, participated in the present study. At the time of pre-testing the participants' age ranged from 16.2 to 25.8 years (*M* = 19.5, *SD* = 2.7) and they had between 5.5 and 19 years (*M* = 12.7, *SD* = 2.6) of experience playing soccer. All participants were randomly assigned to either the control group or the intervention group. There were no significant between-group differences for age or experience. All participants partook in normal pre-season training during the study. Additionally, the SMT group received three sessions of 45–50 min IM training weekly during a 4 weeks period after the pre-test. For group demographics see **Table 1**.

Apparatus

Tests of Timing and Rhythmicity

The IM system was used to assess both the control and SMT groups' timing and rhythm skills at the pre- and post-test sessions. The IM test is run in connection with a Windows based computer program that plays a metronome beat into headphones worn by the participant. The IM assessment used at both pre- and post-test sessions was delivered according to standardized protocol included in the instrument manual (Interactive Metronome® [Equipment], 2012). For the present study, the participants wore headphones to listen to the metronome, contact-sensing gloves on their hands, and they used their feet to tap contact-sensing floor mats. These contact-sensing triggers relay information back to the Windows program about the difference between the time at which a participant makes a tap and the metronome beat. For the purposes of the present study there were two soccer related tasks included in addition to the 14 standard tasks (16 tasks in total). Before starting the tests participants viewed a video demonstration of the 16 tasks. For the tests the metronome was set to 54 bpm, with an inter-onset interval of 1100 ms between each task. The participants received no guide sounds or feedback on their performance. The tests took approximately 20 min to complete. The 16 tasks involve completing both uni- and bilateral hand and foot movements to the metronome beat, e.g., bringing both hands together to clap in time with the metronome. The additional two tasks were a stepping task using both feet to step onto floor sensors in synchrony with the metronome and also to perform a kick with their dominant foot at a sensor placed 50 cm above ground. For the present study IM measures from the pre- and post-test sessions were analyzed. These two measures were the *mean rhythmic ability* and the *mean timing ability* of the participants. The *mean rhythmic ability* measures the inter-response interval, which is measured as how close the participant's response is to their previous response, and the *mean timing ability* measures the millisecond discrepancy between the metronome beat and the participant's responses, which describes the participant's SMS or motor timing skill.

The Stepping Task

Figures 1A,B depicts the experimental lay-out of the stepping task. The instructions that each participant was asked to follow are summarized here. Firstly, the participants were asked stand in the center of a circle of fixated tennis balls, and then to tap the markers with their feet in accordance with a specific digit-series, as many times as possible, while maintaining accuracy, within a 20 s timeframe. The digit-series contained the digits 1–6 (e.g., 1-6-5-2-3-4) and were projected on the screen (placed 2.5 m from the participant at eye level) in front of them throughout the trial, so that they could refer back to the sequence at any time if they forgot the sequence. In other words, the participant had a 20 s period to repeat the sequence as fast and accurate as possible. The participants were instructed to use their left foot to touch markers 1, 3, and 5, and their right foot for markers 2, 4, and 6. Each marker's number was clearly marked and visible for the participant. Before start, it was emphasized that they needed to not only move as fast as possible, but also to ensure that they minimized mistakes by being precise and accurate. Eight different digit-series were presented, in a randomized, counterbalanced order, and presented after one another, with a small pause (approximately 10 s) between each trial. The presentation onset of the digit-series during the experimental conditions was time synchronized with the onset of the movement registrations. Before the actual start of the experimental session, two 20 s warm-up trials were completed by each participant at both pre- and post-tests. Motion data from the two warm-ups were not measured.

Recording and Data Collection

For each trial, the participant's performance was recorded both in 2D and 3D (illustrated in **Figures 1C,D**). The 3D movement data was captured with an Optoelectronic motion capture system (ProReflex® [Equipment], 2008) with four cameras, placed around the player, at a distance of 3.5 m from the center of the tennis ball set-up. The 2D recording was captured with a standard video camera placed in front of the participant recoding at 30 fps. The four camera motion capture system by Qualisys Inc. tracks the real-time position (X, Y, and Z, coordinates) and orientation data in 3D space of small, reflective markers attached to the

TABLE 1 | Participant's mean age, weight, and height, years of experience (±SD), and the number of elite/sub-elite players in both groups.

	N	Age (years)	Weight (kg)	Height (cm)	Experience (years)	Elite-/Sub-elite players (*n*)
SMT	12	18.6 (2.4)	62.5 (5.1)	168.9 (5.0)	12.0 (2.2)	8/4
CTRL	12	20.3 (3.01)	60.7 (6.5)	169.7 (6.05)	13.3 (2.87)	6/6

N, number of participants.

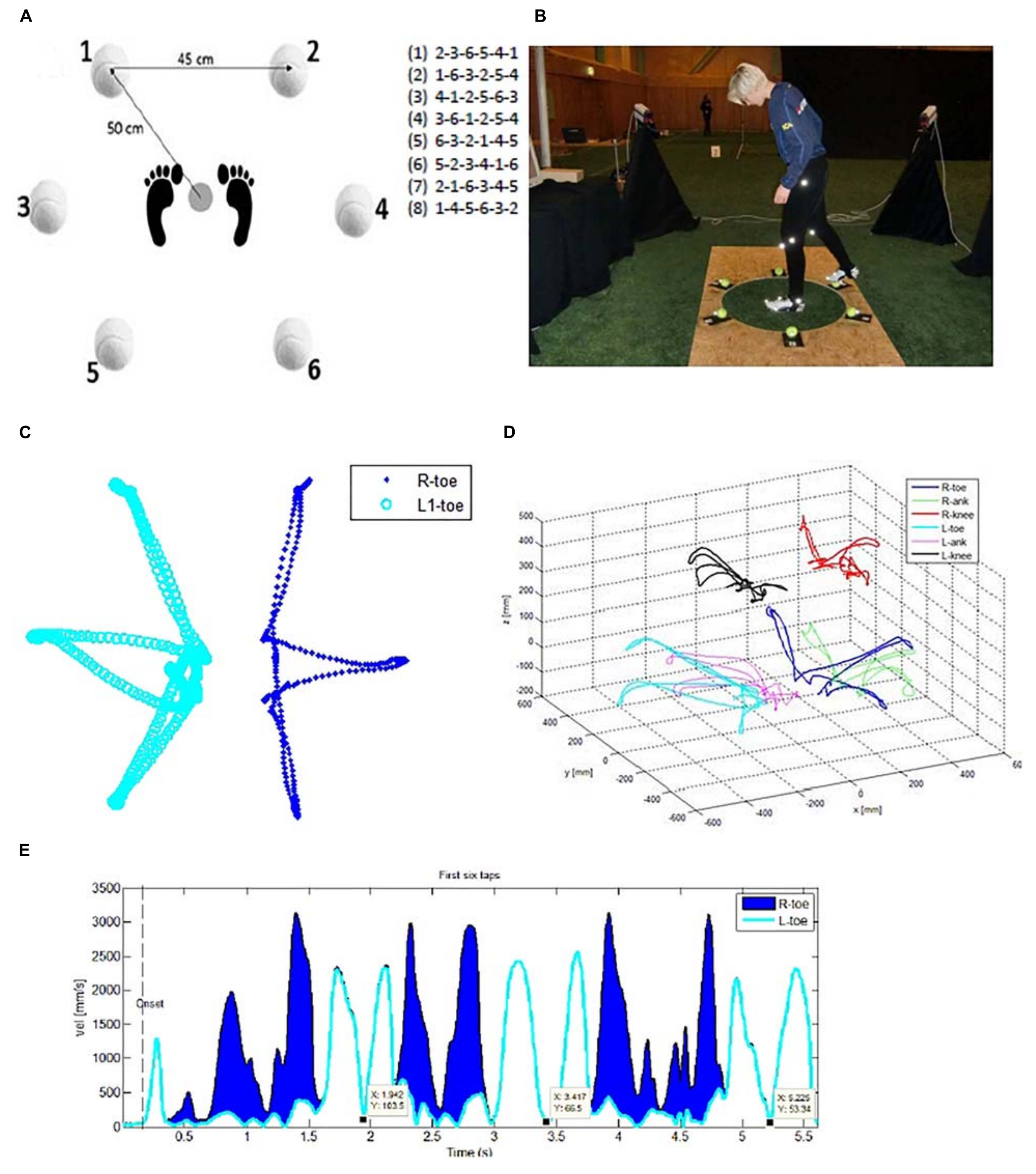

FIGURE 1 | Experimental of protocol illustrating **(A)** the stepping task set-up and example of the eight randomized digit series (e.g., task inducing cognitive-load), contra-balanced (by side), **(B)** photo illustrating the task condition and the marker set-up on the participant, **(C)** example of 2D (x, y) movement trajectories of the right and left foot during the first six step performance (duration 5.7 s) when matching the stepping with the cognitive loaded trial sequence (2/R – 3/L – 6/R – 5/L – 4/R – 1/L) with the actual time position of the three accurate left foot-taps added to the velocity trajectory, and **(D)** the 3D (x-, y-, z-plane) movement trajectories of the right/R and left/L toe, ankle, and knee, respectively, and **(E)** the corresponding velocity trajectories of the right and left toe movements, respectively. The black dots on the velocity trajectory (L-toe) donate the exact moments [time (x) and velocity (y)] of the respectively first three left-foot target hits. Written permission for publication of the photo **(B)** has been reserved from the participant.

participants (illustrated in **Figure 1B**). Each of the six tennis balls had reflective markers attached; these markers provided exact information about the time, precision and accuracy of the participant's foot contact with the ball during the stepping task. The sampling frequency was preset to 120 Hz for all trials, and the quoted accuracy for this system is better than 1 mm for position and 1° for orientation. The cameras were linearized and the system calibrated before the measurement sessions began.

A total of 16 spherical Velcro ProReflex markers were attached to each participant before the stepping task, each marker had a diameter of 7–10 mm. These were placed on each of the hips, knees, ankles, and feet, of the players. Anatomical position is described in **Table 2**, and illustrated in **Figure 1B**. Participant's completed the task with soccer boots on, and so markers for the feet were attached at three positions on each of the soccer boots, other markers were attached to a pair of MoCap pants which have Velcro compatible fabric. In addition, markers were placed on the far side of each tennis ball to aid the 3D analysis (see **Figure 1**). Six of these 16 markers were selected from each participant to be used in the kinematic analyses. Due to technical difficulties at data collection, it was not always possible to take the same six markers from each participant. However, as markers from the knees (2) and feet (3) were positioned in clusters, tests on the data extracted from the Qualisys software showed that there were no significant differences in the average displacement or velocity profile between each of these markers within one cluster. Thus, one marker with the best data quality (without missing values) was selected from within these clusters. The right and left hip-markers were not included in the analysis as a consequence of inconsistent measurement quality due to temporarily hidden hip-markers.

Procedures

The testing and intervention took place 2 months before the start of the competitive Swedish soccer season. Although not playing games during the study time, all participants participated in their regular team trainings under the test period. At the pre-test session all 24 participants completed a screening questionnaire. At the pre- and post-tests all participants completed both the IM assessment of rhythm and timing and stepping task.

TABLE 2 | Labels and anatomical positions of ProReflex Markers.

Label used	Anatomical position	Segment
Left/right foot	(1) Lateral of the base of the fifth metatarsal	Forefoot
	(2) Medial side of the distal phalanx of the liallux (toe)	Hallux
	(3) Proximal base of the first metatarsal	Foot
Left/light ankle	(4) Lateral calcaneus	Hind foot
Left/right knee	(5) The most prominent part of tuberositas tibiae	Thigh/shank
Left/right hip*	(6) Lateral epicondyle	Shank

**Not included in the analyses.*

Both pre- and post-testing of the IM assessment and the stepping task took place under controlled and similar conditions for all participants. The IM assessment and training sessions took place in a specially designed lab-setting for this study; the kinematic assessment of the stepping-task took place on an indoor soccer field (with artificial turf) with controlled temperature and lighting. The participants wore similar clothes and soccer boots, the testing areas were blocked off with black curtains to minimize distractions, and all experimental protocols were the same. There was a 100% retention rate, with all participants completing both the pre- and post-test sessions, and those in the intervention group completed all SMT training sessions.

Ethical Considerations

All participants signed an informed consent form prior to participation. This study is part of a larger research project investigating foot-ball player's performance as regards to the effects of different training methods and assessments, which has received ethical approval by the Umeå Regional Ethical Board (2011/394-31), and conducted in accordance with the Declaration of Helsinki.

The Intervention

Participants in the SMT group received three individual sessions per week of IM training provided over a period of 4 weeks, conducted by a qualified instructor. Each training session lasted 45–50 min, resulting in each participant receiving 9–10 h of IM training between the pre- and post-test assessments. Unlike the IM test, in the training sessions the participants receive feedback on whether their hand/foot contact with contact-sensing triggers was on beat, early, or late. This feedback is provided by guide sounds in the headphones worn by each participant. An on beat contact is defined as being within 15 ms of the metronome, and a high pitched tone is simultaneously played into both ears of the headphones. An early contact, one that is 16 ms or earlier before the metronome results in a low pitch tone in the participant's left ear only. Meanwhile, a late contact, 16 ms or later than the metronome results in a low pitch tone in the participant's right ear only. This feedback is almost instantaneous and guides the participant to make their movements in time with the metronome through allowing them to adjust and correct their errors continually throughout the IM training session. Each training session began with three or four basic warm-up tasks, i.e., clapping both hands together, or a one hand tap to the thigh, and then moved on to the 32 intervention tasks which consisted of both lower-limb and upper-limb movements, many of the movements were designed to employ soccer-specific skills. The metronome speed varied during the training sessions from 54–100 bpm. At the end of each session the participant would receive a breakdown of their performance as a form of feedback that would motivate them to improve on their scores at the next session. After the 12 training sessions each participant in the SMT group had typically engaged in approximately 27000 motor repetitions.

Data Extraction and Analysis

To establish the training effects from the IM intervention, the participant's timing ability and rhythmic ability (measured in milliseconds) from the pre- and post-test sessions were extracted from the IM computer program.

To illustrate the player's performance on the stepping task, two variables were extracted from the 2D video recording, and conferring with the synchronized 3D optoelectronic measures of the pre- and post-test. These variables were number of correct foot taps and time taken (duration) to complete first six taps. Each trial was first analyzed one-by-one to identify and count the total number of successful taps made by the participant and to assess how many of these taps matched the specific digit-series they were instructed to follow for that trial. A successful tap was defined by the soccer boot making clear contact with the tennis ball, taps beside or behind the ball, which did not make contact with the ball were not counted as successful. Due to technical issues during the testing session, not all trials for all participants were recorded correctly and therefore there are some missing data. In total, two trials (or 1% of all pre-test data) from the pre-test (both from SMT group) and four trials (or 2% of all post-test data) from the post-test (three from SMT and one from control) are missing.

Due to the variation in total number of taps made by each participant in the 20 s stepping task the kinematic data analyses was extracted from each trial of the participant's first six taps. The kinematic data from each camera were first transformed into three-dimensional (X, Y, and Z) coordinates by the system software (Qualisys Track Manager). All kinematic data was smoothed prior to analyses using a second-order 10 Hz dual-pass Butterworth filter, and analyzed offline with custom written software in MATLAB (The Mathworks Inc.). The kinematic variables that were extracted for statistical analysis were the cumulative 3D distance (mm), the total number of movement units (MU), and the average velocity (mm/s). Cumulative 3D distance is the total accumulated distance extracted from each marker to gain insight into the energy efficiency of the movement paths (exemplified in **Figures 1C,D**). Movement units describe the segmentation of the movement trajectory and are based on tangential velocity and acceleration data (exemplified in **Figures 1E,F**). The algorithm for calculating MUs was taken from previous studies of movement segmentation by von Hofsten (1991) and Rönnqvist and Domellöf (2006), where one MU is defined as a change from an acceleration or deceleration phase with a rate of change in accumulated velocity of at least 20 mm/s and change in acceleration/deceleration of at least 5 mm/s^2.

The total number of successful kinematic recordings extracted for further analysis was from in total 289 (20 s) stepping trials that represented 76% of all pre- and post-test data. In total 94 trials (24%) of the kinematic recordings were excluded because of poor recording quality. This was due to markers not being measured properly; e.g., >10 frames missing in a row, markers hidden, and/or marker drop-off. Small marker omissions (<10 frames) were pre-set to be gap filled by the system software. All automatic gap fills were visually inspected and adjusted in cases where the fill was deemed incorrect before accepting them. Larger gaps in the recordings (maximum of 20 frames) were manually gap-filled if deemed that it could be done reliably. All larger gap-fills were checked in Z-, Y-, and X-plane, acceleration profile and velocity profile before accepting them.

Statistical Analysis

Tests of homogeneity of variance, normality, and between-groups *t*-tests supported that the sampled data were approximately normally distributed and that the two groups were equal at pre-test in regards to demographic variables, performance on the stepping test, and in kinematic measures. Further, no significant group difference in timing or rhythmic performance was found at the IM pre-test. Where the assumption of homogeneity was not met, Greenhouse-Geisser corrects were applied. Due to the intervention focus of the study effect sizes (partial eta-squared: η_p^2) are provided where applicable, interpretations of these are steered by Cohen's (1969) guidelines: $\eta_p^2 > 0.01$ or 1% = small effect, >0.06 or 6%, medium effect, and >0.14 or 14% = large effect.

To analyze the effect of SMT on the soccer players' timing ability and lower-limbs movement performances in the stepping task, separate mixed analysis of variance test (ANOVAs) with repeated measures were used, with group (SMT – control) as the between-individual factor and "test" (pre-test – post-test) as repeated within-individual factor. Each dependent variable was run in separate tests. Regarding the kinematic variables (cumulative 3D distance, number of MUs, and the average velocity correspondingly) a composite value was calculated from the knee, ankle, and toe markers for the respective right and left leg kinematics. Significant between group and time interactions was followed up by use of *Scheffe's post hoc* comparison. *Pearson* product-moment correlation coefficient was used to explore the relationship between the players' timing ability (mean response time; difference in milliseconds between the moment the beat sounds and the participant's motor response, with longer response time indicating lower time management ability) and the movement performance (number of correct foot taps and duration) and the kinematic outcome parameters (MUs, 3D distance, velocity) from the stepping task. A pre-set alpha level of 0.05 was used as the level of significance for all statistical tests. All statistical analysis was made by using the STATISTICA software (StatSoft 11[1]).

RESULTS

Timing Ability

To analyze the intervention effect of SMT on timing and rhythmic ability (mean response time including all the fourteen standard IM-tasks in milliseconds) were statistically analyzed. The pre- and post-test outcomes from all 14 tasks for respective group are presented in **Figure 2A**. The ANOVA revealed a significant main effect for group; $F(1,22) = 5.24$, $p < 0.05$, $\eta_p^2 = 0.19$, a significant effect of test; $F(1,22) = 21.83$, $p < 0.001$, $\eta_p^2 = 0.50$, and a significant group by test interaction; $F(1,22) = 21.40$, $p < 0.001$, $\eta_p^2 = 0.49$. Partial eta-squared showed that 49.3% of the variance in the improvement of the

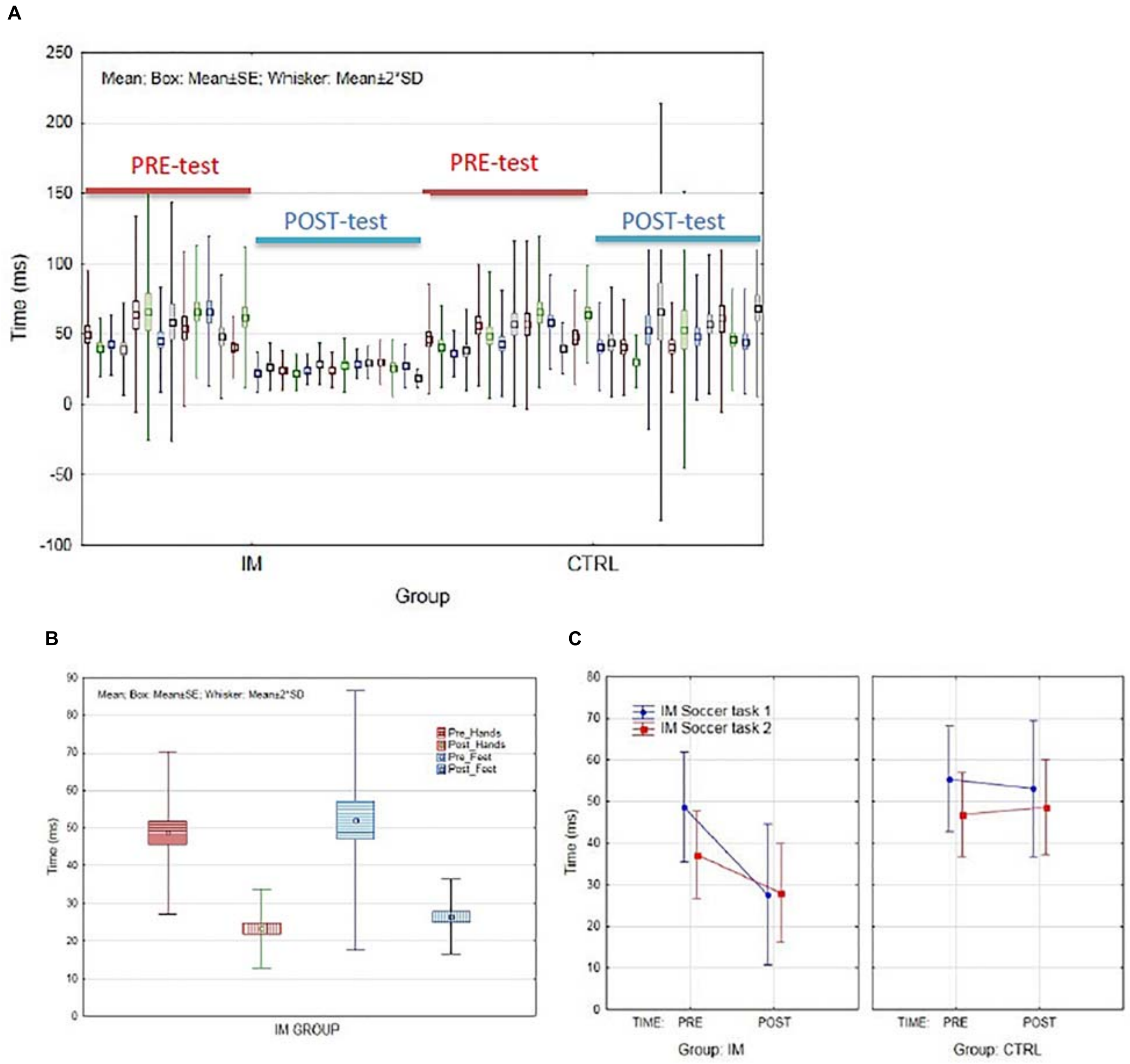

FIGURE 2 | The pre- and post-test mean response time in milliseconds from **(A)** all the fourteen standard IM timing tasks for the SMT group and the control group, respectively, and **(B)** the mean response time from the two IM categories including arms-hands (tasks 1–3, and 14), and legs-feet (tasks 4–9, 12, and 13) as an effect of tests for the SMT group only, and **(C)** the mean response time from the two soccer related tasks (1, stepping task including both feet, and 2, kicking task with the dominant foot) as a function of tests and groups.

