



OPEN ACCESS

EDITED BY

Oxana Eschenko,
Max Planck Institute for Biological
Cybernetics, Germany

REVIEWED BY

Ahmed Khudhur,
University of Kirkuk, Iraq

*CORRESPONDENCE

Atsushi Yokoi
✉ ayokoi@nict.go.jp

RECEIVED 29 September 2025

ACCEPTED 10 October 2025

PUBLISHED 24 October 2025

CITATION

Yokoi A (2025) What can ANS signals tell us
about motor learning? An implication
for better assessment of cognitive
contribution to motor learning.
Front. Behav. Neurosci. 19:1715460.
doi: 10.3389/fnbeh.2025.1715460

COPYRIGHT

© 2025 Yokoi. This is an open-access article
distributed under the terms of the [Creative
Commons Attribution License \(CC BY\)](#). The
use, distribution or reproduction in other
forums is permitted, provided the original
author(s) and the copyright owner(s) are
credited and that the original publication in
this journal is cited, in accordance with
accepted academic practice. No use,
distribution or reproduction is permitted
which does not comply with these terms.

What can ANS signals tell us about motor learning? An implication for better assessment of cognitive contribution to motor learning

Atsushi Yokoi^{1,2*}

¹Center for Information and Neural Networks, Advanced ICT Research Institute, National Institute of Information and Communications Technology, Suita, Japan, ²Graduate School of Frontier Biosciences, Osaka University, Suita, Japan

Motor learning is supported by both explicit and implicit processes. A central question in the field of motor control is how these two processes interact and, critically, how each process can be assessed in an unbiased manner. In this perspective paper, we propose that the autonomic nervous system (ANS) offers an informative window into explicit cognitive processes during motor learning. We first briefly review studies outside the motor learning domain, where ANS activity has been linked to internal cognitive states such as surprise and uncertainty. We then discuss how these ANS-related states can be leveraged to assess the manifestation and influence of explicit processes during motor learning, as well as to explore cognitive computations that may involve central ANS activity, including contextual inference.

KEYWORDS

autonomic nervous system (ANS), cognitive, motor learning, explicit, implicit, cognitive contribution, contextual inference

Introduction

Motor learning is supported by both explicit and implicit forms of learning. While this statement seems self-evident when considering complex motor skills, such as playing a piano sonata, where explicit knowledge of musical notes, melody, and practice strategies (e.g., chunking) is important, it becomes less clear in the context of simpler motor tasks, like reaching to grasp a bottle of wine or hitting a ball with a racket. Although these actions remain complex from a biomechanical perspective, requiring coordination across multiple muscles and joints to move an end-effector from an initial to a target position in space, it is difficult to explicitly describe or implement control over each muscle, especially when accounting for complex multi-joint dynamics solving equations of motion (Hirashima et al., 2008; Kurtzer et al., 2008, 2009; Tanaka and Sejnowski, 2013). Moreover, adaptations to ongoing internal or external changes (e.g., muscle fatigue, or changes in the weight or shape of a tool) are handled almost entirely implicitly. Indeed, studies in amnesic patients have shown that learning of such tasks (e.g., pursuit rotor task, mirror drawing, reach adaptation) is preserved despite damage to the declarative memory system (Brooks and Baddeley, 1976;

Shadmehr et al., 1998; Squire, 2009), reinforcing the view that motor learning is fundamentally an implicit process. As a result, much of the field, particularly in computational motor neuroscience, has focused on implicit learning processes, using relatively simple, multi-joint tasks such as reaching as model behaviors (Shadmehr et al., 2010; Wolpert et al., 2011).