participants' timing ability can be related to the IM intervention. A second ANOVA was performed to test the impact of the IM intervention on the participants' mean rhythmic ability. In line with the outcome from the timing ability, the ANOVA revealed a significant main effect for group; $F(1,22) = 8.20$, $p < 0.01$, $\eta_p^2 = 0.27$, a significant effect of time; $F(1,22) = 17.60$, $p < 0.001$, $\eta_p^2 = 0.44$, and a significant interaction between group and test; $F(1,22) = 14.91$, $p < 0.01$, $\eta_p^2 = 0.40$. Partial eta-squared showed that 40.4% of the variance in the improvement of the participants' rhythmic ability can be related to the IM intervention. The *Scheffe's post hoc* comparisons revealed a significant pre- to post-test improvement for both the timing and rhythmic ability, respectively, for the SMT group ($p < 0.00$). No significant pre- to post-test improvements were found for the control group (timing: $p = 0.99$; rhythmic: $p = 1.0$). As illustrated in **Figure 3A** the variability was evidently decreasing from pre- to post-test for the SMT group. **Figure 2B** highlights the mean response time for the two IM categories including hands (tasks 1, 2, 3, and 14) and feet's (tasks 4–9, 12, and 13), at the respective pre- and post-test for the SMT group only. To analyze the effect of SMT on the timing ability (mean IM response time) for the two specially designed soccer related tasks for this study (1, a stepping task using both feet and 2, a kicking task with the dominant foot) a separate ANOVA was used. The ANOVA revealed no significant

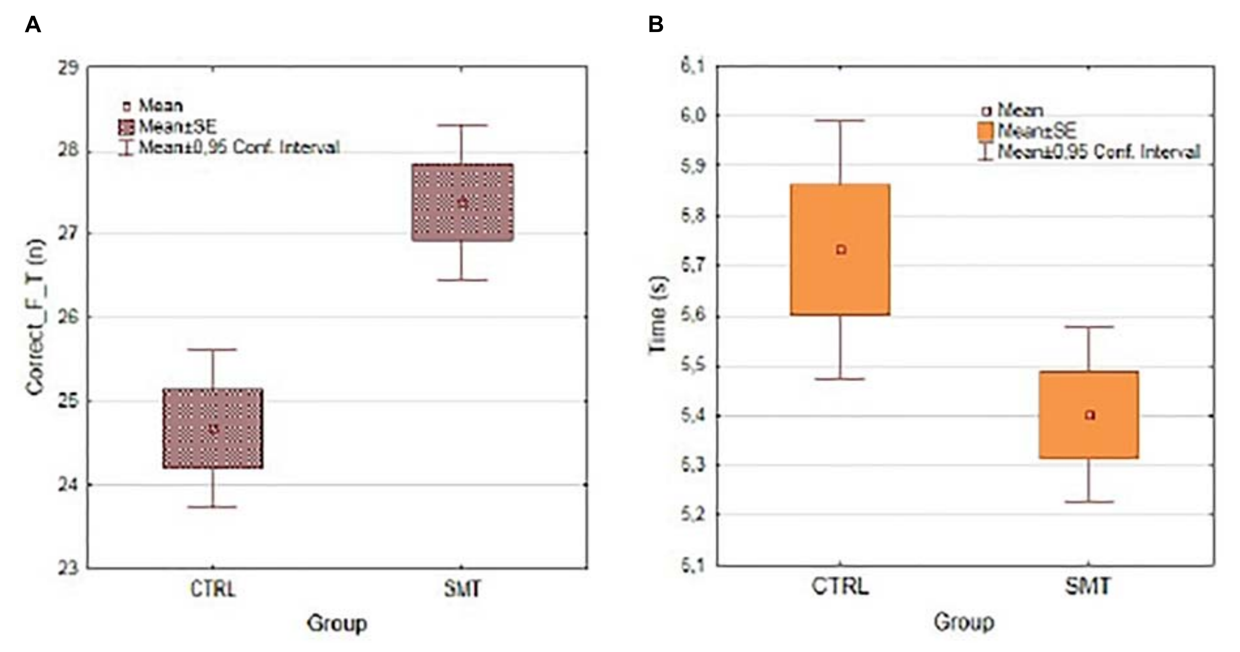

FIGURE 3 | Presenting **(A)** the mean number of correct foot taps during the 20 s stepping task as a function of groups at the post-test comparison, and **(B)** the mean duration to complete the first six steps of the stepping task as a function of group at the post-test comparison.

main effect for group; $F(2,22) = 3.34$, $p = 0.054$, $\eta_p^2 = 0.15$, no significant effect of test; $F(2,22) = 3.39$, $p = 0.051$, $\eta_p^2 = 0.15$, yet a significant interaction between group and test; $F(2,22) = 3.86$, $p < 0.05$, $\eta_p^2 = 0.16$. As presented in **Figure 2C**, the SMT group showed significant improvement by shorter response time at the post-test during the two soccer related IM task, improvements were not found for the control group.

Performance Accuracy and Duration

The ANOVA completed for investigating the effect of improved timing ability on the number of correct taps during the 20-s stepping task revealed no significant main effect of group $F(1,186) = 3.21$, $p = 0.07$, $\eta_p^2 = 0.02$, a significant effect of test $F(1,186) = 25.4$, $p < 0.001$, $\eta_p^2 = 0.12$, and a significant group by test interaction $F(1,186) = 5.20$, $p < 0.05$, $\eta_p^2 = 0.03$. The *Scheffe's post hoc* comparisons confirm that the SMT group significantly improved by means of the number of correct foot taps from pre- to post-test ($p < 0.001$), no such significant improvement was found for the control group ($p = 0.24$), see **Figure 3A**. Regarding the duration to complete the first six steps sequence during the stepping task, the ANOVA revealed no significant main effect for group $F(1,135) = 1.82$, $p = 0.18$, $\eta_p^2 = 0.01$, no significant effect of test; $F(1,135) = 1.96$, $p = 0.16$, $\eta_p^2 = 0.01$, yet a significant interaction between the test and the groups $F(1,135) = 4.64$, $p < 0.05$, $\eta_p^2 = 0.03$. As illustrated in **Figure 3B**, the duration of the first six foot taps was significantly shorter ($p < 0.05$) for the SMT-group at the post-test in comparison to the Control-group who did not show any significant pre- to post-duration change ($p = 0.28$).

Kinematic Outcomes

Number of Movement Units (MUs)

The ANOVA completed to analyze the pre- to post effect on the number of MUs (movement segmentations) made during the first six foot taps sequence (of the 20 s stepping trial) as a function of group and test revealed no significant main effect for group; $F(1,120) = 1.37$, $p = 0.24$, $\eta_p^2 = 0.01$, a significant effect of test $F(1,120) = 8.03$, $p < 0.01$, $\eta_p^2 = 0.06$, and no significant interaction between test and groups; $F(1,120) = 1.38$, $p = 0.24$, $\eta_p^2 = 0.01$. This result shows that independently of groups, a significant increasing number of MUs was found at the post-test ($M = 38.4$, $SD = 6.8$), in comparison to the pre-test ($M = 36.2$, $SD = 9.6$).

Cumulative 3D Distance

The ANOVA completed to analyze the pre- to post-test effect of the cumulative 3D distance revealed no significant main effect of group; $F(1,120) = 0.08$, $p = 0.76$, $\eta_p^2 = 0.001$, a significant effect of test $F(1,120) = 9.71$, $p < 0.01$, $\eta_p^2 = 0.07$, and no significant interaction between test and groups $F(1,120) = 1.44$, $p = 0.23$, $\eta_p^2 = 0.01$. This result shows that independent of group, a significant shorter 3D movement distance was found at the post-test ($M = 270.3$ cm, $SD = 30.6$ cm) in comparison to the pre-test ($M = 288.9$ cm, $SD = 33.4$ cm).

Average Velocity (mm/s)

The ANOVA completed to analyze the pre- to post-test effect of the average velocity revealed no significant main effect of group $F(1,120) = 2.95$, $p = 0.09$, $\eta_p^2 = 0.02$, a significant effect of test $F(1,120) = 9.49$, $p < 0.01$, $\eta_p^2 = 0.07$, and a significant interaction between test and group $F(1,120) = 4.05$,

$p < 0.05$, $\eta_p^2 = 0.03$. This result shows that independent of group, a decreasing average velocity was found at the post-test (*M* = 506 mm/s, *SD* = 0.79 mm/s), in comparison to the pre-test (M = 482 mm/s, *SD* = 0.60 mm/s). In addition, the *Scheffe's post hoc* comparisons confirmed a significant difference ($p = 0.04$) between the SMT and the control group; whereas only the control group showed a significant decreasing velocity profile at the post-test (*M* = 460 mm/s, *SD* = 63 mm/s), in comparison to the pre-test (*M* = 504 mm/s, *SD* = 81 mm/s).

Associations Between Outcomes

As would be expected, a strong significant correlation between timing and rhythm performance outcomes was found (pre-test; $r = 0.895$; post-test; $r = 0.910$), this is because these are two related measures of the overall motor timing ability.

A significant correlation was observed between the IM response time and the number of correct foot taps performed (based on individual mean number of correct foot taps over 20 s task interval) for the SMT group ($r = -0.557$, $p < 0.01$), indicating that a decreasing IM response time associates with an increasing number of correct foot taps at the post-test. There were no statistical significant correlations found for either group regarding the relationship between the IM response time and the kinematic outcomes variables from the stepping task.

However, when the correlations between the IM response time, stepping performance, and kinematic outcomes (MUs, 3D distance, and velocity) are based on individual task performances independent of group, some interesting associations appears. As presented in **Table 3**, a significant negative correlation was found between the IM response time (timing ability) and the number of correct foot taps among the soccer players at both the pre- and post-test ($r = -0.486$, $p < 0.05$; $r = -0.588$, $p < 0.01$). This correlation indicates that the participants with a longer response time (poorer timing ability) are those who preform less correct foot-taps at both the pre- and the post-test. In addition, at the post-test a significant positive correlation was found between the IM response time and the six steps duration ($r = 0.700$, $p < 0.01$), indicating that a shorter response time (better timing ability) at the post-test links with a shorter step duration. In addition, a significant negative correlation between the IM response time and the average velocity ($r = -0.458$, $p < 0.05$) was found, indicating that better timing ability is also related with faster movements.

Independently of groups, correlations between stepping performance (number of correct foot taps and duration) and the kinematic outcome variables based on individual trials at post-test are presented in **Figure 4**. Significant correlation was found between number of correct foot taps and (a) 3D distance ($r = 300$ $p < 0.05$); (b) number of MUs ($r = 453$, $p < 0.01$); and (c) average velocity ($r = 544$, $p < 0.01$). Significant correlations were also found between the duration of the first six foot taps and (d) the 3D distance ($r = 530$, $p < 0.01$); (e) the number of MUs ($r = 770$, $p < 0.001$); and (f) the average velocity ($r = -732$, $p < 0.001$). These findings of significant correlations indicate that the increasing number of correct foot taps during the stepping task is related to shorter 3D movement distance, less MUs, and a higher average movement velocity. Moreover, that a decreasing performance duration of the first six foot taps is associated with a shorter 3D distance, less MUs and increasing movement velocity. Similar significant correlations and relationships between kinematics and stepping task performance were also found at pre-test when based on all individual trial outcomes (independently of groups).

TABLE 3 | Correlations between the IM response time (means based of 14 IM standard tasks) and stepping-task parameters (means based on number of correct foot taps/20 s, and duration of the first six foot taps) and kinematic measurements (MUs, 3D distance, and velocity), independent of group.

	IM response time	
Parameters	**Pre-test**	**Post-test**
Correct F_T (n)	−0.486*	−0.588*
Duration Six F_T (s)	0.373	0.700**
MUs (n)	0.116	0.362
Distance (mm)	0.228	0.337
Velocity (mm/s)	−0.244	−0.458*

$*p < 0.05$, $**p < 0.01$.

DISCUSSION

There is a growing body of studies confirming that timing and rhythmicity training programs are beneficial in a variety of rehabilitation settings, clinical conditions, and in affecting a variety of human behaviors. For example, motor planning, sequencing, and cognitive functions, such as academic achievement and attention. Based on these cross-domain findings, the concept of timing training has also gained popularity in applied fitness settings to enhance sport performance. For instance, a recent study where the use of rhythm was used to improve a cycling (motor) task (Bertollo et al., 2015); both external (i.e., focusing attention on a metronome) and internal (e.g., focusing on pacing) strategies were found to be effective. Yet, there are few scientific studies that have investigated the efficacy of synchronized timing training and its effect on sport performance and athletic achievement. As far as we know, there has not previously been any study investigating what possible effect SMT might have on lower-limb performance and kinematics. The present study was designed to determine potential effect of SMT on sensorimotor timing ability, and also, to investigate whether improved timing ability may provide additive value to traditional soccer training.

In line with our expectations, and with previous findings from studies including golfers and soccer players, as well as various groups of clinical populations and children suffering from various impairments, it was found that IM training produced significant improvements in timing and rhythmicity, manifested in reduced response time. This finding confirmed timing improvements also in the highly experienced and physically well-trained soccer players who took part of the IM intervention in this study. This timing improvement was found after just 9–10 h of IM training over a 4-week period. This was seen by means of evident decreasing response time between pre- and post-test.

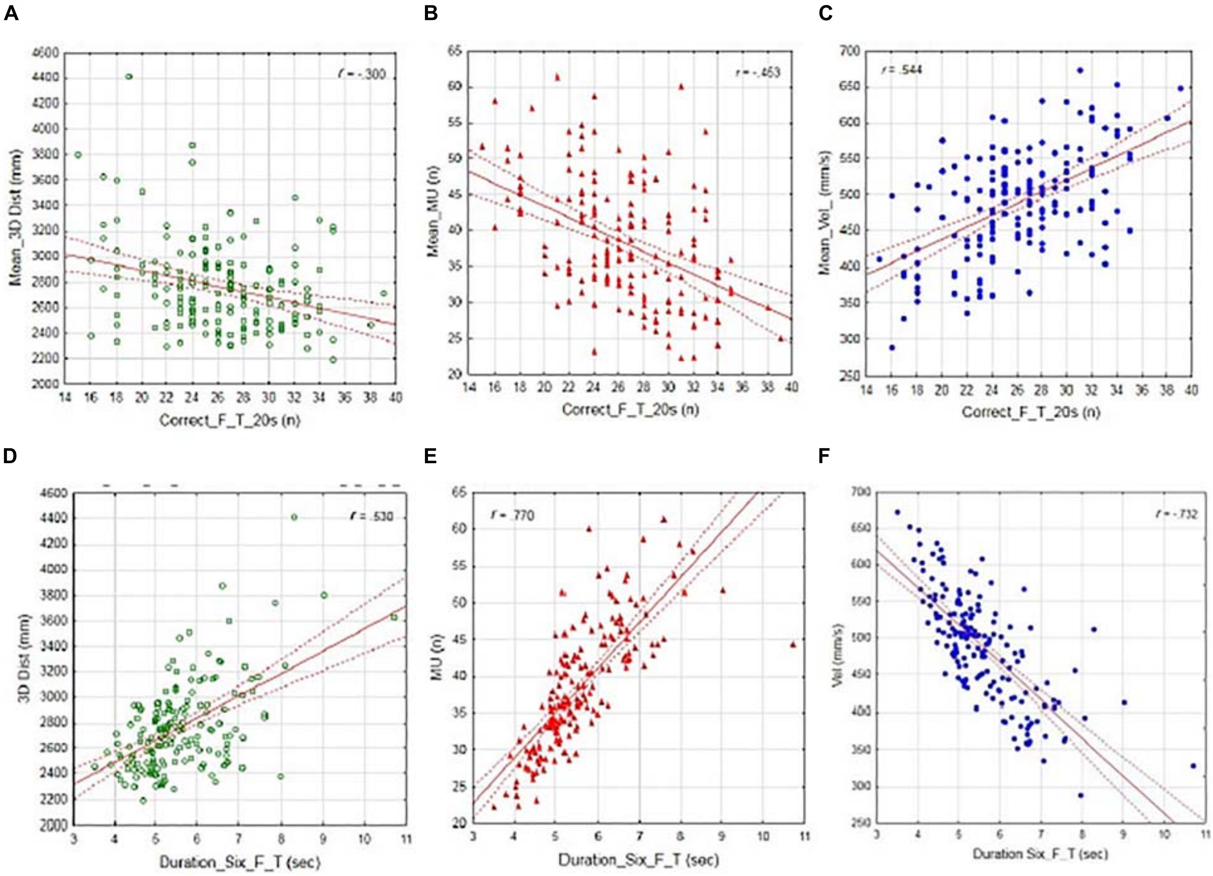

FIGURE 4 | Scatter plots of the relationship between the two respective stepping performance variables: mean number of correct taps during 20 s **(A–C)**; mean duration of the first six taps **(D–F)**, and the kinematic variables: 3D distance, number of MUs, and average velocity. The dotted lines represent 95% confidence intervals.

Accordingly, decreasing intra- as well as inter-individual timing variability was seen as an effect of IM training. In addition to this, the two specifically designed soccer-related IM tasks that were added confirmed timing improvements for the SMT group. Thus, these findings support the suggested explanation that improvements on the underlying brain network related to sensorimotor communication and synchronization, and that IM interventions may improve the resolution and efficiency of an individual's temporal processing (Taub et al., 2007, 2015; McGrew, 2013).

Effects of SMT on the Stepping Task Performance

It was expected that both groups would improve on the stepping task since, at pre-test the task was novel to all participants, and there was only 4 weeks between the tests. Still it was assumed that the rate of improvement between the two groups would differ, favoring the SMT group. The analysis confirmed this expectation as significant improvements were found for the SMT group only. The SMT group showed a significant, increasing number of correct foot taps and took on average a shorter time to complete the stepping task at the post-test in comparison to the pre-test. These results add to previous findings of improvement in outcome accuracy as an effect of SMT found on golfers' performance (Libkuman et al., 2002; Sommer and Rönnqvist, 2009); reduced variability and enhanced precision of soccer cross-passes in soccer players (Sommer et al., 2018); and to findings from similar timing training programs that have reported associations between rhythmic competences and improved tennis performance (Sogut et al., 2012).

Because motor planning was a key part to the cognitively loaded stepping task used in this study, it recruited working memory, attention and other executive functions, which are vital to good motor planning ability. Thus, understanding these results within the context that SMT improves motor planning through improving motor timing and rhythmicity (Stemmer, 1996; Rossini and Pauri, 2000; Diamond, 2003; Mauk and Buonomano, 2004; Koziol et al., 2012); the findings from the present study provide support for the explanation that SMT may strengthen the neural pathways within the spatiotemporal network, and thereby improve motor planning ability. Due to the fact that the stepping task introduced in the present study involves simultaneous coordination of a motor and a cognitive task (to learn and process the digit sequence and meanwhile, plan and produce precise, coordinated stepping movements, and in the right order), the positive SMT effect found by means of stepping accuracy (number of correct taps) and decreased duration, may also be explained as increasing efficiency of working memory; thus, that ultimately results in more efficient complex information processing. This explanation is in line with the suggestion that IM-based training may increase the efficiency of attentional and inhibitory control, and thus result in an increase in automatization and efficient performance of working memory (Taub et al., 2015). Thus, suggesting domain-general influences of SMT on the underlying brain-based sensorimotor control and planning strategies may explain the improved lower-limb movement performance found for the cognitive demanding stepping task.

In the present study, we did not confirm previous findings of changes in the kinematic properties and dynamics (found in the golf swing) as an effect of SMT (Sommer et al., 2014). When comparing the pre- to post-test data and possible group differences, no apparent effect of SMT was found from the kinematic data investigated. This study focused on movement segmentation (MUs), 3D distance, and the average velocity, and thus the kinematic variables extracted during the stepping task describe possible changes in lower limbs movement dynamics and efficiency after SMT. One possible interpretation of the lack of kinematic changes in this study is that the working memory resources involved in the processing of the stepping task may interfere with the motor performance during the foot tapping serials. Thus, that the use of the high cognitive loaded task may create substantial higher-order processing competition between the motor and the cognitive domains. This interpretation is in line with the dual-task interference phenomena described by Johannsen et al. (2013), who suggested that the effect of dual-task interference predominantly concerns the timing accuracy of movement control and not the kinematics (findings based on timing of periodic ankle movements). Another possible explanation might be that even if the representation of a timing skill is reorganized in the brain shortly after an internal model has been acquired, this reorganization may not have been established in the kinematic properties; it may still contribute to increased stability of the representation of the sensorimotor timing improvements. Thus, this explanation is in line with the suggested sequential stages of motor memory consolidation (Shadmehr and Holcomb, 1997).

The findings that both the control and the SMT groups showed changes by means of increasing number of movement segmentations (MUs), shorter movement trajectories, and a decreasing performance speed (average velocity) at the post-test may be interpreted as a test–re-test effect. Yet, it may also be considered alongside Bernstein's theory on skill acquisition in complex movement performance. Bernstein (1967) suggested that the mastery of complex motor skills is dependent upon increased availability of redundant degrees of freedom (DOF); this increase in DOF available to the individual that has mastered a complex movement allows them to become more efficient, and more flexible, in their motor performance. Therefore, the pre- to post-test changes found by means of increasing number of MUs may be interpret as reflecting the availability of more DOF presented as a test-task-training-effect. Thus in line with Verrel et al.'s, (2013) interpretation of the increased availability of DOF in the context of skilled string instrumentalists who need to make fast and efficient changes of direction: a skill also necessary in the stepping task used in the present study. The decreasing performance speed found at post-test for the control group, although with a small effect size, may be explained as a speed-accuracy trade-off effect, usually described as competing demands of response speed and response accuracy (Belkin and Eliot, 1997).

It was expected that there would be a relationship between participants' pre- to post-test IM response time and the stepping task performance after completing the SMT intervention. In other words, that those who improved most on the IM test (by means of decreasing response time) would improve most in the stepping task. In line with this prediction a significant correlation was found between the IM response time and the number of correct of steps performance. This finding supported previous findings describing the relationship between improved sensorimotor timing skills and improved sport performance and accuracy, as an effect of SMT. Yet, as seen from the results of the pre- and post-test comparison from the ANOVAs, no significant relationships between the IM generated timing improvements and the kinematic outcomes were found for either group. These findings indicated that the effect of SMT had a stronger impact on the soccer players' sensorimotor planning ability (as a possible result of enhanced executive functions and attention), than on the spatial-temporal aspects of kinematic properties, *per se*. Thus, these results are contrary to previous findings from kinematic outcome analyses based on upper-limb performance during the golf swing; which suggested that SMT may not only effect golf performance accuracy, but also influence the underlying coordinative structures and temporal synchronicity (Sommer et al., 2014). Essentially, these comparisons of kinematics are from two different motor tasks, with different demands, and based on different movement performance and sports.

Even though the present study did not show any evident pre- to post-test effect of SMT on the kinematic properties, some attention-grabbing findings emerge from correlations made between the kinematics (on individual task levels) and movement performance independently of group. These correlations indicate that the increasing number of correct foot taps during the stepping task is related to better timing ability (shorter response time), a shorter 3D movement distance, less movement segmentations (MUs), and a higher average movement velocity. Moreover, decreasing performance duration of the first six foot taps was associated with a shorter 3D distance, and fewer MUs, as well as with increasing movement velocity. These findings are most likely associated with the inter-individual variations in the nature of higher-order cognitive processing capacity in the participants and emphasized due to the demands of the cognitive-load added to the stepping task. In addition, sensory-motor synchronization, coordination, and sequencing during complex actions may be associated with individual variations in the nature of the neuro-anatomical constraints that determine the control of goal-directed lower-limb movements. Recent studies have suggest that executive functions (EFs; the cognitive control processes that regulate thoughts and actions), are critical for high performance in soccer. For instance, it has been demonstrated that elite young soccer players showed higher scores in general EF tests than non-elite youth players (Huijgen et al., 2015; Vestberg et al., 2017). Similar results have also been reported in hockey players (Lundgren et al., 2016). A positive relationship between successful sport performances in young soccer talents and their cognitive creativity in general have also been described by Kovac (1996). Relationships between elite soccer players' EF and the number of goals they scored two seasons later have also been observed (Vestberg et al., 2012, 2017), leading the authors to suggest a causal role of the soccer players' cognitive function and their future soccer success. Hence, these findings of EFs and performances are in agreements with the well-established findings of associations between cognitive control processes and timing ability in general based on chronometric tasks; reaction time, inspection time, time discrimination, and interval production (Ullén et al., 2008; Holm et al., 2017). Additionally, neuroimaging data have also suggest that timing tasks load more on cognitive control as they become sensory rather than motor (Lewis and Miall, 2003; Rammsayer and Troche, 2014).

A shortcoming of the present study is that we did not include information outcomes from standardized neuropsychological assessment regarding the participants' general executive functions; further studies should employ these assessments. Another limitation was that we were unable to include the kinematic recordings from the hip markers due to measurement-technical problems. Furthermore, application of time series analysis of the leg dynamics may give added information of the soccer players' stability and variability and of the leg dynamics (joint inter-couplings) during the stepping task, as a possible effect of SMT.

Future Research

It is recommended that further studies should address the effect of SMT on movement performance and kinematics by comparing different levels of athletes with non-athletes, and during different level of task complexity; with- and without cognitive-load(s). This would provide evidence on the effects of SMT in groups with differing levels of experience/training, and therefore provide information on its efficacy in different populations and sports. In addition, more neuroimaging (fMRI) studies to investigate the effect of SMT on structural-functional brain activation and locations in relation to different aspects of performance are requested for. In addition, the possible long-term effects of SMT are fairly unknown and in need of evaluation. Follow up data would provide information on whether the effects of SMT are long lasting, and optimally, provide further important knowledge about consolidation and task-general transfer effects. To elucidate the relationship between cognitive and sport performance, further experiments are needed that directly test the causal relationship between both internal and external timing ability and cognitive performance and EF in athletes.

CONCLUSION

Being the first study to utilize 3D kinematic analysis to assess the effects of SMT in the context of soccer player's leg movements, the present study provides new and meaningful information about the effects of SMT on sensorimotor efficiency, motor planning, and performance. The results support the suggested explanations that improvements of the underlying brain network relate to sensorimotor communication and synchronizations, and that the IM training may improve the resolution and efficiency of an individual's temporal processing. The results also provide support for the theoretical and empirical link between efficient cognitive capacity and sensorimotor performance and accuracy. To conclude, even if physical strength and mental ability are of high importance in all sport performance, sensorimotor timing ability may be the key factor. The present study emphasizes the importance of improving the cognitive-motor planning ability and sensorimotor timing skills, especially in team sport such as soccer where the players have to rely on accurately timed actions on milliseconds level. It is clear from the results that synchronized sensorimotor timing abilities should be acknowledged as a critical factor for soccer player's performance. Additionally, that SMT also may be beneficial for both general motor planning and in other sports performance and situations of complex, high cognitive-motor demanded tasks, and dynamic contexts.

AUTHOR CONTRIBUTIONS

LR and MS conceived and designed the work, and acquired the data. LR, MS, and RM contributed in analysis and interpretation of the data, drafted the work, revised the work, contributed in final approval of the version to be published, and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Focusing Attention on Muscle Exertion Increases EEG Coherence in an Endurance Cycling Task

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The aim of this study was to examine EEG coherence before, during, and after time to exhaustion (TTE) trials in an endurance cycling task, as well as the effect of effort level and attentional focus (i.e., functional external, functional internal, and dysfunctional internal associative strategies—leading to Type 1, Type 2, and Type 3 performances) on brain functional connectivity. Eleven college-aged participants performed the TTE test on a cycle-ergometer with simultaneous EEG and rate of perceived exertion (RPE) monitoring. EEG data from 32 electrodes were divided into five effort level periods based on RPE values (Baseline, RPE 0-4, RPE 5-8, RPE 9-MAX, and Recovery). Within subjects RM-ANOVA was conducted to examine time to task completion across Type 1, Type 2, and Type 3 performance trials. RM-ANOVA (3 performance types × 5 effort levels) was also performed to compare the EEG coherence matrices in the alpha and beta bands for 13 pairs of electrodes (F3-F4, F3-P3, F4-P4, T7-T8, T7-P3, C3-C4, C3-P3, C4-P4, T8-P4, P3-P4, P3-O1, P4-O2, O2-O1). Significant differences were observed on TTE performance outcomes between Type 1 and Type 3, and between Type 2 and Type 3 performance states ($p < 0.05$), whereas Type 1 and Type 2 performance states did not differ. No significant main effects were observed on performance type ($p > 0.05$) for all frequency bands in any pair of electrodes of the coherence matrices. Higher EEG coherence values were observed at rest (Baseline) than during cycling (RPE 0–4, 5–8, 9–MAX) for all pairs of electrodes and EEG frequency bands irrespective of the type of performance (main effect of effort, $p < 0.05$). Interestingly, we observed a performance × effort interaction in C3–C4 in beta 3 band [$F_{(4,77)} = 2.62$, $p = 0.038$] during RPE 9-MAX for Type 3 performance as compared to Type 1 and Type 2 performances. These findings may have practical implications in the development of performance optimization strategies in cycling, as we found that focusing attention on a core component of the action could stimulate functional connectivity among specific brain areas and lead to enhanced performance.

Keywords: functional brain connectivity, focus of attention, MAP model, RPE, effort, performance

INTRODUCTION

Physical exercise is commonly known to result in changes of brain cortical activity measured by EEG techniques (Schneider et al., 2009a). It is also generally accepted that exercise can cause temporary changes of the EEG activity in the alpha and beta bands (Crabbe and Dishman, 2004). Specific brain changes are related to different kinds of exercise and to the participants' preferences for physical exercise (Schneider et al., 2009a,b). Moreover, the effects of exercise on brain cortical activity are reflected in specific brain regions. For example, research findings from studies comparing running and cycling revealed an increased alpha activity in the frontal regions, involved in emotional processing, immediately after treadmill exercise on those participants who displayed a clear preference for running. On the other hand, participants who preferred cycling showed increased alpha activity in the parietal regions, which play an important role in integrating sensory information, after bike exercise (Schneider et al., 2009b). These studies have shown the occurrence of brain activity changes as a result of exercise. However, few studies have examined these changes during exercise. For example, Bailey et al. (2008) documented increased EEG power spectra during graded-exercise to fatigue; in particular, they found increased power in the theta, alpha, and beta bands during exercise at different electrode sites (i.e., F3, F4, F7, F8, C3, C4, P3, P4). Findings suggest that brain activity may be related to exercise intensity, which could have an impact on brain waves; in particular, increases in EEG activity in alpha and beta bands seem to reflect augmented ventilatory rate.

In a cycling study, Hottenrott et al. (2013) found cortical activity to be influenced by cadence. Specifically, EEG data indicated that cadence not only directly increased metabolic and cardiac activity, but also influenced cortical parameters. In detail, the U-shaped curve of EEG spectral power over time suggests a central activation that decreases with the onset of fatigue.

Hilty et al. (2011), in addition, demonstrated that there is a fatigue-induced increase in communication between the mid/anterior insular and the motor cortex during cycling exercise. The authors provided basis to further investigate the cortical mechanisms of supraspinal fatigue. Moreover, in different tasks, Babiloni et al. (2011) speculated on the physiological meaning of inter- and intra-hemispheric connectivity during performance; in a golf putting task, for instance, they suggested that the increase of bilateral parietal central coherence in alpha band is due to the recruitment of central-parietal resources related to global attention. However, there is scant research examining brain activity before, during, and after endurance tasks or under stressful conditions.

Interaction among brain processes, cognition, and performance has been recently studied using the multi-action plan (MAP) model (Bortoli et al., 2012; Robazza et al., 2016) as a theoretical framework (for a review, see di Fronso et al., 2017). This model provides practical indications to help athletes reach and maintain optimal performance also under strenuous or stressful situations. The MAP model is based on the notion that different attentional strategies lead to optimal and suboptimal performance states, which are related to specific psychophysiological (Bertollo et al., 2013; Filho et al., 2015), neural (Bertollo et al., 2016; di Fronso et al., 2016), or affective responses (Robazza et al., 2016). The MAP model is conceptualized in function of distinct performance levels (i.e., optimal or suboptimal) and attentional demands (i.e., automatic or controlled). The interplay between performance and attention leads to four performance states: (a) Type 1, optimal-automated performance, characterized by an automatic ("flow" like) attentional mode; (b) Type 2, optimal-controlled performance, typified by an associative focus directed toward core components of a given task/action; (c) Type 3, suboptimal-controlled performance, characterized by a focus directed toward irrelevant information and/or a dysfunctional control of automated action components; and (d) Type 4, sub-optimal-automated performance, typified by a low level or a lack of focus of attention. In particular, former studies showed that athletes can achieve optimal performances (Type 1, Type 2) with different type of effort, attention, and investment of cognitive resources (Furley et al., 2015; Carson and Collins, 2016; Robazza et al., 2016). In brain studies, high levels of anxiety are commonly associated with beta activity increase and alpha activity decrease (e.g., Carvalho et al., 2013). Similarly, efficient and inefficient processing during performance were shown to be modulated by the degree of effort and attentional demands of the task, with a clear Event-Related Synchronization in Type 1 performance and Desynchronization in Type 3 performance (Bertollo et al., 2016).

Drawing on the MAP model assumptions, the effect of different internal and external associative strategies on endurance performance has been investigated (Bertollo et al., 2015). Participants were required to direct attention externally on pacing (Type 1 performance), focus internally on a core component of the cycling action (Type 2), or attend to muscular exertion (Type 3). Findings showed that participants in Type 1 and Type 2 performance states attained optimal performance. On the other hand, Type 3 performance condition led to poor performance because of enhanced feelings of fatigue. Type 4 performance was not considered in this earlier study and in the current investigation because of the difficulty to instate in participants involved in a laboratory task a mental attitude of real disengagement featuring a Type 4 performance state. In a study testing the association between cortical functional networks and the performance types foreseen in the MAP model in cycling (Comani et al., 2014), coherence analysis has been used as an adequate metrics to quantify the functional correlation between active brain areas at the sensor level, as also suggested in more recent studies (Srinivasan et al., 2007; Bowyer, 2016). Comani et al. found that performance types relied on fronto-occipital and inter-hemispheric frontal coherence in the alpha band.

Drawing on the MAP model assumptions, we conducted a counterbalanced repeated measure trial to investigate the effect on cortical coherence (i.e., functional connectivity; Florian et al., 1998; Srinivasan et al., 2007) of internal and external attentional strategies during the different periods (i.e., effort levels) of a time to exhaustion (TTE) cycling task. At Baseline, before the TTE test, we expected to observe in participants a higher functional connectivity in the alpha and beta bands as compared to the periods of TTE execution and Recovery, because of a readiness for task execution that translates in a greater communication within all brain regions (Hypothesis 1-effort level effect). Furthermore, we expected to observe a significant interaction between type of performance and effort level (i.e., Baseline, RPE 0-4, RPE 5-8, RPE 9-MAX, Recovery) on functional connectivity (Hypothesis 2-Performance × effort level interaction). In particular, Type 3 performance should result in a higher level of coherence in the beta band (the biomarker that most reflects motor binding; Cheron et al., 2016), during the last stages of the TTE task, due to the attentional focus on dysfunctional feelings, which increases the communication among sensory motor areas and should differ from Type 1 and Type 2 performances. On the other hand, Type 1 "flow-like" experience should be characterized by reduced functional connectivity, related to cortical inhibition (Klimesch, 1996; Pfurtscheller, 2003; Klimesch et al., 2007) and brain regions deactivation (Knyazev et al., 2011). Because of the limited research on this topic, the current investigation could be considered exploratory in nature. Specifically, alpha band analysis could provide information about global resting state, whereas beta band could offer information about sensory motor integration (beta1), perception-action coupling (beta2), and selective attention related to the motor task (beta3) (Laufs et al., 2003; Donner and Siegel, 2011; Kilavik et al., 2013; Cheron et al., 2016).

METHOD

Participants

We recruited 12 college-aged students. One student discontinued participation from the experiment due to health reasons. Therefore, 11 students (4 women and 7 men, $M_{\text{age}} = 24.29$ years, $SD = 4.91$ years) completed the experimental protocol, consisting of five visits to our exercise physiology laboratory. All volunteers participated regularly in different physical activities of low or moderate intensity and some of them were professional cyclists (see **Table 1**). After being briefed on the general purpose of the study, the participants agreed to participate and signed a written informed consent. The study was conducted in accordance with the declaration of Helsinki and received approval from the local university ethics committee (University "G. d'Annunzio" of Chieti-Pescara) with application ref. n. 10-21/05/2015.

Ratings of Perceived Exertion (RPE)

RPE was measured through the CR-10 Scale (Borg and Borg, 2001) ranging from "0" (no effort) to "•" (maximal sustainable effort). The verbal anchors were: 0 = nothing at all, 0.5 = extremely weak, 1 = very weak, 2 = weak, 3 = moderate, 5 = strong, 7 = very strong, 10 = extremely strong, • = absolute maximum (a score of 11 is assigned to this anchor). No verbal anchors were used for 4, 6, 8, and 9; the use of CR-10 Scale is instrumental in diminishing ceiling effects, and its ratings are linearly related to various physiological parameters such as VO2max, lactate, and heart rate (Borg, 1998).

Procedure

Similarly to a previous study (Bertollo et al., 2015), five visits to the laboratory were arranged, with inter-visit intervals of 48–72 h in order to permit physiological Recovery of participants. Two qualified researchers collected the data. Data collection occurred in a quiet (no music playing, and no other people allowed in the laboratory) and safe environment to warrant the comfort of the participants. During the first visit, participants received standard instructions about the use of RPE on the CR-10 scale and performed an incremental test to determine their anaerobic threshold (AT) and individual optimal pedaling rate in revolution/minute (rpm). Heart rate, VO_2, and VCO_2 were continuously monitored with the Schiller CS 200 system. During the second visit, an EEG was acquired during a TTE test to check the setting and EEG equipment. At the same time, the precision of the estimated AT and the pedaling rate were verified to proceed as accurately as possible with the other three visits to our laboratory that were important for data collection and the subsequent analysis. The time to exhaustion interval is defined as the maximum interval for which the subject can maintain an exercise intensity equal to AT + 5%, and/or after which he/she reaches volitional exhaustion. During the last three visits, participants performed the TTE test on a monark Cyclo-Ergometer (939 E) with simultaneous EEG monitoring. The TTE test was performed adopting a counterbalanced design. During each visit, one of three MAP-based strategies was randomly used during the constant load phase of the protocol:

1) An external associative strategy—focus on an external pacing-metronome set at the individual optimal pedaling rate—leading to Type 1 performance (instructions for participants: "… during the whole constant load phase, a metronome reproducing your optimal pedaling rate will be activated. Please focus your attention on the pacer and follow the pedaling rhythm…");
2) A functional internal associative strategy—focus on the internal individual optimal pedaling rate (core component)—leading to Type 2 performance ("…during the whole constant load phase maintain your optimal pedaling rate which is estimated to be *n* revolutions per minutes-RPM. Please, focus your attention on your feet to maintain that rhythm…");
3) A dysfunctional internal associative strategy—focus on muscle exertion (perception of tension, stiffness, fatigue, soreness, etc.) related to pedaling—leading to Type 3 performance ("…during the whole constant load phase, please focus your attention on your muscle exertion…").

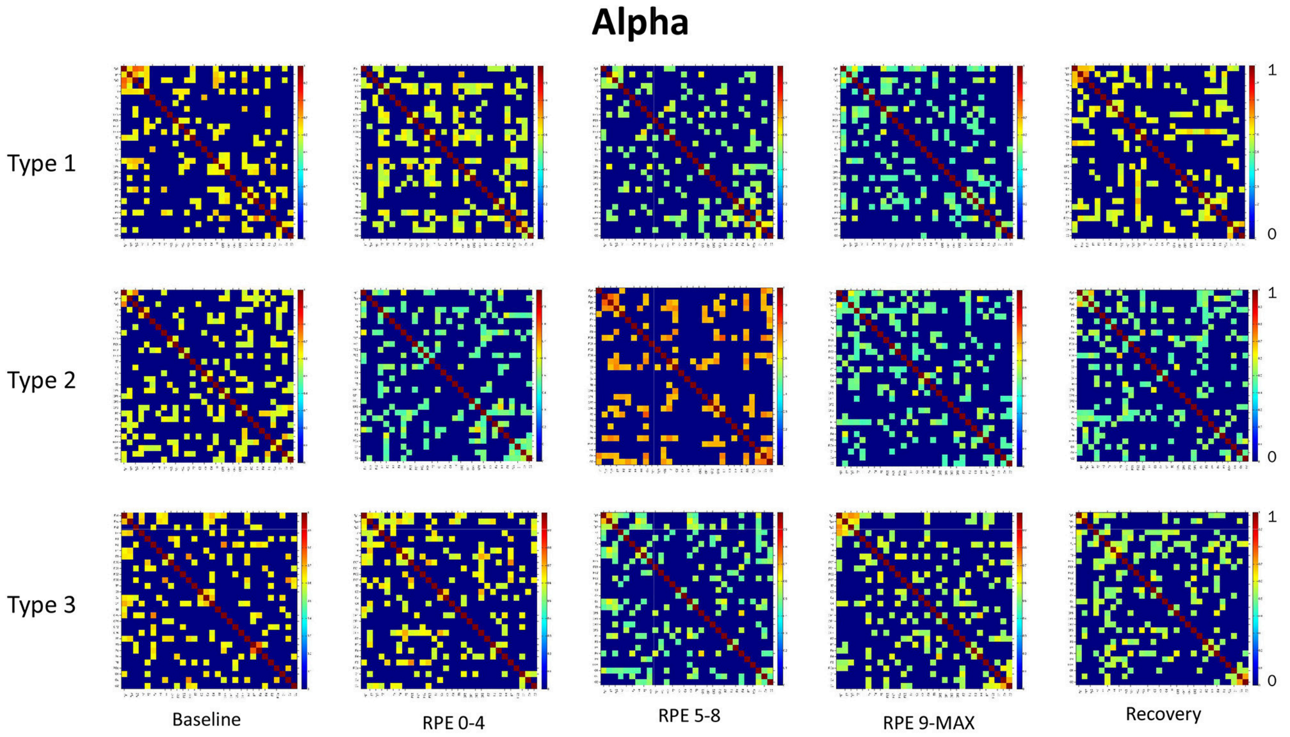
At the end of the task, participants were asked to complete a manipulation check questionnaire using a 10-point frequency scale with anchors 1 (never) and 10 (always). The questionnaire contained one of the following questions: "How often did you focus your attention on the metronome?" (Type 1 performance condition), "How often did you focus your attention on your feet to maintain individual RPM pacing?" (Type 2 performance condition), and "How often did you focus your attention on your muscle exertion?" (Type 3 performance condition). A frequency adherence under 4, which was considered "often enough," was adopted as an exclusion criterion.

Incremental Test (First Visit)

After a warm up (4 min at 75 watt), oxygen uptake (VO_2) and carbon dioxide production (VCO_2) were measured using an incremental protocol on a monark cycle ergometer (939 E). Heart rate, VO_2, and VCO_2 were continuously monitored using the Schiller C2 200 System, as above mentioned, to obtain all the physiological parameter useful to identify AT. AT was measured using the V-SLOPE method (Wasserman et al., 1994). Pedaling rate was maintained at 70 rpm, and the workload power output, initially set at 75 Watt, was step-wise increased by 25 Watt every

TABLE 1 | Mean (M) and Standard Deviations (SD) of Anaerobic Threshold (AT) and Individual Optimal Pedaling Rate (IOPR) obtained with incremental test, and minutes on constant load phase of Time to Exhaustion Test (TTE) in the three types of performance for the participants.

Participants	Age	Gender	Expertise	AT-VO2 (l/min)	AT-VO2 (ml/kg/m)	AT-VCO2 (l/min)	AT-power (Watt)	IOPR	AT-HR	Time to exhaustion (min)		
										Type 1	Type 2	Type 3
1	24	M	Novice	1.29	20.50	1.28	145	83	140	13	16	15
2	32	M	Amateur	2.04	26.80	2.27	150	100	152	18	16	9
3	33	M	Elite	1.88	24.40	2.83	200	100	138	19	10	10
4	20	F	Novice	1.12	18.70	1.43	85	68	150	16	14	11
5	28	M	Novice	1.69	20.10	1.85	120	78	161	10	15	13
6	33	M	Amateur	3.01	45.50	3.15	225	80	165	14	12	12
7	19	M	Elite	2.27	37.10	2.26	175	70	169	23	31	19
8	25	M	Novice	2.66	30.09	3.21	170	75	159	13	9	8
9	27	F	Novice	1.21	22.80	1.19	90	54	176	11	12	9
10	24	F	Novice	1.15	21.00	1.00	90	60	138	27	26	20
11	21	F	Novice	1.38	25.5	1.48	90	73	186	12	15	10
Mean	24.29			1.79	26.59	1.99	140	76.45	157.63	16	16	12.36
SD	4.91			0.64	8.2	0.8	48.98	14.38	15.84	5.31	6.69	4.05



Note: The order of the electrodes in the axis, from top to bottom and from left to right, is: Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3,Pz, P4, P8, POz, O1,OZ, O2.

FIGURE 1 | Coherence matrices for each type of performance during different time periods of the protocol in the alpha band. Red color indicates high values of coherence whereas the blue color indicates low values of coherence.

2 min until exhaustion. After the incremental test, participants were given a 20-min rest period. After this period, participants were asked to pedal at AT + 5% for 10 min to identify their individual optimal pedaling rate, while familiarizing themselves with the study procedures.

TTE Test at Individual Constant Load (Second to Fifth Visit)

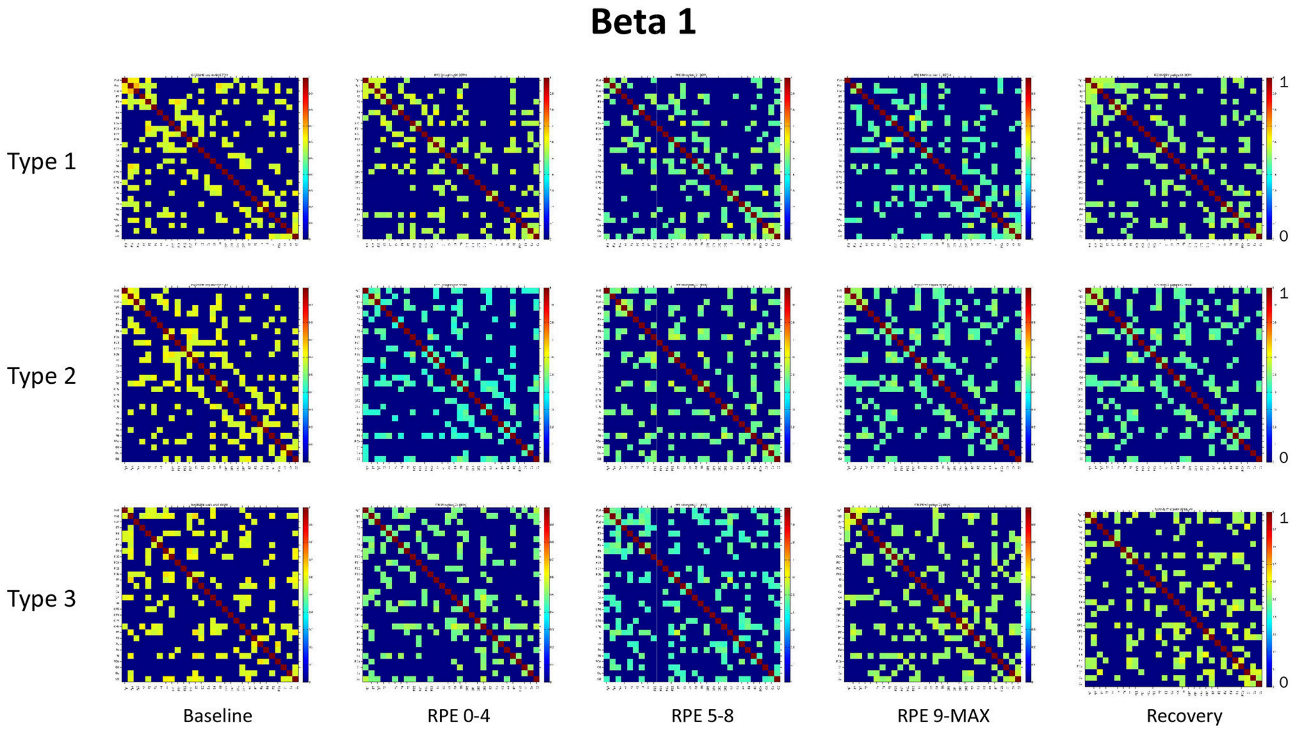
During the second visit participants familiarized with TTE protocol. After a resting period of 2 min (no movement for Baseline EEG recording) and a warm up period of 4 min on the cycle ergometer at 60% of AT in Watt, participants performed a constant load exhaustive test at individual constant load (AT + 5%) reporting at the same time their RPE, with pedaling rate fixed at their individual optimal pedaling rate. After exhaustion (absolute maximum effort), there was a Recovery period of 4 min at 60% of AT and a further resting period of 2 min without movement. RPE scores were collected 5 s before the end of each minute during the entire protocol. During the following visits to the laboratory (i.e., 3rd, 4th, and 5th), participants were assigned to one of the three experimental conditions, each defined in a random order and occurring on different days. In order to verify the adherence to the experimental assignments, the above-mentioned manipulation check questionnaire was administered.

EEG Recording and Pre-processing

Electroencephalographic data were continuously recorded during the whole protocol using the 32 channels EEG ASAlab system with Waveguard cap (Advanced Neuro Technology, Enschede, Netherlands). This system is supplied with shielded wires to make recordings less susceptible to external noise and movements. Sampling frequency was 512 Hz. The ground electrode (AFz) and common average reference were positioned between Fpz and Fz to ensure low impedance values (< 10 KΩ). The 32 electrodes were distributed over the scalp according to the 10/5 system (Oostenveld and Praamstra, 2001). The EEG data were band-pass filtered between 0.3 and 40 Hz. Epochs showing instrumental, ocular, and muscular artifacts were detected using the ASA (Advanced Source Analysis) software (Zanow and Knösche, 2004) with the PCA (Principal Components Analysis) method. Data epochs showing residual artifacts were visually identified by two independent experts and excluded from further analysis.

EEG Data Analysis

Pre-processed EEG signals were divided based on the TTE test structure and on the RPE scores. We identified 7 periods: Baseline, warm up, RPE 0–4, RPE 5–8, RPE 9–MAX, Recovery, and rest. We retained the Baseline, RPE 0–4, RPE 5–8, RPE 9–MAX, and Recovery periods for further analysis. Unfortunately,



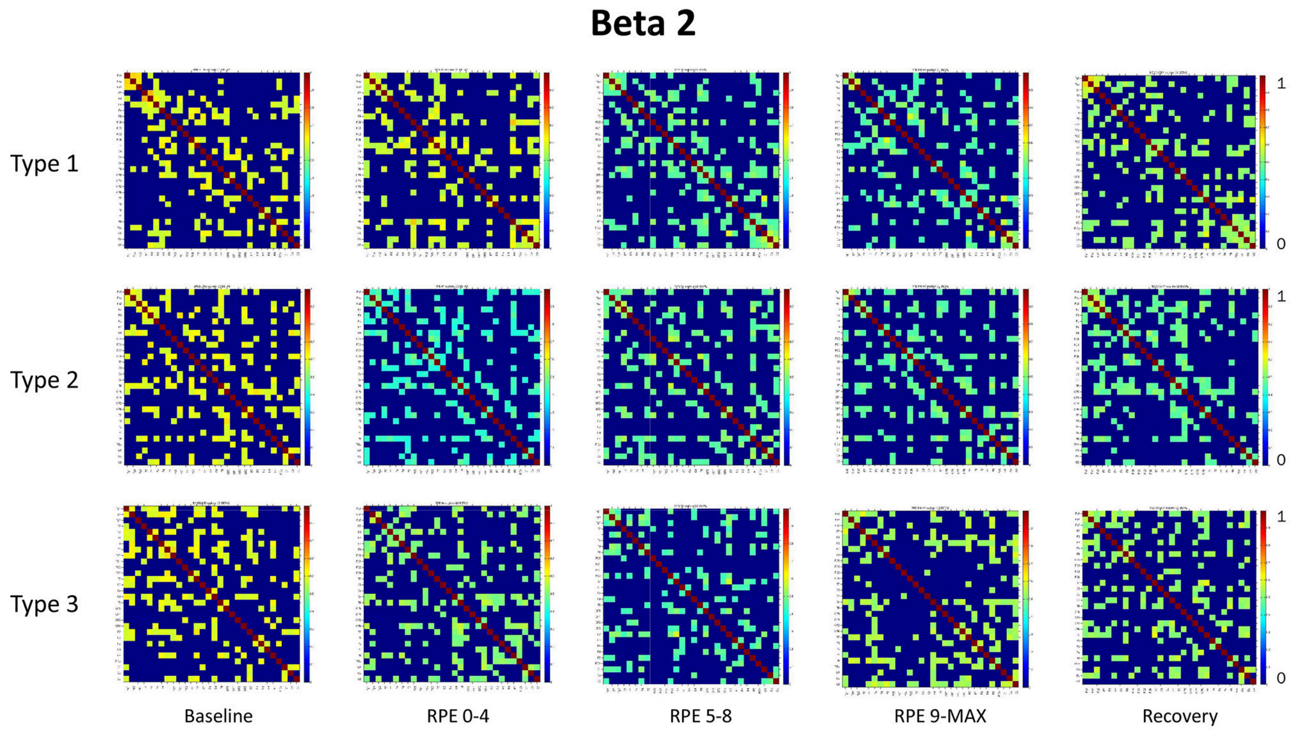
Note: The order of the electrodes in the axis, from top to bottom and from left to right, is: Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3,Pz, P4, P8, POz, O1,OZ, O2.

FIGURE 2 | Coherence matrices for each type of performance during different time periods of the protocol in the beta 1 band. Red color indicates high values of coherence whereas the blue color indicates low values of coherence.

rest periods, where participants were requested to stop pedaling, could not be analyzed because of sweating artifacts due to the autonomic nervous system response, which irremediably affected EEG signals. Warm up, instead, was not a period of interest because attention manipulation was not implemented. For each period we analyzed the EEG intervals of 4 s duration from −6 to −2 s prior to RPE evaluation. Four-seconds epochs were averaged at individual level when part of similar categories of RPE periods (e.g., participant 1: Baseline = 2 epochs for each type of performance; RPE 0–4 = 5 epochs for Type 1; 6 for Type 2; 7 for Type 3; RPE5–8 = 4 epochs for Type 1; 6 for Type 2; 4 for Type3; RPE 9–MAX = 4 epochs for Type 1; 3 for type 2; 4 for Type 3; Recovery = 4 epochs for each type of performance). Therefore, the grand average of the eleven participants was performed resulting in a total of 22 epochs for Baseline; 44 epochs for Recovery, 53 (±10 epochs) for RPE 0–4, 50 (±2) for RPE5–8 44 (±6) for RPE 9-MAX.

Coherence analysis of the EEG data was performed to detect cortical connectivity patterns in relation to the different attentional strategies and time periods. The complex coherence between two signals X_1 and X_2 (recorded by two given electrodes) was calculated as the cross-spectrum between the signals and normalized by the square root of the power spectrum product of the two signals. Given that coherence is a normalized measure of the correlation between two signals, and consists of complex values, its amplitude can vary from 0 to 1. For each period, mean coherence matrices were calculated in the alpha (8–12 Hz), beta 1 (12–18 Hz), beta 2 (18–23 Hz), and beta 3 (23–30 Hz) bands (ASA-Lab software). We divided the beta band in three sub-bands to better study sensory motor processes, perception-action coupling, and selective attention (Laufs et al., 2003; Donner and Siegel, 2011; Kilavik et al., 2013; Cheron et al., 2016).

For each of the four frequency bands (i.e., alpha, beta1, beta2, beta3) we obtained 15 reference coherence matrices (3 performance types × 5 time periods) by averaging the mean coherence matrices of the 11 participants. To retain only significant functional connections across EEG signals, we adopted the approach proposed by Berchicci et al. (2015) and thresholded each reference coherence matrix on the basis of its own coherence value distribution, which is expected to be non-Gaussian. We then calculated the Median and Median Absolute Deviation (MAD) of the coherence value distribution for each reference coherence matrix, and defined a new thresholded coherence matrix where only the coherence values > (Median + 1 MAD) were considered as meaningful functional connections and retained, whereas all other coherence values were set equal to zero (Li et al., 2015; Chella et al., 2016). Each thresholded coherence matrix is composed of the coherence values of each pair of 30 electrodes with this order of labels: Fp1, Fpz, Fp2, F7,



Note: The order of the electrodes in the axis, from top to bottom and from left to right, is: Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3,Pz, P4, P8, POz, O1,OZ, O2.

FIGURE 3 | Coherence matrices for each type of performance during different time periods of the protocol in the beta 2 band. Red color indicates high values of coherence whereas the blue color indicates low values of coherence.

F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, POz, O1, OZ, O2.

Statistical Analysis

Before considering cortical data, we analyzed performance outcomes in TTE test, running a within-subjects repeated measure analysis comparing the time to complete the task during each type of performance (Type 1, Type 2, Type 3).

Afterwards, a series of within-subjects repeated measures ANOVA was performed with 3 (performance types) × 5 (effort level = Baseline, RPE_0–4, RPE_5–8, RPE_9–Max, Recovery) on each pair of electrodes. According to a previous study (Del Percio et al., 2011), representative electrodes are F3, F4, C3, C4, P3, P4, T7, T8, O1, O2. We analyzed cortical activity by combining these electrodes in pairs representative of inter-hemispheric (F3–F4, C3–C4, T7–T8, P3–P4, O2–O1) and intra-hemispheric (F3–P3, F4–P4, T7–P3, T8–P4, C3–P3, C4–P4, P3–O1, P4–O2) connectivity across the frontal, central, parietal, temporal, and occipital regions in alpha and beta bands.

RESULTS

Performance Outcomes Comparison

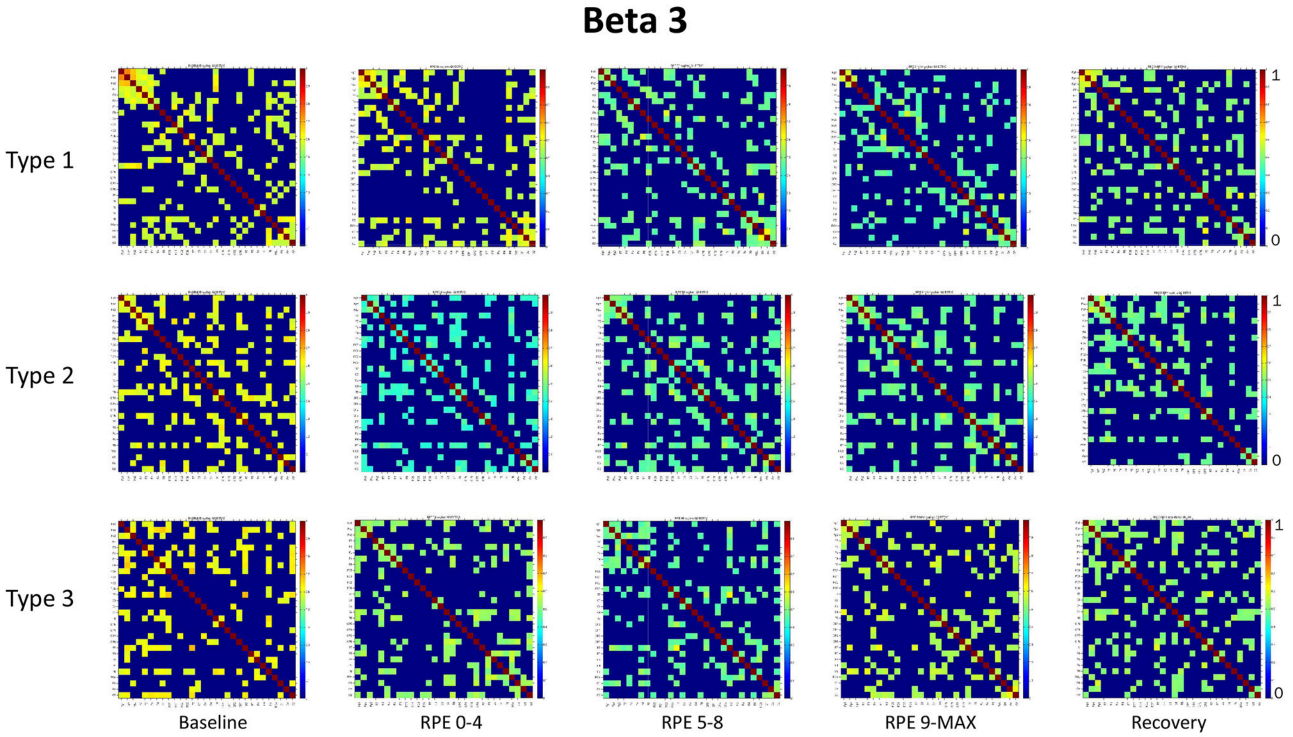
Within-subjects RM-ANOVA for TTE (see **Table 1**) showed significant differences among performance outcomes, $F_{(2,9)} = 7.323$, $p = 0.013$, $\eta_p^2 = 0.619$, Power = 0.827. *Post-hoc* pairwise comparisons with Bonferroni correction, showed significant differences between Type 1 and Type 3 ($p = 0.037$) performance states, and between Type 2 and Type 3 ($p = 0.024$), but not between Type 1 and Type 2 ($p = 1.000$).

Manipulation Check

Manipulation check results showed that participants adhered satisfactorily to the experimental conditions. During Type 1 performance condition, response ratings ranged from 4 to 9, which corresponded to an adherence frequency from “often enough” to “almost always” ($M = 6.80$, SD = 1.83). In Type 2 performance state, the response ratings ranged from 5 to 10 (“often” to “always”; M = 7.36, SD = 1.80), whereas in Type 3 performance state the response ratings ranged from 4 to 10 (“often enough” to “always,” $M = 7.27$, $SD = 1.79$).

EEG Coherence Results

For each frequency band (alpha, beta1, beta2, beta3) we calculated coherence matrices for each type of performance (Type 1, Type 2, Type 3) and for each effort level (Baseline, RPE 0–4; RPE 5–8; RPE 9–MAX, Recovery). These matrices are shown in **Figures 1–4**. Furthermore, the averaged coherence values of all electrodes in the alpha and beta bands are included in Supplementary Materials to provide a comprehensive picture of brain activity at the sensor level (see Figures 1S—4S).



Note: The order of the electrodes in the axis, from top to bottom and from left to right, is: Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3,Pz, P4, P8, POz, O1,OZ, O2.

FIGURE 4 | Coherence matrices for each type of performance during different time periods of the protocol in the beta 3 band. Red color indicates high values of coherence whereas the blue color indicates low values of coherence.

Alpha Band

RM-ANOVA 3 (performance) × 5 (effort level) showed significant effects on effort level for almost all pairs of chosen electrodes (see Table 1S). *Post-hoc* analysis showed differences between Baseline and periods of TTE task (effort level), mainly between Baseline and RPE 5–8 and between Baseline and 9-MAX period (see **Table 2**).

Beta Bands

RM-ANOVA 3 (performance) × 5 (effort level) showed significant effort level effects for almost all pairs of chosen electrodes in all beta bands (see Tables 2S—4S). *Post-hoc* comparisons on effort level showed differences mainly between Baseline and RPE 5–8, and between Baseline and Recovery (**Table 3**). Moreover, performance × time interaction was found for C3–C4 electrodes pair in beta 3 band (Table 4S). *Post-hoc* pairwise comparisons showed significant differences between Type 3 and Type 1 performances, as well as between Type 3 and Type 2 performances, but not between Type 1 and Type 2 during RPE 9-MAX (**Table 4**).

DISCUSSION

Current results, derived from EEG coherence analysis of data collected before, during, and after TTE, corroborated previous behavioral findings (Bertollo et al., 2015) and helped clarifying the brain mechanisms underpinning endurance task performance. Specifically, results related to performance outcomes confirmed that participants were able to optimally perform using an external associative strategy by focusing their attention on the metronome (Type 1 performance). Similarly, participants were able to achieve optimal performance also using an internal associative strategy with a focus of attention directed to the core component of the action (Type 2 performance). On the other hand, participants' performance was poor when

TABLE 2 | *Post-hoc* pairwise comparisons on effort level in alpha band.

Elec Pair	Baseline mean coherence values	Other periods mean coherence values	*P*
F3-P3	0.542	RPE 5–8, 0.422	0.034
F4-P4	0.551	RPE 5–8, 0.397	0.000
T7-T8	0.576	RPE 5–8, 0.460	0.041
	0.576	RPE 9–MAX, 0.475	0.042
T7-P3	0.545	RPE 5–8, 0.406	0.000
	0.545	RPE 9-MAX, 0.400	0.032
C3-C4	0.549	RPE 5–8, 0.414	0.011
C3-P3	0.551	RPE 5–8, 0.442	0.001
	0.551	Recovery, 0.453	0.012
C4-P4	0.570	RPE 5–8, 0.427	0.012
	0.570	RPE 9–MAX, 0.439	0.003
T8-P4	0.540	RPE 5–8, 0.420	0.003
P3-P4	0.580	RPE 5–8, 0.425	0.003
	0.580	Recovery, 0.483	0.039
P4-O2	0.573	RPE0–4, 0.454	0.021
	0.573	RPE5–8, 0.449	0.016
	0.573	RPE 9-MAX, 0.446	0.003
	0.573	Recovery, 0.441	0.022

Only significant results are reported.

TABLE 3 | *Post-hoc* pairwise comparisons on effort level in beta bands.

Bands	Elec Pair	Baseline mean coherence values	Other periods mean coherence values	*P*
Beta 1	F3-F4	0.542	Recovery, 0.443	0.001
	F3-P3	0.516	RPE 5–8, 0.370	0.009
	T7-P3	0.502	RPE 5–8, 0.414	0.046
	C3-P3	0.548	Recovery, 0.465	0.028
	C4-P4	0.546	RPE 5–8, 0.421	0.003
		0.546	RPE 9–MAX, 0.465	0.005
	P3-P4	0.559	RPE 5–8, 0.438	0.001
		0.559	Recovery, 0.458	0.045
	P4-O2	0.532	RPE 5– 8, 0.437	0.046
		0.532	RPE9–MAX, 0.413	0.030
		0.532	Recovery, 0.428	0.027
	O2-O1	0.591	RPE 0–4, 0.473	0.040
Beta 2	F3-F4	0.565	RPE 5–8, 0.416	0.029
		0.565	Recovery, 0.444	0.001
	F3-P3	0.539	RPE 5–8, 0.391	0.025
		0.539	Recovery, 0.416	0.047
	F4-P4	0.514	RPE 5– 8, 0.365	0.001
	C3-C4	0.572	RPE 5–8, 0.441	0.005
	C3-P3	0.555	RPE 5–8, 0.433	0.000
		0.555	RPE 9–MAX, 0.448	0.043
		0.555	Recovery, 0.447	0.049
	C4-P4	0.523	RPE 5–8, 0.400	0.005
	T8-P4	0.503	RPE 5– 8, 0.383	0.005
	P3-P4	0.523	RPE 5–8, 0.420	0.002
		0.523	Recovery, 0.428	0.013
	P3-O1	0.508	RPE 5–8, 0.422	0.046
		0.508	Recovery, 0.394	0.036
	P4-O2	0.524	Recovery, 0.430	0.006
Beta 3	F3-F4	0.549	RPE 5–8, 0.411	0.019
		0.549	Recovery, 0.438	0.002
	F3-P3	0.560	RPE 5–8, 0.388	0.000
		0.560	RPE 9–MAX, 0.419	0.002
		0.560	Recovery, 0.420	0.000
	T7-T8	0.555	RPE 5–8, 0.425	0.044
	T7-P3	0.526	RPE 5–8, 0.415	0.003
	C3-C4	0.563	RPE 5–8, 0.415	0.010
	C3-P3	0.538	RPE 5–8, 0.424	0.029
		0.538	Recovery, 0.459	0.000
	C4-P4	0.535	RPE 5–8, 0.408	0.010
		0.535	RPE 9–MAX, 0.449	0.030
		0.535	Recovery, 0.436	0.026
	T8-P4	0.531	RPE 5–8, 0.406	0.000
		0.531	RPE 9–MAX, 0.445	0.050
	P4-O2	0.543	RPE 5–8, 0.435	0.008
		0.543	Recovery, 0.430	0.001
	O2-O1	0.610	Recovery, 0.496	0.026

Only significant results are reported.

TABLE 4 | *Post-hoc* pairwise comparisons for C3-C4 electrodes pair on performance × effort level interaction (red color indicates $p < 0.05$).

	T1 Baseline	T1 RPE 0–4	T1 RPE 5–8	T1 RPE 9–MAX	T1 Recovery	T2 Baseline	T2 RPE 0–4	T2 RPE 5–8	T2 RPE 9–MAX	T2 Recovery	T3 Baseline	T3 RPE 0–4	T3 RPE 5–8	T3 RPE 9–MAX	T3 Recovery
	Mean =0.57	**Mean =0.56**	**Mean =0.41**	**Mean= 0.43**	**Mean =0.49**	**Mean =0.57**	**Mean= 0.39**	**Mean =0.42**	**Mean =0.41**	**Mean =0.47**	**Mean =0.54**	**Mean =0.47**	**Mean =0.40**	**Mean =0.55**	**Mean =0.48**
Effort levels (periods)	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***
Baseline		0.97	0.00	0.01	0.10	0.86	0.00	0.00	0.00	0.05	0.55	0.05	0.00	0.76	0.07
RPE 0–4	0.97		0.00	0.01	0.11	0.83	0.00	0.00	0.00	0.06	0.57	0.05	0.00	0.80	0.08
RPE 5–8	0.00	0.00		0.68	0.13	0.00	0.59	0.85	0.88	0.22	0.01	0.24	0.73	0.01	0.18
RPE 9–MAX	0.01	0.01	0.68		0.27	0.00	0.34	0.82	0.57	0.42	0.03	0.44	0.45	0.02	0.35
Recovery	0.10	0.11	0.13	0.27		0.07	0.04	0.18	0.09	0.76	0.30	0.73	0.06	0.18	0.86
Baseline	0.86	0.83	0.00	0.00	0.07		0.00	0.00	0.00	0.04	0.44	0.03	0.00	0.64	0.05
RPE 0–4	0.00	0.00	0.59	0.34	0.04	0.00		0.47	0.70	0.08	0.00	0.09	0.85	0.00	0.06
RPE 5–8	0.00	0.00	0.85	0.82	0.18	0.00	0.47		0.73	0.30	0.02	0.32	0.59	0.01	0.24
RPE 9–MAX	0.00	0.00	0.88	0.57	0.09	0.00	0.70	0.73		0.17	0.01	0.18	0.85	0.00	0.13
Recovery	0.05	0.06	0.22	0.42	0.76	0.04	0.08	0.30	0.17		0.18	0.97	0.12	0.10	0.90
Baseline	0.55	0.57	0.01	0.03	0.30	0.44	0.00	0.02	0.01	0.18		0.17	0.00	0.76	0.23
RPE 0–4	0.05	0.05	0.24	0.44	0.73	0.03	0.09	0.32	0.18	0.97	0.17		0.13	0.09	0.87
RPE 5–8	0.00	0.00	0.73	0.45	0.06	0.00	0.85	0.59	0.85	0.12	0.00	0.13		0.00	0.09
RPE 9–MAX	0.76	0.80	0.01	0.02	0.18	0.64	0.00	0.01	0.00	0.10	0.76	0.09	0.00		0.13
Recovery	0.07	0.08	0.18	0.35	0.86	0.05	0.06	0.24	0.13	0.90	0.23	0.87	0.09	0.13	

they focused their attention on muscle exertion. These results suggest that individuals may perform well not only in a flow-like performance state (Type 1), but also when they pay attention to specific action components (Type 2 state). Therefore, identifying the core components of action linked to functional performance patterns and focusing attention on this fundamental movement can improve performance and help individuals counteract the discomfort and pain deriving from muscle soreness and fatigue in endurance tasks.

The main purpose of this study was to examine, within the theoretical framework of the MAP model, the effect of attentional strategies on brain functional connectivity during different periods of effort. In summary, findings from the entire scalp (averaged coherence of all electrodes) in the alpha and beta bands showed:

1) Higher coherence values at rest (Baseline) than during task execution (RPE 0–4, 5–8, 9–MAX periods) for all performance types (Hypothesis 1-effort level effect). *Post-hoc* pairwise comparisons showed significant differences between Baseline and the two periods of high effort (RPE 5–8; RPE 9–MAX) in both alpha and beta bands. Differences between Baseline and Recovery were found especially in the beta bands.
2) Higher coherence values in Type 3 performance as compared to Type 1 and Type 2 performances during RPE 9-MAX (Hypothesis 2-Performance × effort level interaction). It is interesting to observe that performance × effort level interaction on the C3–C4 electrodes pair in beta 3 band most likely reflected the effect of focusing attention on muscle exertion (Type 3 performance state), that led to higher inter-hemispheric communication between motor areas during the exhausting phase (i.e., RPE 9-Max).

These results are consistent with previous findings which associate high values of coherence with functional coupling (Thatcher et al., 1986), information exchange (Petsche et al., 1997; Pfurtscheller and Andrew, 1999), and functional coordination (Gevins et al., 1989) among brain regions. High coherence values suggest an increased functional synchronization among two or more brain areas related to the preparation for task execution (Pfurtscheller and Andrew, 1999).

Our findings also highlighted that coherence was generally lower during those periods characterized by movement and high effort such as at RPE 5–8 and particularly at RPE 9–MAX (especially in Type 1 and Type 2 performance).

Our results are partially consistent with the finding that after a fatiguing cycling exercise there is an increase in the communication between the mid/anterior insula and the motor cortex (Hilty et al., 2011), similar to what observed for the Baseline period. Indeed, from a statistical point of view, we found differences for inter- and intra-hemispheric coherence when comparing Baseline and TTE, but not when comparing TTE and Recovery. This occurred not only in the alpha but also in the beta band, the biomarker that best reflects motor binding (Cheron et al., 2016). Therefore, we can argue that our first hypothesis was confirmed to a large extent, although further research is necessary to compare TTE and Recovery immediately after exercise, eventually considering longer periods of post-exercise Recovery.

We also noticed that coherence patterns during Baseline periods were similar for all types of performance. This finding indicates an extensive exchange of background information among all brain regions before task execution and movement (Petsche et al., 1997; Pfurtscheller and Andrew, 1999). Even if, in general, we did not observe significant results on performances by effort interactions, it is worth noting that Type 1 performance was usually typified by higher coherence as compared to the other performance types during low effort (RPE 0–4 period) in the alpha and beta bands. This result could be related to the external associative strategy adopted that can initially engage a broader functional connectivity across brain areas, as well as to the nature of the task that requires a sustained movement (Comani et al., 2014). Lower coherence in Type 2 and Type 3 performances could be related to negative feelings associated with fatigue or the internal focus of attention (Wilson et al., 2011). Of note, during maximum effort (RPE 9–MAX period) Type 1 performance was characterized by lower coherence that could be due to fatigue effects. These may lead to a reorganization of the brain network (Berchicci et al., 2013) irrespective of the functional strategy adopted. Moreover, we can hypothesize that task execution during the final period of the TTE becomes more automatic and needs less information exchange, especially when an external associative strategy is adopted (Hatfield and Kerick, 2007). This result can be also partially interpreted within the framework of the neural efficiency hypothesis, which reflects a general reduction in neural activity as task execution becomes more automated and less controlled (Callan and Naito, 2014). We also found that an external associative strategy was effective and possibly leading to flow like experiences, as demonstrated by cortical inhibition and therefore by the low coherence values obtained during maximum effort (Knyazev et al., 2011).

It is worth considering that during the Recovery phase there was no attention manipulation and, consequently, cognitive and attentional demands were low; these low demands could have contributed to the retrieval of coherence patterns similar to those observed during Baseline. From the visual inspection of the coherence matrices, indeed, we observed, especially in the alpha band, high coherence values during Recovery in Type 1 performance, similarly to coherence in Type 3 performance. We can hypothesize that after maximum effort a counteracting mechanism restores the same pattern of functional connectivity among brain areas as during Baseline. Indeed sensory-related thalamic nuclei information, which serves as gate to the primary sensory areas in the cortex during TTE (Beiser and Houk, 1998), is absent during Baseline. We also observed another difference between Type 1 and Type 3 performance states: coherence values in beta 3 were significantly higher for Type 3 during maximum effort in C3–C4. This may be due to the focus of attention on muscle exertion that leads to an increased inter-hemispheric communication between motor areas devoted to the motor input in the bilateral cycling task (Comani et al., 2014). We could argue that an enhancement of alpha and beta interhemispheric coherence, particularly in C3–C4, may reflect the primary activation of the somatosensory cortex in noxious processing (Chen and Rappelsberger, 1994). This difference was also observed between Type 2 and Type 3 performance, but not between Type 1 and Type 2 performance. These findings corroborate the MAP model perspective because the two optimal performances (Type 1 and 2) showed similar functional connectivity patterns, which were different from those observed for Type 3 performance (Bertollo et al., 2016; di Fronso et al., 2016, 2017). However, our findings are not conclusive in regard to our second hypothesis, and further investigation is needed to more deeply explore sensory motor integration and perception-action coupling. From an applied perspective, this study suggests the use of bio-neurofeedback not just to help people divert their attention away from dysfunctional sensations (Bertollo et al., 2015), but also to stimulate functional connectivity among specific brain areas for performance optimization, according to the explanation provided by Poldrack (2015) on neural efficiency theory. He suggested that “the total amount of energy consumed by neuronal computations depends not just upon the function of individual neurons, but also on how those neurons are connected to one another” (p. 16). Neurofeedback training could be used together with relaxation and mental skills training to help athletes modulate alpha or beta brain waves, and therefore self-regulate their functional arousal level (di Fronso et al., 2017).

Some limitations of the current study need to be addressed in future research. From a methodological point of view, performing EEG studies in sport is still hard due to different types of artifacts affecting the EEG recordings. We conducted this study with a stationary EEG system and wet electrodes, which did not totally allow to avoid the artifacts in low frequency ranges. More advanced EEG equipment (e.g., mobile EEG systems, dry-electrode technology) and new algorithms for EEG data pre-processing (Stone et al., 2018; Tamburro et al., 2018) could allow to consider also the theta band, hence paving the way to a better interpretation of EEG data in the light of the neural efficiency hypothesis. From a theoretical point of view, it might be important to investigate also cortico-muscolar coherence during voluntary movements (Marsden et al., 2000), as it could provide useful information on specific functional connections between the cortex and the engaged muscles (Travis et al., 2002), and a better understanding of the brain-body interaction and integration (Tang and Bruya, 2017). Finally, future studies should engage a larger number of participants to provide more reliable results, especially about peak performance experiences that are rare to find and difficult to reproduce. Research should also be extended to different endurance sports and more experienced athletes to attain more generalizable findings. Other functional neuroimaging techniques (e.g., NIRS) and analytic procedures (i.e., LORETA) could also enable a better understanding of structure-function and brain-body connections.

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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SUPPLEMENTARY MATERIAL

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Reach-To-Grasp Movements: A Multimodal Techniques Study

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The aim of the present study was to investigate the correlation between corticospinal activity, kinematics, and electromyography (EMG) associated with the execution of precision and whole-hand grasps (WHGs). To this end, motor-evoked potentials (MEPs) induced by transcranial magnetic stimulation (TMS), EMG, and 3-D motion capture data have been simultaneously recorded during the planning and the execution of prehensile actions toward either a small or a large object. Differences in the considered measures were expected to distinguish between the two types of grasping actions both in terms of action preparation and execution. The results indicate that the index finger (FDI) and the little finger (ADM) muscles showed different activation patterns during grasping execution, but only the FDI appeared to distinguish between the two types of actions during motor preparation. Kinematics analysis showed that precision grips differed from WHGs in terms of displayed fingers distance when shaping before object's contact, and in terms of timing and velocity patterns. Moreover, significant correlations suggest a relationship between the muscular activation and the temporal aspects concerned with the index finger's extension during whole-hand actions. Overall, the present data seem to suggest a crucial role played by index finger as an early "marker" of differential motor preparation for different types of grasps and as a "navigator" in guiding whole-hand prehensile actions. Aside from the novelty of the methodological approach characterizing the present study, the data provide new insights regarding the level of crosstalk among different levels concerned with the neuro-behavioral organization of reach-to-grasp movements.

Keywords: reach-to-grasp, transcranial magnetic stimulation, kinematics, MEP, EMG

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INTRODUCTION

A large amount of behavioral and neurophysiological studies have identified specific kinematic patterns and neural activations for grasping of differently shaped objects (for review, see Castiello, 2005). Effective grasping implicates the ability to coordinate multiple configurations of finger movements, depending on the properties of the object to be grasped (e.g., size, shape, and weight). This process first involves a progressive opening of the grip with straightening of the fingers during reaching, followed by a closure of the grip until it matches object size and shape. Precision grip (PG; i.e., the opposition of the thumb to the index finger) on small objects requires smaller hand aperture. Increasing object size, instead, lowers the spatial accuracy demands, permitting a larger grip to emerge in a whole-hand grasp (WHG; i.e., the opposition of the fingers to the palm). Interestingly, subpopulations of neurons in the primary motor cortex (M1) of non-human primates are active while conducting a PG, but not during a WHG (Muir and Lemon, 1983). This indicates that the control of fingertip actions with a PG engages neural circuits that are different to those engaged during the phylogenetically older WHG (Napier, 1980).

Despite the interest on motor preparation and execution of different types of grasps, the functional connection between these two processes still needs to be clarified (Prabhu et al., 2007). A very useful measure of motor planning is provided by the amplitude of the motor-evoked potential (MEP) in response to a standard single pulse of transcranial magnetic stimulation (spTMS) over M1 (Priori et al., 1998). Transcranial magnetic stimulation (TMS) was first introduced as a method to investigate the integrity of the corticospinal (CS) outflow from cerebral motor cortex to the spinal cord (Rothwell, 1997). The TMS pulses penetrate the skull and carry an electric stimulating current into the cortex. Depolarization of neurons is produced by virtue of an induced current, as prescribed by Faraday's law (Epstein, 2008). In the motor area, action potentials leads to activation of pyramidal neurons, conduction of impulses to the spinal cord, and eventually to contraction of muscles on the contralateral side of the body (Davey, 2008). The M1 and its descending projection to the spinal cord in the CS tract, in particular, are crucial for the control of hand and finger movements (Muakkassa and Strick, 1979; Godschalk et al., 1984; Matelli et al., 1986; Dancause et al., 2006). Much of the work involving magnetic stimulation of the human motor cortex, therefore, has focused on electromyographic (EMG) responses in hand muscles during action execution (Lemon et al., 1995). Interestingly, the TMS pulses tend not to activate the pyramidal output neurons directly, but instead to stimulate the axons of neurons that synapse onto them. Thus, the size of the response produced by a given stimulus is sensitive to the excitability of synaptic connections within the cortex, giving an indirect measure of the excitability of intrinsic cortical circuits within the conscious brain (Quartarone et al., 2006).

In terms of action execution, motion-capture technology has allowed researchers to build up a detailed and complex picture of how action kinematics vary depending on the relationship between types of prehensile actions and intrinsic object properties (Gentilucci et al., 1991; Castiello et al., 1993, Castiello et al., 1996). In particular, the dimension of an object influences how it is manipulated, with the maximum grip aperture (MGA; i.e., the opening of the fingers while approaching the object) varying linearly as a function of the size of the object (Jeannerod, 1981; Marteniuk et al., 1990). Moreover, different types of grasping (i.e., PG and WHG) are characterized by different temporal patterns, with the time of MGA occurring earlier for PG than for WHG (Gentilucci et al., 1991).

Given the vast interest on the mechanisms underlying the execution of prehensile actions, here we specifically devised a multi-methodological study in order to unveil for the first time the relationship between the neural underpinning of motor preparation and the unfolding of hand shaping – as identified, respectively, by CS excitability, EMG, and kinematics. We recorded MEPs and EMG from two intrinsic hand muscles: the first dorsal interosseous (FDI) and abductor digiti minimi (ADM) during the planning and execution of precision and WHGs. Since FDI is a prime mover in PG, whereas the ADM abducts the little finger to open the hand in the WHG (Cattaneo et al., 2005; Davare et al., 2009, 2010; Cavallo et al., 2011), we predict facilitation effects for those muscles during the preparation and execution of the respective action sequences. Moreover, MEP literature also highlights FDI modulation during the observation of a WHG, in correspondence to the maximal finger aperture phase (e.g., Gangitano et al., 2001). This aspect might be crucial when considering potential correlations between FDI activity during action execution and kinematics. In addition to MEPS and EMG recording, motion capture was applied to measure hand kinematics. In terms of crosstalk between CSE, EMG, and kinematics, no firm predictions can be made given that this is the first study investigating the activity sequence from action preparation to action execution, at both the neural and behavioral levels.

MATERIALS AND METHODS

This experiment investigated the reciprocal contribution of CS activity, kinematics, and EMG associated with the preparation and execution of precision and WHGs.

Participants

Twenty-five naïve volunteers (15 female and 10 male, aged between 21 and 30 years, mean age 23.92 ± 2.4 years) took part in the experiment. All participants were right-handed, as assessed with the Edinburgh Handedness Inventory (Oldfield, 1971), with normal or corrected-to-normal visual acuity. They were all screened for TMS exclusion criteria and for neurological, psychiatric, and medical problems (Wassermann, 1998; Rossi et al., 2009). The experiment was approved by the ethics committee of the University of Padua, in accordance with the Declaration of Helsinki (sixth revision, 2008). All participants gave their written informed consent and were financially compensated for their participation.

Experimental Stimuli

The participants sat comfortably in front of a table (∼90 cm wide, ∼90 cm long) upon which a cup (∼12 cm height, ∼9 cm diameter) with a spoon (∼20 cm long) inside it and a starting platform (∼2 cm wide, ∼4 cm long) were placed. The cup was positioned alongside the participants' midsagittal plane at a 30 cm distance from the starting platform. Participants placed their right hand in pinch position on the starting button at the outset of each trial (**Figure 1A**).

Procedure

Participants were tested individually in a single experimental session lasting 1 h. They were seated in a comfortable chair with the right elbow positioned on an adjustable armrest, the head on a fixed headrest, and the right hand's ulnar styloid process

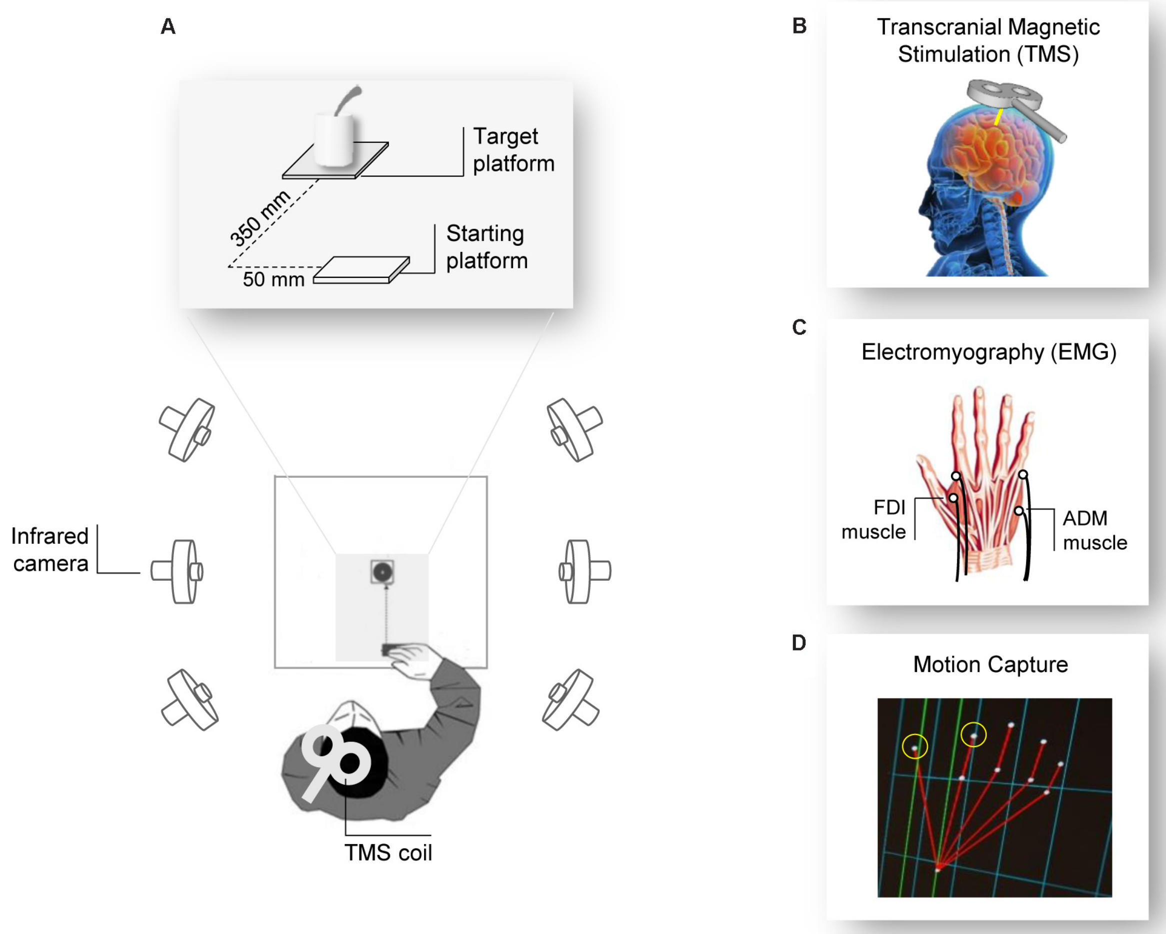

FIGURE 1 | Experiment setup. **(A)** The participants were seated in front of a table surrounded by six infrared cameras. The participant's hand was positioned in front of the object they had to grasp after the Go signal (TMS pulse). **(B)** The TMS coil was placed over the participant's left M1 and **(C)** MEPs and EMG activity were measured from electrodes placed over the FDI and the ADM muscles of the right hand. **(D)** Two infrared reflective markers taped to the participant's index and thumb fingers were used to track the right hand's kinematics.

laying on the starting platform with the hand in pinch position (**Figure 1A**). They were instructed to remain as still and relaxed as possible between each trial and to keep their eyes open. At the beginning of each block, participants were verbally instructed on the type of action they would have to perform. The order of the actions was counterbalanced between participants. TMS pulse served as a "Go" signal, after which participants were required to either (a) release the start button, reach and grasp the cup with a WHG, and lift it, or (b) release the start button, reach and grasp the sugar spoon with a PG, and move it. At the end of each action (WHG, PG), participants were requested to place the object at its original position and then return to the starting position. Participants performed a total of 32 trials, divided in four blocks of eight repetitions each; therefore, they performed 16 repetitions for each type of action. For each trial, right hand TMS-induced MEPs from the participants' FDI and ADM muscles were recorded during action preparation, together with EMG activity and kinematics recordings during action execution.

Transcranial Magnetic Stimulation

Single-pulse TMS was administered using a 70 mm figure-of-eight coil connected to a Magstim Bistim2 stimulator (Magstim Co., Whitland, United Kingdom). Pulses were delivered on the participant's left primary motor cortex (M1), in correspondence with the right hand representation. The coil was placed on the head with a 45° angle relative to the inter-hemispheric fissure, with the handle pointing laterally and caudally (Brasil-Neto et al., 1992; Mills et al., 1992; **Figures 1A,B**). The optimal scalp position (OSP), which is defined as the scalp position at which the minimum level of stimulation elicits the largest MEPs from both the ADM and the FDI muscles, was determined by moving the coil in approximately 0.5 cm steps around the presumed hand motor area. The OSP was then marked on a tight-fitting cap worn by the participants ensuring a correct coil placement throughout the experiment. During the experiment, the coil was held by a tripod and continuously checked by the experimenters to maintain a constant positioning with respect to the marked OSP. The stimulation intensity was then set at 120% of the rMT (see below). TMS stimulation was managed by E-Prime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, United States).

Electromyographic Recording

Electromyographic activity was recorded through two pairs of surface Ag/AgCl electrodes (1 cm diameter) placed in a belly-tendon montage (**Figure 1C**). After skin cleaning, electrodes containing a small amount of water-soluble EEG conductive paste were placed and fixed on the target positions. The active electrode was placed over the muscle belly (determined by palpation during maximum voluntary contraction) and the reference over the proximal interphalangeal juncture. The ground electrode was positioned over the participant's right wrist. The electrodes and wires were secured and positioned so that they did not restrict the participants' movements. Skin impedance, evaluated at rest prior to beginning the experimental session, was considered of good quality when below the threshold level (5 **Ω**). Electrodes were connected to an isolable portable ExG input box linked to the main EMG amplifier for signal transmission via a twin fiber optic cable (Professional BrainAmp ExG MR, Munich, Germany). A high-pass filter of 30 Hz and a low-pass filter of 1000 Hz were applied to the raw myographic signal, which was amplified prior to being digitalized (5 KHz sampling rate), and stored on a computer for offline analysis. MEPs and EMG activity were recorded simultaneously from the FDI and ADM muscles of the participant's right hand. We also determined the individual resting motor threshold (rMT) as the minimum TMS intensity able to produce MEPs with an at least $\geq$50 μV peak-to-peak amplitude in a relaxed muscle in 5 out of 10 consecutive pulses (Rossini et al., 1994) in the higher threshold muscle (ADM). rMT ranged from 28 to 52% (mean = 40.1%, SD = 5.5) of the maximum stimulator output. EMG recordings were managed by E-Prime V2.0 (Psychology Software Tools Inc., Pittsburgh, PA, United States) and Brain Vision Recorder (Brain Products BmbH, Munich, Germany) software.

Kinematics Recording

Movements were tracked using the 3-D optoelectronic SMART system (Bioengineering Technology and Systems, B| T| S|, Milan, Italy) equipped with six infrared cameras (sampling rate 60 Hz), placed in a semicircle at a distance of 1–1.2 m from the table (**Figure 1A**). Two semi-spherical reflecting markers (∼0.25 mm diameter) were attached to the participants' right hand on the radial side of the index nail and on the ulnar side of the thumb nail (**Figure 1D**). The index finger and thumb markers served to measure the manipulation component of the grasping action. Cameras position, roll angle, focus, zoom, brightness, and threshold were set before the experimental sessions to optimize markers' tracking. Static and dynamic calibrations were then performed for 3-D space reconstruction. For the static calibration, a three-axis frame of markers at known distance was placed at the center of the table, allowing to determine the spatial coordinate system. For the dynamic calibration, a three-marker wand was moved up and down several times parallel to each axis throughout the workspace of interest. The SD of the reconstruction error was below 0.3 mm for all the axes (x, y, and z).

Data Analysis

MEP Data

Individual peak-to-peak MEP amplitudes (mV) were analyzed off-line using Brain Vision Analyzer (Brain Products BmbH, Munich, Germany). The MEP peak-to-peak amplitude for FDI and ADM muscles was determined as a measure of participants' CS excitability. Trials in which any EMG activity greater than 100 μV was present in the 100 ms window preceding the TMS pulse were discarded to prevent contamination of MEP measurements by background EMG activity (<1%).

EMG Data

Electromyographic activity was analyzed offline using Brain Vision Analyzer (Brain Products BmbH, Munich, Germany). The EMG signal from the FDI and ADM muscles during action execution was rectified (Rectify function of the Brain Vision Analyzer software; no smoothing) and the area under the curve of the rectified EMG track (mV*s) was calculated for each muscle and each trial to quantify muscular activity when executing the grasping actions (PG, WHG). To explore the variations of EMG activity over time for each type of action, EMG activity was measured within a time window starting 500 ms after the TMS-go signal pulse up to 4500 ms. This window was subdivided in four time bins of 1 s each. The four time bins were defined as follows: (T_1) 500–1500 ms; (T_2) 1500–2500 ms; (T_3) 2500–3500 ms; and (T_4) 3500–4500 ms. In order to better take into account possible time differences across participants, for each participant and type of action, we calculated a 1-s time window based on the time at which the maximum distance between the thumb and index finger was reached (TMGA, see the next paragraph), comprising 500 ms before and after it ($T_{\text{individualized}}$).

Kinematics Data

Following kinematic data collection, the 3-D markers positions as a function of time were reconstructed, filtered (Butterworth filter with a 6 Hz cutoff), and analyzed by means of the SMART-D Tracker and SMART-D Analyzer software packages (B| T| S). Jeannerod (1981, 1984) coded grasping in terms of changes in grip aperture – the separation between the thumb and the index finger – and described two major components for prehensile behavior: the transport and the grasp components. The transport component brings the hand in the vicinity of the object and it is analyzed on the basis of the 3-D position of the wrist in time. The grasp component, instead, is concerned with finger pre-shaping during transport and finger closing around the object. Given that we aimed at investigating the crosstalk between finger muscles' EMG and kinematics, analyses were confined to the grasp component. Notably, the FDI is an intrinsic hand muscle that receives the strongest cortical input as it closes around the object (Lemon et al., 1995) and it is specifically implicated in grip aperture (Jeannerod, 1981). The following kinematic parameters were then extracted for each individual movement to measure the manipulation component:

Reaction times (RTs): The time at which participants released the start button after the "Go" signal.

Maximum grip aperture: The maximum distance reached by the 3-D coordinates of the thumb and index finger.

Time of maximum grip aperture (TMGA): The time at which the distance between the 3-D coordinates of the thumb and index finger was maximum from movement onset.

% Time of maximum grip aperture (TMGA%): The percentage of time at which the distance between the 3-D coordinates of the thumb and index finger was maximum with respect to grasping time.

Maximum grip velocity (MGV): The maximum velocity reached by the 3-D coordinates of the thumb and index finger during grip aperture.

Time of maximum grip velocity (TMGV): The time at which the tangential velocity of the 3-D coordinates of the thumb and index finger was maximum from movement onset.

% Time of maximum grip velocity (TMGV%): The percentage of time at which the tangential velocity of the 3-D coordinates of the thumb and index finger was maximum with respect to grasping time.

Statistical Analysis

SPSS 23 (SPSS Inc., Chicago, IL, United States) was used for statistical analysis. A repeated-measure ANOVA (rmANOVA) with condition (PG, WHG) and muscle (FDI, ADM) as within-subject factors was performed on MEP amplitudes. An rmANOVA on EMG activity was performed with condition (PG, WHG) muscle (FDI, ADM) and time (T_1–T_4) as within-subject factors. Moreover, to deeply investigate inter-individual time variations in muscular activation, an rmANOVA on EMG activity was performed on $T_{\text{individualized}}$ with condition (PG, WHG) and muscle (FDI, ADM) as within-subject factors. For kinematics parameters, the mean values for each parameter of interest (RT, MGA, TMGA, TMGA%, MGV, TMGV, and TMGV%) were determined for each participant and entered into separate rmANOVAs with action (PG, WHG) as within-subjects factor. The partial eta square (η_p^2) value was calculated as an estimate of effect size. In the presence of significant interactions, *post hoc* comparisons were performed. To explore the crosstalk between MEP and EMG measures and between EMG and kinematics, correlations were computed using the Pearson correlation coefficient. Each *p*-value obtained was corrected with Bonferroni correction. A significance threshold of $p < 0.05$ was set for all statistical analyses.

RESULTS

Grasp Preparation: MEP

The ANOVA on MEP amplitudes showed a main effect of muscle [$F_{(1,24)} = 6.037$, $p = 0.022$, $\eta_p^2 = 0.201$], action [$F_{(1,24)} = 8.847$, $p = 0.007$, $\eta_p^2 = 0.269$], and a significant interaction of muscle by action [$F_{(1,24)} = 8.556$, $p = 0.007$, $\eta_p^2 = 0.263$]. *Post hoc* contrasts revealed that MEP amplitudes for the FDI muscle were higher while preparing a PG compared to a WHG ($p = 0.004$). Moreover, the preparation for a PG was characterized by an increase in MEP amplitudes of the FDI compared to the ADM muscle ($p = 0.006$). Results are graphically summarized in **Figure 2A**.

Grasp Execution: Electromyography

The ANOVA on EMG activity across time bins (T_1–T_4) showed a main effect of time [$F_{(1,24)} = 26.834$, $p < 0.001$, $\eta_p^2 = 0.528$], a significant interaction of muscle by action [$F_{(1,24)} = 40.843$, $p < 0.001$, $\eta_p^2 = 0.630$], muscle by time [$F_{(1,24)} = 2.849$, $p = 0.043$, $\eta_p^2 = 0.106$], and muscle by action by time [$F_{(1,24)} = 13.431$, $p < 0.001$, $\eta_p^2 = 0.359$]. Results are graphically summarized in **Figure 3**. In PG trials, the FDI was more active compared to the ADM muscle at T_2 ($p = 0.001$), T_3 ($p = 0.001$), and T_4 ($p = 0.020$; **Figure 3A**). In WHG trials, the ADM was more active compared

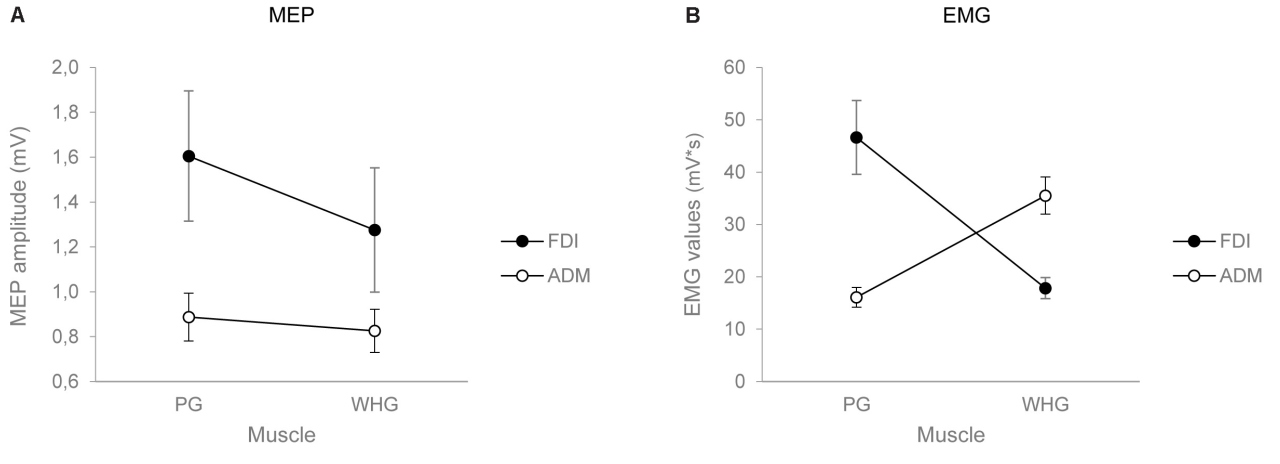

FIGURE 2 | Graphical representation of the mean values for the MEP amplitude **(A)** and the EMG activity in $T_{\text{individualized}}$ **(B)** for the FDI (black circles) and the ADM (white circles) muscles when participants performed either a PG or a WHG. Bars represent SE of the mean.

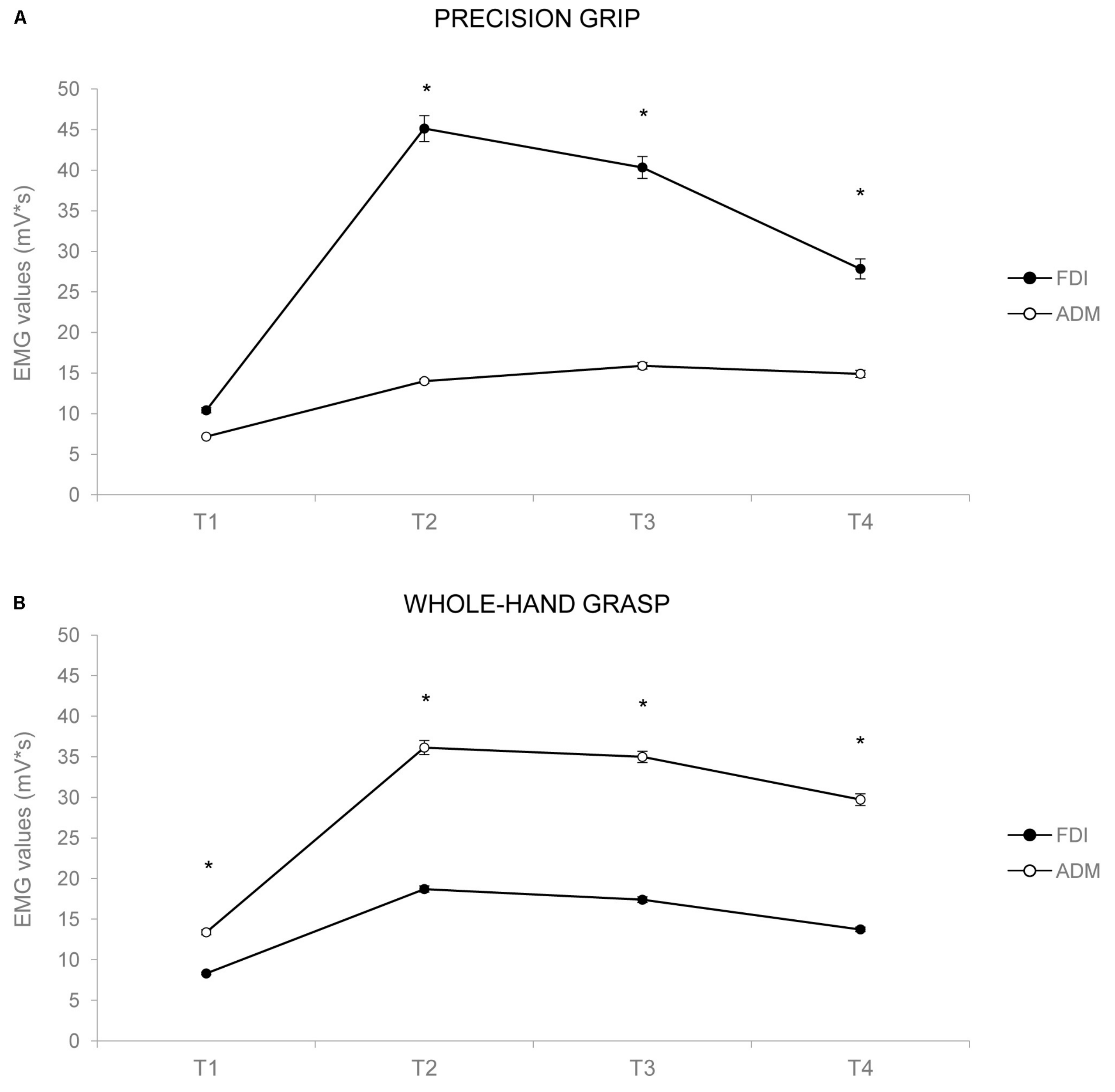

FIGURE 3 | Graphical representation of the mean values for the EMG activity across the 1-s time bins (T_1–T_4) for the FDI (black circles) and the ADM (white circles) muscles during PG **(A)** and WHG **(B)**. Bars represent SE of the mean. Asterisks indicate statistically significant comparisons ($p < 0.05$).

to the FDI muscle throughout all the four time bins (T_1–T_4, $p_s < 0.001$; **Figure 3B**). FDI was more activated in PG than WHG from T_2 to T_4 ($p_s < 0.020$), whereas ADM was more activated in WHG than PG in all time bins (T_1–T_4, $p_s < 0.001$). Moreover, the FDI muscle during both PG and WHG was less activated during the first time bin in T_1 compared to later time bins (i.e., T_2–T_4, $p_s < 0.05$), and during T_4 compared to T_3 ($p = 0.006$ and $p = 0.021$, respectively). Similarly, the ADM muscle during both PG and WHG was less activated during the first time bin in T_1 compared to T_2–T_4 ($p_s < 0.013$). The ANOVA on EMG activity at $T_{\text{individualized}}$ showed a significant interaction of muscle by action [$F_{(1,24)} = 39.706, p < 0.001, \eta_p^2 = 0.623$]. In PG trials, the FDI was more active compared to the ADM muscle ($p < 0.001$); conversely, in WHG trials, the ADM was more active than the FDI muscle ($p < 0.001$). FDI muscle showed a greater activation in PG compared to WHG trials ($p < 0.001$), whereas the ADM muscle was more activated in WHG than in PG trials ($p < 0.001$). Results are graphically summarized in **Figure 2B**. As concerns the temporal distribution of $T_{\text{individualized}}$, we calculated that for PG trials, the TMGA occurred within the first time bin (T_1) for the 20% of participants and within the second time bin (T_2) for the 80% of participants. For WHG trials, the TMGA occurred within the first time bin (T_1) for the 12% of participants, within the second time bin (T_2) for the 76% of participants, and within the third time bin (T_3) for the 12% of participants. Overall, the TMGA occurred within T_2 for the most of the participants.

Grasp Execution: Kinematics

The ANOVA on RT did not show any statistically significant effect [$F_{(1,24)} = 0.010$, $p = 0.921$, $\eta_p^2 < 0.001$]. The ANOVA on MGA showed a main effect of action [$F_{(1,24)} = 1356.217$, $p < 0.001$, $\eta_p^2 = 0.983$], with WHG requiring a greater hand aperture compared to PG due to different object sizes (**Figures 4A,C**). The ANOVA on TMGA showed a significant main effect of action in both absolute [$F_{(1,24)} = 156.387$, $p < 0.001$, $\eta_p^2 = 0.867$; **Figure 4B**] and relative [$F_{(1,24)} = 82.637$, $p < 0.001$, $\eta_p^2 = 0.775$] terms, with a delayed peak of MGA for the WHG compared to the PG. The ANOVA on MGV showed a significant main effect of action [$F_{(1,24)} = 45.742$, $p < 0.001$, $\eta_p^2 = 0.656$], with a faster grip aperture for the WHG compared to the PG (**Figures 4D,F**). The ANOVA on TMGV showed a significant main effect of action in both absolute [$F_{(1,24)} = 38.093$, $p < 0.001$, $\eta_p^2 = 0.61$; **Figure 4E**] and relative [$F_{(1,24)} = 61.356$, $p < 0.001$, $\eta_p^2 = 0.72$] terms, with an earlier velocity peak for PG execution compared to the WHG.

Correlations Between MEP and EMG

No significant correlations emerged when correlating MEP amplitudes with the EMG activation neither during $T_{\text{individualized}}$ ($p_s > 0.05$) nor for T_1–T_4 bins ($p_s > 0.05$).

Correlations Between EMG and Kinematics

When correlating EMG activations during $T_{\text{individualized}}$ and kinematics, negative correlations emerged between the EMG activity of the FDI muscle and both the TMGA% and TMGV% [$r_{(23)} = -0.547$, $p = 0.019$, **Figure 5A**; $r_{(23)} = -0.676$, $p < 0.001$, **Figure 5B**, respectively]. In particular, an increased activation of FDI occurred when MGA (TMGA%) and peak velocity of grip aperture (TMGV%) were anticipated. Notably, when performing the same correlations for all the time bins (T_1–T_4), we found that only for T_2 negative correlations emerged between the EMG activity of the FDI muscle and both the TMGA% and TMGV% [$r_{(23)} = -0.554$, $p = 0.033$; $r_{(23)} = -0.593$, $p = 0.014$, respectively]. No other significant correlations emerged for either the FDI muscle during PG or the ADM muscle during PG or WHG ($p_s > 0.05$).

DISCUSSION

The aim of the present study was to unveil the relationship between the neural underpinning of motor preparation and the unfolding of hand shaping – as identified by CS excitability, EMG, and kinematics, respectively. Results confirmed previous literature on motor preparation showing that planning a PG entailed an increased MEP amplitude in the FDI muscle with respect to the ADM muscle (not recruited in the PG) and with respect to the preparation of a WHG, that requires minor intervention from the index finger muscle. Results from the

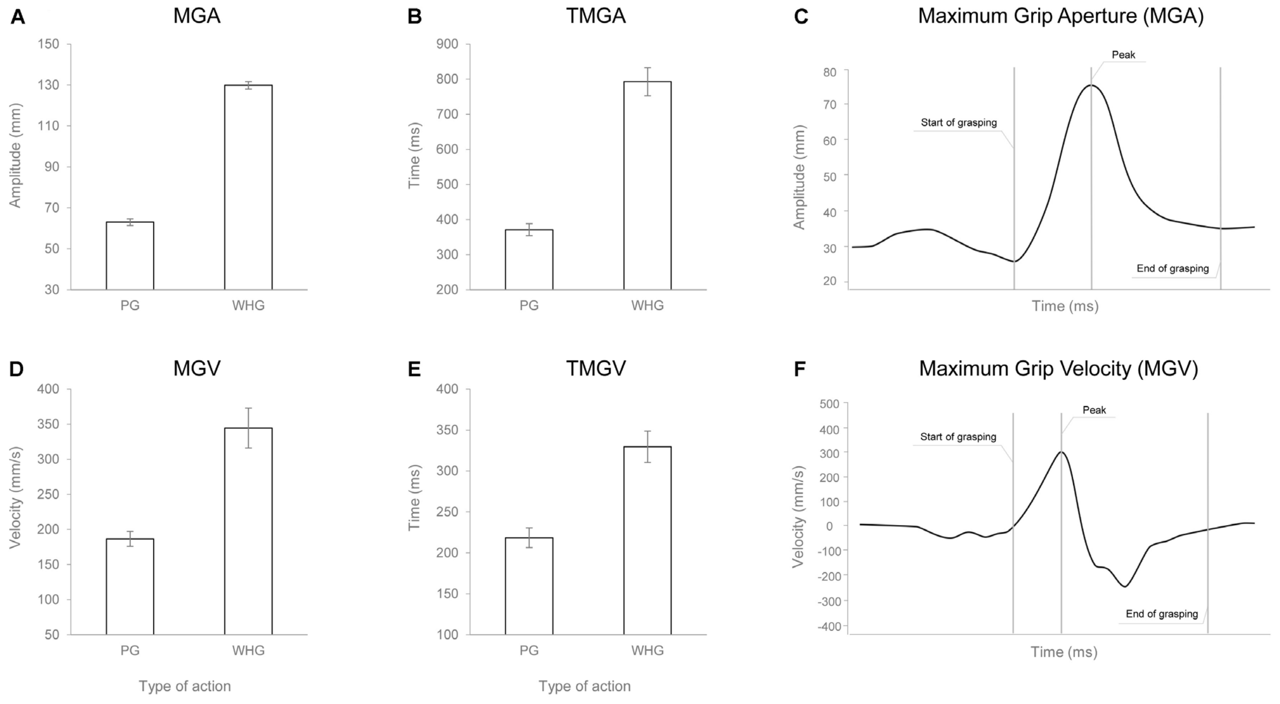

FIGURE 4 | Graphical representation of the mean values for MGA **(A)**, TMGA **(B)**, MGV **(D)**, and TMGV **(E)** when participants performed either a PG or a WHG. Bars represent SE of the mean. Example of the measure of the MGA **(C)** and MGV **(F)** peaks from a representative participant.

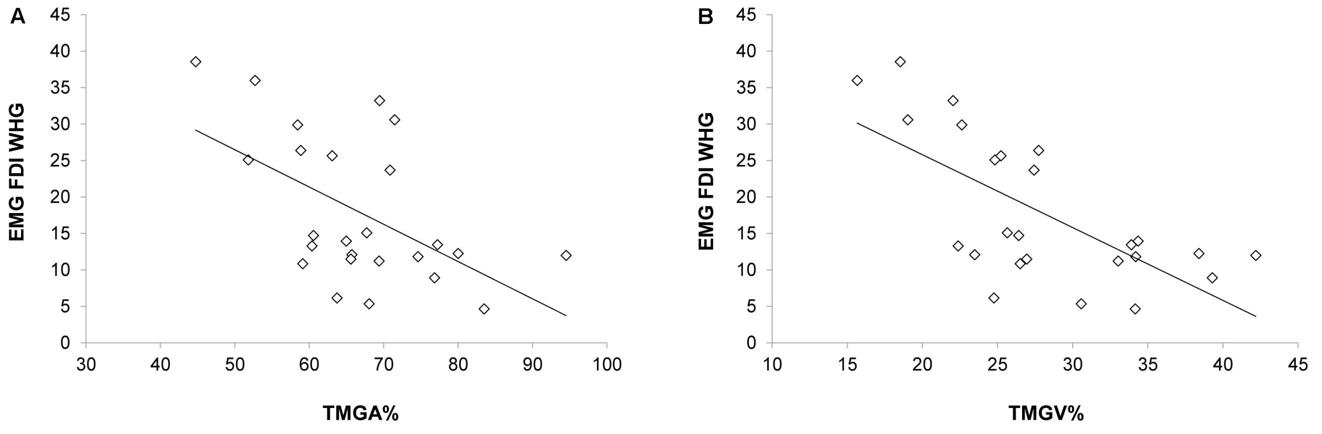

FIGURE 5 | Negative correlations between the EMG activity ($T_{\text{individualized}}$) in the FDI muscle during the WHG and **(A)** the time at which the grip aperture was maximum from movement onset and **(B)** the time at which the velocity of grip aperture was maximum from movement onset.

EMG extended these results to the ADM muscle and showed that during PG trials the FDI muscle was more active compared to both the ADM and during WHG trials. Moreover, during WHG trials, the ADM muscle was more active compared to both the FDI and to muscle activity during PG trials. No significant correlations emerged when correlating MEP amplitudes during action preparation with EMG activity during action execution. In terms of kinematics, results confirmed the linear relationship between grip aperture and object size, with smaller aperture for PG and larger for WHG (Gentilucci et al., 1991). Moreover, an early peak of MGA and MGV was found for the PG compared to the WHG, indicating that performing a PG required a more precise determination of contact points, resulting in an anticipated hand aperture (Gentilucci et al., 1991). When correlating EMG activations and kinematics of grasping during action execution, significant correlations emerged for the FDI muscle during WHG. In particular, the more MGA and MGV were anticipated, the more FDI was activated.

Different Planning Strategies for Different Types of Grasping

When the participants prepared for a PG, the muscle specifically involved in this action (the FDI) was facilitated to a greater extent than when preparing a WHG. In contrast, the ADM did not lead to significantly larger MEPs when preparing a WHG relative to preparing a PG. Interestingly, this a-specific pattern for the ADM muscle is convergent with previous findings during finger observation (Kaneko et al., 2007; Naish and Obhi, 2015). Hence, it is possible that the motor representation of the ADM is simply weaker/smaller than that of the FDI, being the former more frequently activated during, for instance, pointing movements or in synergy with the thumb to grasp and manipulate objects. In contrast, the little finger abduction is a relatively infrequent movement. A feature of the current design (and most studies of this type) that must be considered is that a single hot spot was chosen for stimulating both the FDI and ADM cortical maps and the intensity of stimulation was set based on the intensity required to elicit responses in the less excitable (higher threshold) muscle (ADM). So, it is possible that the FDI muscle might have been "over-stimulated," with respect to its motor threshold, compared to the ADM. Both these hypothesis would be confirmed by the fact that MEPs elicited in FDI were greater than those triggered in ADM. Moreover, the WHG is phylogenetically older than the PG (Napier, 1980) and requires a different temporal unfolding, with a tardive abduction of the little finger on the object (Castiello et al., 1993). In contrast, the PG requires a precocious maximum aperture, which might be specified in advance in order to anticipate the closing phase. To sum up, it is possible that differences in motor representations, cortical maps, relative stimulation intensity, and temporal recruitment could have influenced our pattern of results, and this is a factor to bear in mind for future studies in both action preparation and execution.

Dissociating Planning and Online Control

Planning and online control of action are two specialized processes serving different purposes and utilizing distinct visual representations (Glover, 2004). Choosing an appropriate motor plan depends on perceived information about the object and final goals. In particular, the planning process involves three aspects: (i) perceiving task-specific object properties; (ii) selecting a grasp strategy; and (iii) planning a hand location and orientation. Online control, instead, is feedback-based and it takes place during movement execution. Are these two processes independent one from each other? This is a highly controversial issue (Goodale and Westwood, 2004). Since no correlation was found here between MEPs and EMG, we might presume that a dissociation takes place between motor preparation and action execution. We must be cautious in interpreting these results, though, since no modulation was shown in the MEPs recorded from the ADM muscle. In this connection, we propose a more cautious approach when choosing the target muscles in future studies.

The Index Finger Pattern

As concerns the significant correlation between the myographic and the kinematic components of the index finger movement during the WHG, we might advance a specific hypothesis. In a previous study with a similar whole-hand grasping task (Sartori et al., 2011), we demonstrated that participants adopted a particular motor pattern depending on the end-goal: the index finger tended to move away from the surface of the stimulus during the more demanding condition (i.e., pouring compared to moving). This strategy possibly allows for greater control (stabilizing mechanism) when stimulus dynamics become increasingly difficult (see also Crajé et al., 2011). To some extent, the index finger can be regarded as a "navigator" during computation of a hand trajectory toward a target (Sartori et al., 2011; Ansuini et al., 2015). Careful placement of the digits driven by the index finger is considered a prerequisite for a stable grasp (Kinoshita et al., 1995; Santello and Soechting, 2000). The present results, showing a correlation between index finger muscular activity and kinematics, specifically occurring within the time window including the MGA, seem to indicate that maximum aperture is the crucial event leading to index finger modulation. Notably, here grip aperture is much more expanded during the WHG with respect to the PG (12.99 vs. 6.3 cm, respectively). The greater finger extension needed to perform the WHG, therefore, might signify that the index finger act as a "navigator" and this might be the key to understand why we found a correlation only for whole-hand actions. To conclude, these results seem to suggest that the index finger may play a crucial role in driving the grasp component of whole-hand prehensile actions.

Theoretical Implications

Over the past two decades, neuroscience research has largely modified the traditional view of the motor system. The simultaneous discovery of mirror neurons in the ventral premotor cortex of macaques (di Pellegrino et al., 1992) and the application of TMS to the human primary motor cortex (M1) during action observation (Fadiga et al., 1995) gave birth to the hypothesis of a neural system matching action observation and execution in humans as well as in monkeys. Nowadays, a considerable amount of data suggests that EMG responses in hand muscles recorded while an object is grasped exactly replicate the pattern of MEPs elicited by spTMS during action observation (e.g., Gangitano et al., 2001, 2004; Fadiga et al., 2005; De Stefani et al., 2013; Naish et al., 2014). So far, the combined TMS/MEP technique has taken research on the perception–action coupling mechanism a step further, producing original data with regard to the observation–execution matching system. Specifically, it has answered the questions of how and when observing another person's actions produces motor facilitation in an onlooker's corresponding muscles. In the light of this massive literature, the present data suggest a more cautious approach. In particular, the lack of correlation between MEPs and EMG and the poor sensitivity of ADM muscle must be taken into account in future studies.

CONCLUSION

The present results confirm and extend the existing literature on motor preparation and execution indicating that the considered measures reliably distinguish between precision and whole-hand grasping actions. Moreover, significant correlations suggest a crosstalk between the muscular activation and the temporal unfolding of hand shaping. These findings offer new insights regarding the organization of reach-to-grasp movements and might have relevant translational implications on the literature concerning motor preparation and action execution.

AUTHOR CONTRIBUTIONS

SB and LS designed the study. SB, GZ, and SG collected, analyzed, and interpreted the data. SB, GZ, and LS wrote the manuscript. UC critically revised the manuscript.

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Musical Agency during Physical Exercise Decreases Pain

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Objectives: When physical exercise is systematically coupled to music production, exercisers experience improvements in mood, reductions in perceived effort, and enhanced muscular efficiency. The physiology underlying these positive effects remains unknown. Here we approached the investigation of how such musical agency may stimulate the release of endogenous opioids indirectly with a pain threshold paradigm.

Design: In a cross-over design we tested the opioid-hypothesis with an indirect measure, comparing the pain tolerance of 22 participants following exercise with or without musical agency.

Method: Physical exercise was coupled to music by integrating weight-training machines with sensors that control music-synthesis in real time. Pain tolerance was measured as withdrawal time in a cold pressor test.

Results: On average, participants tolerated cold pain for ~5 s longer following exercise sessions with musical agency. Musical agency explained 25% of the variance in cold pressor test withdrawal times after factoring out individual differences in general pain sensitivity.

Conclusions: This result demonstrates a substantial pain reducing effect of musical agency in combination with physical exercise, probably due to stimulation of endogenous opioid mechanisms. This has implications for exercise endurance, both in sports and a multitude of rehabilitative therapies in which physical exercise is effective but painful.

Keywords: pain, musical agency, cold pressor test, endurance, sport, endorphin

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INTRODUCTION

Musical Agency

Control over musical sound (musical agency) is experienced by singers and musicians on a regular basis during music performance. Such experience of agency in music seems to be perceived as highly relevant to the performers, who are highly capable of recognizing their own performances at later time points (Repp and Knoblich, 2004; Keller et al., 2007; Repp and Keller, 2010; Sevdalis and Keller, 2014). Non-musicians, however, can also experience musical agency, especially when the "musical instruments" are appropriately adapted to their capabilities.

Jymmin-Paradigm

In a paradigm using weight training machines with musical feedback, muscular effort can be closely coupled to musical sound, giving any participant the opportunity to experience a possibility for musical expression and the broad range of positive psychological and physiological effects that follow (Fritz et al., 2013a,b, 2015). This approach, dubbed *Jymmin* (gym + jammin), combines exercise machines designed for weight training with sensors to control music production software in real time. Integrating exercise and musical agency in this way stimulates improvements in mood, reductions in perceived effort, and enhanced muscular efficiency compared to control conditions where participants engaged in the same exercises but without their movements affecting the music (Fritz et al., 2013a,b). On a physiological level, the positive effects of this intervention on mood (as measured on mood subscale of the Multidimensional Mood Questionnaire Steyer et al., 1997) may result from a release of endogenous opioids in the central nervous system.

Opioids and Pain Sensitivity

Physical exercise is known to be an effective trigger of opioid activity (Sforzo, 1989; Droste et al., 1991; Goldfarb and Jamurtas, 1997; Boecker et al., 2008), which has also been implicated in mediating improved mood and decreased pain sensitivity when listening to/participating in music (Västfjäll, 2001; Dunbar et al., 2012; Roy et al., 2012). With regard to hypoalgesic effects of physical exercise, previous meta-analytic data from healthy participants suggested that isometric exercise over durations ≥ 5 min can have large effects on pain sensitivity ($d = 1.74$; $SD = 0.75$; Naugle et al., 2012). Because there is also a relation of endorphin levels and grooming in non-human primates, it has been suggested that music-making may represent a form of social interaction that allows for expansion of cohesive groups beyond the limits imposed by the requirements of one-to-one grooming interactions thus for example facilitating bonding even in large choirs (Weinstein et al., 2016).

The previously observed effects of Jymmin on mood give rise to the hypothesis that temporal coupling between muscular effort and musical sound is a particularly effective trigger for the release of endogenous opioids, highlighting the potential utility of musical agency in sports endurance and rehabilitative therapy.

Assessment of endogenous opioids in the central nervous system is complicated by the fact that they do not easily cross the blood brain barrier (Dearman and Francis, 1983; Kalin and Loevinger, 1983). Existing methods for direct measurement are highly invasive, requiring intravenous injection of radioactive tracers or the extraction of cerebrospinal fluid (Hosobuchi et al., 1979; Boecker et al., 2008). Here we use pain sensitivity as a proxy for central opioid levels. This approach is common in human behavioral research (Zillmann et al., 1993; Depue and Morrone-Strupinsky, 2005; Cohen et al., 2010; Dunbar et al., 2012) and supported by the link between analgesia and opioids in medicine (Mayer and Hayes, 1975; Hosobuchi et al., 1979; Bandura et al., 1987; Fields, 2000; Zubieta et al., 2001, 2003).

Inter-individual variability in experimentally determined pain sensitivity has been shown to be substantial (Dionne et al., 2005; Fillingim, 2005). Medical studies of chronic opioid abuse have shown that down-regulation of the endogenous opioid system (mu receptors) can result in increased pain sensitivity (hyperalgesia), as well as painful responses to normally non-painful stimuli (allodynia)(Sprouse-Blum et al., 2010). These results imply that individual pain sensitivity relates to the activity and regulation of endogenous opioids, modulating the effects of endorphin release, such that increased pain sensitivity is associated with decreases in hypoalgesic effects of endorphin. Because inter-individual variability in baseline pain sensitivity can be substantial, it is critical to consider this important source of variation in pain research (Dionne et al., 2005; Fillingim, 2005).

An approximation of individual pain sensitivity can be achieved with the Pain Sensitivity Questionnaire (PSQ). It is a self-rating instrument that involves making pain intensity ratings of daily life situations (Ruscheweyh et al., 2009). It includes two sub-scores, one based on items referring to mildly painful situations (the PSW-minor), and one based on items referring to moderately painful situations (the PSQ-moderate). Correlations between PSQ scores and ratings of experimentally induced pain are highest for the PSQ-minor score, indicating that it is a better predictor of individual pain sensitivity than either the PSQ-moderate or PSQ-total (perhaps because mildly painful situations are perceived to be manageable). The PSQ may thus be reduced to the PSQ-minor items without losing relevant information (Ruscheweyh et al., 2009, 2012).

Relevance of Study, Research Questions

In the context of the present study, it is important to note that regardless of the precise mechanism underlying changes in pain sensitivity, it is clear that a method to systematically reduce pain associated with physical exercise would be of high medical relevance, with applications ranging from sports medicine to the prevention of injury and rehabilitation in non-athletes. Indeed, patients suffering from various forms of physical injury and/or neural disorders, as well as many elderly often display activity avoidance, rejecting highly effective physical exercise therapy because for them it is painful (Geisser et al., 2000; Mannerkorpi and Iversen, 2003; Crombie et al., 2004).

Here we investigated an influence of musical agency during physical exercise on pain threshold. We hypothesized that the pain threshold is heightened after performing physical exercise with musical agency as compared to the same type of physical exercise performance with passive music listening. We tested this hypothesis in a cross-over design in which every participant performed both, the experimental and control condition.

MATERIALS AND METHODS

Participants

Twenty-two healthy human participants took part in this study (12 female; mean age = 25 years; age range = 21–29; $SD = 2.41$). None of the participants had mental or motor disorders, and none had a history of cardiovascular disease or chronic pain based on self-report. Exclusion criteria also included professional musicians, athletes or body builders. Participants were run in pairs. The association of participants into pairs was random, and an examination of influences of gender was not addressed in the current study. Participants received monetary compensation after completion of the second-day of the experiment. Ethical approval was obtained from the Ethics Committee of the University of Leipzig, and the experiment was carried out in accordance with the guidelines of the local institutional review board at the University of Leipzig. Informed consent was obtained from all participants after explanation of the experiment and the risks involved in participation. Participants were also made aware that they could withdraw from the study at any time without further consequences.

Three of the 22 participants were excluded from the analysis because they either did not show up for the second session, the cooling-system for the cold pressor task failed, or they completed the cold pressor test without reporting pain. One participant (whose partner did not turn up on the second day) had to perform with a substitute partner [with the same gender (female) as the original partner and within the age range of the participant group] allowing us to retain her data in the analysis. Accordingly, the statistical analysis included 19 participants (10 male; mean age = 25.11 years; age range = 21–29; *SD* = 2.45).

Experimental Design

Participants worked out in groups of two (randomly assigned to group, no prior relationship). Each pair participated in two experimental conditions in a within-subjects design. Both conditions involved operating exercise machines while listening to music, followed by administration of a CPT. In the *agency* condition exercise movements controlled the music. In the *no-agency* condition exercise movements did not control the music, which was instead a recording of the *agency* condition of a different participant pair (with the exception of the first pair, who listened to a recording of their own *agency* condition in the *no-agency* condition). Each condition was run in a separate session on a separate day with at least one night and maximum of nine nights between sessions. The order in which participants performed the conditions was counterbalanced across pairs (allocation ratio 1:1). In addition to controlling for traditional order effects, this counterbalancing was also aimed at controlling for potential biases in pain sensitivity based on having previous experience with the CPT. All experimental data were acquired within 2 weeks.

Musical Feedback Equipment

Two physical exercise machines were used in this study, a cable lat pulldown machine and an abdominal trainer, both of which have been used in previous music feedback studies with a similar paradigm (Fritz et al., 2013a,b, 2015). These standard fitness machines allow for guided movements designed to train specific muscle groups. The cable lat pulldown machine consisted of a metal bar attached via cable and pulley to an adjustable weight stack that was moved vertically. Using an underhand (supinated) grip, participants pulled the metal bar down to lift the stack, bilaterally training the latissimi dorsi and biceps muscles. Hypoalgesic effects of biceps training has been described previously (Naugle et al., 2012). The abdominal trainer used the participant's own body mass as resistance to a "sit-up" motion designed to train the abdominal muscles. Because previous work suggested that participants were quickly exhausted by this exercise, they were allowed to use their arms for assistance via a semi-circular handle attached to the machine's backrest. Nevertheless, it was not possible to execute the sit-up motion without abdominal engagement. Sensors placed on the weight stack on the lat-pulldown and on the back support of the abdominal trainer transduced their configuration into digital signals used to manipulate music under the control of computer software (Ableton Live 8$^{\text{TM}}$; see **Figure 1**). Movement related weight shift parameters during both the experimental condition (musical feedback) and control condition were monitored and recorded.

Music

The music consisted of a set of synchronized repeating musical loops at a tempo of 130 beats per minute, which in previous experiments was perceived as appropriate for physical exercise by participants (Fritz et al., 2013a,b, 2015). The music consisted of a simple 4:4 drum beat (bass drum, hi-hat, and cymbals), a bass line (electric bass guitar), and a continuously fluctuating melody line (synthesizer) that could be varied in pitch. In the *agency* condition (described below), the movements of each machine were mapped to modulate different acoustic parameters. The pull-down machine controlled the cutoff frequencies of bandpass filters on the drum beat and bass line loops such that the more the bar was pulled down, the more the frequencies in the higher part of the spectrum were audible (an effect typically used by disc jockeys to modify sound spectra). The abdominal trainer controlled the pitch of the melody line such that more abdominal engagement resulted in synthesizer sounds with higher pitch. These effects were calibrated so that audible changes in the music

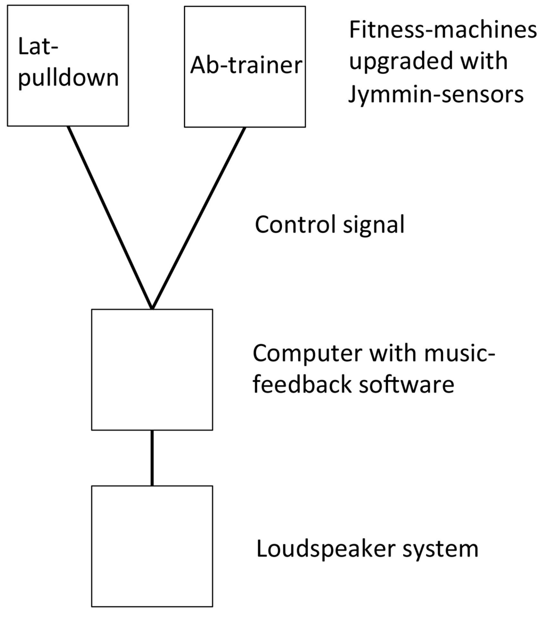

FIGURE 1 | Schematic illustration of experimental setup.

could be created along the entire movement range. Audio was presented over loudspeakers in both conditions (amplitude = ~65 dBA). The non-agency condition included music recordings from the agency conditions of other participants (except the first group who listened to a music piece performed during their own agency condition), which could not be modified by participants. This was done to avoid that effects could be due to different basic acoustical features of the music during the agency and non-agency conditions.

Recently it was shown that physical exertion by participants in music making results in a positive perceptual bias that increases the aesthetic quality of music (the "band effect"; Fritz et al., 2016). It is thus reasonable to assume that, in the context of this exercise-based music experiment, participants perceived the musical feedback compositions as rather enjoyable and motivational. Note that previously conducted experiments with a similar design (Fritz et al., 2013a,b, 2015, 2016) used similar parameters with respect to tempo (130 bpm), beat (4:4), and instrumentation (which included drums, bass line). While these parameters could certainly be varied, we decided to keep them consistent with those used in previous studies.

Cold Pressor Test (CPT)

Pain tolerance was measured using the cold pressor test (Turk et al., 1984; Hsieh et al., 2010). In this test, participants placed their non-dominant hand and lower arm into cold water for as long as they could tolerate it. The time until withdrawal was used as a measure of pain tolerance. Water entry and withdrawal times were recorded with a stopwatch (values rounded to the nearest hundredth of a second). Accuracy was facilitated by a mechanical lever in the water that responded to the weight of a participant's hand by producing a clear visual signal. To prevent tissue damage, the CPT was always stopped after 5 min. The test apparatus itself consisted of a water tank with a built-in refrigeration unit that was adjusted to cool the water to 2°C. Water temperature was measured immediately after the procedure to account for the temperature variations that occur as a result of the cooling process (which uses a thermostat to switch water cooling on and off) as well as changes caused by the procedure itself (e.g., warming of the water caused by the temperature and surface area of the submerged limb).

Pain Sensitivity Questionnaire

Individual differences in sensitivity to pain in everyday life were assessed using the Pain-Sensitivity-Questionnaire (PSQ; Ruscheweyh et al., 2009). The PSQ consists of 17 items (14 pain related and 3 non-pain related), each comprised of a statement describing a painful situation (e.g., pricking your fingertip on a thorn), followed by a rating of projected pain intensity on an eleven-point scale (ranging from 0 "no pain at all" to 10 "most severe pain imaginable"). The PSQ consists of two subscales, the PSQ-minor and the PSQ-moderate, which divide the items into those describing mildly painful (mean rating <4) and moderately painful situations (mean rating 4–6). PSQ scores have been shown to have high internal consistency and are independent of age and gender (Ruscheweyh et al., 2009).

Procedure

Upon arrival at the lab (Max Planck for Human Cognitive and Brain Sciences) for the first session, each participant pair was given a brief description of the procedure during the study before providing written informed consent. The description included that they would perform physical workouts in two sessions, each with a duration of 10 min, and that they could abort the experiment at any time if they felt unwell. They were then allowed to test the fitness machines (without music) to decide who would use which machine. The machines were placed facing each other so that the participants could see each other during the exercise. For the lat-pulldown machine the participant could decide how much weight, 10 or 15 kg, felt comfortable—this was a procedure that in previous studies was successfully used to individually adapt the workout to differences in muscle strength between participants (Fritz et al., 2013a,b, 2016). Participants were required to use the same machine and the same amount of weight in both conditions. The experimenter demonstrated how to use the machines safely, and in the *agency* condition also briefly showed how the movements were mapped to the musical sounds. The participants then exercised using the machines for 10 min. Although this type of exercise is somewhat uncommon, in previous experiments it has been successfully applied to evoke positive psychological and physiological effects in participants (Fritz et al., 2013a,b, 2016). It has furthermore been argued that when associated with musical feedback it may constitute a more healthy fitness machine workout (Fritz, 2017). Immediately following completion of the exercise, participants were taken one at a time into a separate room for CPT administration. The order in which the members of each pair took the CPT was the same for both conditions. Following completion of the CPT in the first session, participants completed the PSQ. The choice to administer the PSQ at the end of the session as opposed to the beginning was made because we wanted to avoid any potential include of participant's reflecting on painful situations on their behavior in the CPT.

Data Analysis

CPT: The CPT data were analyzed using SPSS (version 22). A two-tailed independent samples t-test with the water temperature values after the *agency* and *no-agency* conditions was calculated to examine the possibility of significant differences between conditions. An analysis of covariance (ANCOVA) was performed to compare pain sensitivity between the *agency* and *no-agency* conditions (repeated measures). The PSQ-minor scores were included as a covariate in this analysis because of their previously established relationship to experimental pain ratings, and because individual differences in pain sensitivity are likely to modulate the hypoalgesic effects of with exercise through differences in the activity and effects of endogenous opioid systems (see Introduction). Gender and the order of conditions were also included in the model as between-subjects factors. Data were not included in the statistical analysis if participants did not participate in the second experimental session (on the second day), the cooling-system for the cold pressor task failed, or they completed the cold pressor test without reporting pain (to prevent tissue damage the CPT was stopped after 5 min).

Movement Data

Movement related weight shift data was extracted from the MIDI signals produced by the physical exercise machines. For each 10 min exercise session, an array of weight shift data comprising values between 0.00 and 1.00 (corresponding to the MIDI value range of 1–127), and timestamps between 0 s and 600 s (10 min) was recorded with a temporal resolution of 265.6 samples per second.

The total distance of how much the respective weight on each machine was shifted was calculated with the formula:

$$\sum_{n=1}^{v_{max}} |v_{n-1} - v_n|$$

where the parameter v corresponds to weight position (0.00–1.00). Weight shift distance here is an abstract value and without unit. Weight shift distance was compared between the *agency* and *no-agency* conditions for each participant.

RESULTS

Three of the 22 participants were excluded from the analysis (see Methods/Participants). Accordingly, the statistical analysis included 19 participants (10 male; mean age = 25.11 years; age range = 21–29; $SD = 2.45$).

Pain Tolerance

The results of the pain tolerance assessments following the *agency* and *no- agency* conditions are shown in **Figure 2**. On average, participants tolerated cold stimulation for 45 s following the *no-agency* condition ($SD = 24$) and 50 s following the musical *agency* condition ($SD = 26$ s). Comparison of individual pain tolerance scores with the results of the PSQ showed a significant correlation with the PSQ-minor subscale scores ($r = -0.505$, $p = 0.027$). The difference in pain tolerance between the *agency* and *no-agency* conditions was thus assessed for statistical significance using a repeated measures ANCOVA, in which PSQ-minor scores were included as a covariate. Gender and the order of conditions were also included in the model as between-subjects factors. The results showed significant effects of musical agency [$F_{(1,\,13)} = 5.974$, $p = 0.028$, $\eta^2 = 0.250$] and PSQ-minor score [$F_{(1,\,13)} = 4.652$, $p = 0.049$, $\eta^2 = 0.236$] on pain tolerance. This indicates that 23.6% of the total variance in pain tolerance was explained by participants' baseline pain sensitivity (as assessed by the PSQ-minor), and 25.0% of the residual variance was explained by the experimental manipulation of musical agency, with higher pain tolerance following the agency condition. Neither gender nor the order of conditions had significant effects on pain tolerance [$F_{(1,\,13)} = 0.087$, $p = 0.772$; and $F_{(1,\,13)} = 0.029$; $p = 0.867$ respectively].

Movement Data

Movement related weight shift data were analyzed separately for the two different exercise machines, the abdominal trainer and lat-pulldown machine. Average weight shift distance for the abdominal trainer was slightly higher in the *no-agency* condition than in the *agency* condition ($N = 10$, mean = 165.07, $SD = 60.01$; and $N = 11$, mean = 118.24, $SD = 56.04$ respectively), but this difference was not significant [$t_{(19)} = -1.849$, $p = 0.080$ (two-tailed), 95% CI = (−99.83, 6.17)]. For the lat-pulldown machine, however, average weight shift distance was determined to be significantly greater in the *no-agency* compared to *agency* condition [$N = 11$, mean = 85.88, $SD = 57.09$; and $N = 10$, mean = 194.81, $SD = 74.55$ respectively; $t_{(19)} = -3.781$, $p = 0.001$ (two-tailed), 95% CI = (−169.23, −48.62)].

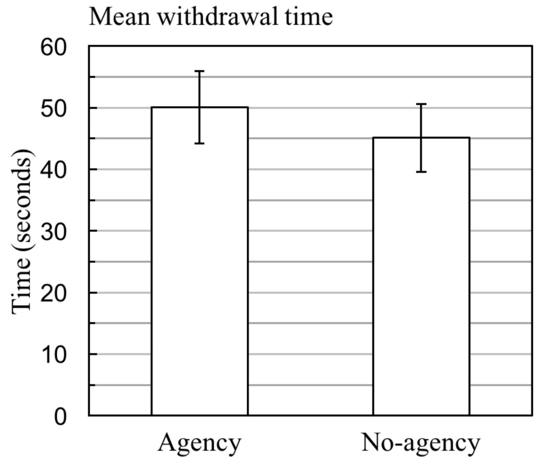

FIGURE 2 | Pain tolerance following exercise with and without musical agency. Mean withdrawal times following exercise with and without musical agency (error bars represent ± SE). Statistical significance was assessed by the ANCOVA described in the main text. In the final sample, 13 out of the 19 participants started with the musical *agency* condition.

Water Temperature

The two-tailed independent samples t-test with temperature values after the *agency* and *no-agency* conditions showed a significant difference [$t_{(32)} = -3.049$, $p < 0.005$, 95% CI = (−1.28, −0.25)]. Closer inspection showed that the mean water temperature in the CPTs was lower after the *agency* (*mean* = 1.56°C, $SD = 0.81$) than the *no-agency* condition (*mean* = 2.33°C, $SD = 0.65$).

DISCUSSION

The results of this experiment demonstrate that systematically coupling physical exercise to music making enhances pain tolerance compared to physical exercise while simply listening to music. While passive music listening has previously been shown to have the capacity to already increase pain tolerance, we here show a greater effect of active musical engagement that is specific to having agency over sound. The CPT withdrawal times and the PSQ-minor results corroborated each other in that participants who tolerated the cold water for longer durations also tended to rate questionnaire items as less painful. Factoring the PSQ-minor results into the analysis of CPT withdrawal times allowed us to separate variance attributable to individual differences in generalized baseline pain sensitivity from variance attributable to the experimental manipulation of musical agency. Results suggest that in participants with high baseline pain tolerance, the analgesic effects of the intervention have a greater positive impact, and could therefore in such individuals more strongly ameliorate quality of life and to avoiding the development of chronic pain. Given that individuals who cite pain as a barrier to do physical workout will likely have low baseline pain tolerance, it remains to be examined in training studies with a longer horizon if they can derive a benefit from the intervention.

Amount of physical activity (workload) has previously been shown to be positively correlated with CPT withdrawal times, probably due to a greater release of endorphins in conditions with greater physical exertion (Sforzo, 1989; Droste et al., 1991; Goldfarb and Jamurtas, 1997; Boecker et al., 2008). In the current experiment, workload (assessed terms of weight shift distance) was determined to be significantly greater in the *no-agency* condition, although only significantly so for the lat-pulldown machine. Critically, this indicates that the longer CPT withdrawal times associated with the musical agency condition are unlikely to be explained as the result of higher exertion levels stimulating greater opioid release. On the contrary, the longer CPT times following the *agency* condition appear to have occurred despite lower levels of exertion. This provides strong evidence that the combination of physical exercise with musical feedback is highly effective in stimulating hypoalgesia, and does so beyond physical exercise with passive music listening. The current data furthermore support previous findings suggesting that biceps training can have hypoalgesic effects (Naugle et al., 2012), and for the first time provide evidence that abdominal training can have a hypoalgesic effect.

Movement measurements showed that for the lat-pulldown machine average weight shift distance was greater in the *no-agency* compared to *agency* condition. This corresponds to the more stereotypical movement pattern exhibited by the performers during the no-agency condition, which has been shown to comprise a greater degree of isotonic movement and a smaller degree of isometric movement than in the agency condition (Fritz et al., 2013a).

Temperature measurements showed that the water was significantly colder after the CPT in the *agency* compared to *no-agency* condition (by -0.77°C). This could be due to temperature variations resulting from the nature of the cooling process (which entailed a thermostat switching water cooling on and off), or because the limbs of participants in the *no-agency* condition were at a higher temperature than those in the *agency* condition as a result of higher exertion levels. Regardless of the cause of this difference, it has been shown that even small differences in water temperature can have large effects on pain intensity and pain tolerance such that lower temperatures result in higher pain intensity and lower tolerance (Mitchell et al., 2004). Critically, the temperature data provide no support for the possibility that the longer CPT withdrawal times associated with the *agency* condition here can be explained by colder water. In fact, it is more likely that the opposite is true. Despite the water temperature being lower after the *agency* condition, which one would expect to result in greater pain intensity and lower tolerance, the opposite was the case: participants after *agency* actually remained in the water for longer.

Given the medical link between opioids and analgesia (Zubieta et al., 2001, 2003; Hsu et al., 2013), as well as the invasive and ethically more problematic nature of procedures for measuring endogenous opioid activity directly (e.g., PET scanning or lumbar puncture; Weinstein et al., 2016), measures of pain sensitivity have become a common proxy in human behavioral research (Cohen et al., 2010; Dunbar et al., 2011). Nevertheless, it is important to emphasize that although the enhancement of pain tolerance following exercise with musical agency suggests a role for endogenous opioids mechanisms in mediating the positive effects of musical agency, caution is warranted regarding this interpretation because opioid activity was not directly observed or manipulated. There are non-opioidergic mechanisms through which analgesia can arise (Bandura et al., 1987; Hebbes and Lambert, 2013) and the perception of pain is also mediated by a host of contextual factors, including attention, motivation, expectation, and emotional state (Fields, 2000; Rainville, 2002; Mannion et al., 2007; Wiech et al., 2008).

Beyond these remaining mechanistic questions, however, the fact that musical agency can be applied to reduce pain associated with physical exercise has immediate consequences for sports medicine as well as clinical injury prevention and rehabilitation. In many cases, physical exercise is the most effective form of treatment for patients suffering from physical injury (e.g., musculoskeletal damage, burn damage, and recovery after surgery) as well as neurological damage/disorders (e.g., stroke, spinal cord injury, fibromyalgia and chronic pain). In such cases exercise restores strength, increases range of motion and improves quality of life (Mior, 2001; Edgar and Brereton, 2004; Jacobs and Nash, 2004; Kwakkel et al., 2004; Houglum, 2010; Busch et al., 2011; Kroll, 2015). But pain can present a significant obstacle to the success of physical exercise rehabilitation, increasing negative affect and decreasing patient motivation (Jack et al., 2010). The capacity of musical agency to reduce pain, reduce sense of exertion (Fritz et al., 2013a) and improve mood (Fritz et al., 2013b) is thus likely to increase patient motivation and commitment, ultimately contributing to rehabilitation success. Secondary benefits include a decreased requirement for external encouragement and supervision and increased therapeutic efficiency. Musical feedback provides real-time encouragement, guiding the attention of patients toward targeted muscles and movements, increasing efficiency (Fritz et al., 2013a) and potentially facilitating the recovery of optimal control at the neuromuscular level. Finally, musical feedback technology is flexible and cost-effective (given that it can be used without constant supervision by a therapist). The only requirements are a computer, music production software, position sensors, and standard exercise equipment.

A limitation to the current study is that the age range investigated in the present study is not representative of the age range most relevant in the rehabilitation context. Further experiments may investigate if similar results can be found in a cohort of elder participants. Another limitation to the current study may be that strictly speaking we have investigated pain sensitivity immediately after the sports workout, and not during the sports workout. However, in a rehabilitation context where participants may experience pain due to physical training, it would be most relevant to quantify pain levels during the fitness workout. Tests during workouts are problematic, however, because attention to task performance is likely to be a confounding parameter. Another potential limitation is that we did not assess differences in how the participants in our study generally respond to music and/or use music during exercise. Note, however, that because the music was similar in both conditions, differences in individual response to music are unlikely to have been a confounding factor. Furthermore, it would be interesting to assess how much control each individual perceives to have over the music during the *agency* condition, and how this relates to the magnitude of the observed effects. While the percept of control should always be higher during the *agency* condition, this may vary between individuals, for example in relation to their musical skills or auditory processing capabilities. In addition, in regard of literature on Self Determination Theory and autonomy (Deci and Ryan, 1985; Ryan and Deci, 2000) we have come to the conclusion that our classification of agency has to be regarded as rather rough. For future studies a more elaborate assessment of the Self-Determination Continuum will be beneficial, especially with respect to how much the activity is perceived as extrinsically or intrinsically motivated (Ryan and Deci, 2000). Note that participants were tested in pairs, and thus influenced the music together with their actions. Their physical exercising has accordingly been a joint action, such that the experimental situation had a social aspect, which was not systematically investigated in the current study, but may have had an important influence on the shift in pain sensitivity as a result of the musical agency condition. It is a limitation that the current experiment has an imbalance of order in which participants undertook the conditions. While counterbalancing in the planning and scheduling of the experiment was accurate, unreliability on behalf of several participants (who had to come in on several days to do different conditions) required an adaptation of testing schedule, creating the imbalance. We here also want to emphasize the necessity to use cold pressor equipment that ensures a highly precise constant temperature of circulating water, as has previously been argued (Mitchell et al., 2004). While it can be a challenge to precisely control for water temperature throughout the measurement procedure, especially when the time of CPT intervention is not flexible but has to be performed at exact time points (in the current study at the end of each physical exercise intervention). This is of essential importance because the effects of the *agency* condition on pain would have been irrevocably confounded if the water temperature had by chance turned out to have been lower after the control condition. Finally, because the current paradigm used recordings of the *agency* condition in the *no-agency* condition, the first group listened to the music they created in the agency condition twice. This is relevant because familiarity with music can lead to a greater appreciation of the same style of music (North and Hargreaves, 1995). Note, however, that this was only the case for the first pair of participants and that these participants (#1 and 2; see Supplementary Table 1) did not show striking differences such that in this group the difference between *agency* and *no-agency* were not smaller than in the other groups).

At a broader level, the positive effects of musical agency may be deeply rooted in human biology. Almost all cultures exhibit some form of movement coupled to music, typically in the context of ritual or celebration (McNeill, 1997; Brown and Jordania, 2013). On such occasions, music and dance can persist for many hours and in some cases even days (McNeill, 1997). Paradoxically, such experiences tend to be associated with euphoria rather than exhaustion, suggesting that they engage powerful neurophysiological mechanisms capable of modulating bodily perceptions, leading to greater physical endurance. Using Jymmin technology and musical agency in high performance sports has the potential to increase individual endurance, using it in clinical rehabilitation therapy has the potential to harness these mechanisms for patient health and well-being.

AUTHOR CONTRIBUTIONS

TF, LS, JG, and AV: Study design; AL and FH: Data acquisition; OC, LS, and EB: Analysis; TF and DB: Manuscript writing.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2017.02312/full#supplementary-material

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Conflict of Interest Statement: The Max Planck Society has applied for intellectual property for specific aspects of the Jymmin technology at the European and U.S. patent offices, and has registered Jymmin as a trademark.

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