However, recent studies in the same field have increasingly emphasized the role of explicit cognitive processes in motor learning (Krakauer et al., 2019; Tsay et al., 2024). This growing body of research highlights that explicit learning mechanisms significantly contribute even to relatively simple motor tasks, such as reaching movements (Bond and Taylor, 2015; Krakauer et al., 2019; McDougle et al., 2016; Tsay et al., 2024). One form of explicit strategy appears at the level of action selection or decision-making, for instance, aiming deliberately away from a target to compensate for predictable external disturbances like visuomotor rotation (Taylor et al., 2014; Taylor and Ivry, 2012). A hallmark of such explicit adjustments is that they rapidly disappear once participants are instructed to stop using the strategy or detect that the perturbation is no longer present (Benson et al., 2011; Morehead et al., 2015). This stands in stark contrast to implicit learning, in which behavioral changes, such as shifts in reach direction, can persist even when participants are fully aware that the perturbation has been removed (Morehead et al., 2015; Shadmehr et al., 2010). Here, implicit learning is more like a gradual, experience-driven modification of low-level sensorimotor mappings (or internal forward models), rather than a deliberate adjustment of the movement goal itself. Thus, our tentative definition of explicit motor learning processes in the current paper is any adaptive behavioral change that does not fall into sensorimotor recalibration (change in internal model).

Given this, key questions now concern how to objectively quantify the contributions of each learning process to observed behavior, how explicit learning is initiated, and how explicit and implicit processes interact. Currently, the assessment of explicit learning component relies in large part on verbal report by participants (Bond and Taylor, 2015; McDougle et al., 2016; Miyamoto et al., 2020). Therefore, the most important issue is how to quantify explicit contributions without interfering with the learning process itself, as frequent reports during learning can bias participants' strategies (Maresch et al., 2021a,b). Relatedly, it is also not clear *a priori* that how much of explicit cognitive processes contributing to motor behavioral change is ready for verbalization. It is likely that the strategic re-aiming is one of many forms for explicit cognitive contribution in motor adaptation which work on top of the implicit sensorimotor recalibration. Some of them could be difficult to verbalize and other may express even without conscious awareness. Under such circumstances, there is the growing need for non-verbal methods to assess the cognitive contributions to motor learning.

In this perspective, we propose that the autonomic nervous system (ANS) may offer a promising window into explicit cognitive processes during motor learning. This is not to suggest that ANS activity serves as a direct readout of explicit learning components (e.g., aiming direction), but rather that it may reflect internal states that influence the deployment of such explicit strategies. A growing body of research in cognitive psychology and psychophysiology has used peripheral ANS indices, such as pupil diameter, skin conductance, and heart rate, to monitor participants

while they perform various cognitive tasks. These studies have yielded important insights into how both peripheral ANS signals and central ANS-related brain networks contribute to cognitive processes, including error detection, performance monitoring, action selection, and decision-making (Critchley, 2005; De Berker et al., 2016; Hajcak et al., 2003; Joshi and Gold, 2020; Nassar et al., 2012; Ullsperger et al., 2014; van der Wel and van Steenbergen, 2018; Zénon, 2019).

In the following section, we first briefly review studies outside the domain of motor learning, in which ANS activity has been linked to various internal states relevant to cognitive tasks. We also highlight ANS responses to conscious/unconscious errors. Next, we present findings from motor learning research that emphasize cognitive contributions even in seemingly simple actions like reaching movements and suggest similarity between motor and cognitive learning paradigms. Finally, we discuss how ANS-related internal states can be leveraged to assess the expression and influence of explicit processes during motor learning, as well as to explore common cognitive computations across cognitive and motor tasks that may engage central ANS mechanisms.

Autonomic nervous system activity reflects internal cognitive states

Beyond its well-known association with emotional states and threat responses (Canon, 1915; Roelofs and Dayan, 2022), ANS indices, such as pupil diameter and heart rate, have been widely used in cognitive psychology and neuroscience to probe internal state changes during non-motor (or minimally motor) cognitive tasks. For example, tasks involving mental arithmetic or working memory elicit sympathetic upregulation, reflected in increased pupil diameter (Ahern and Beatty, 1979; Beatty, 1982; Hess and Polt, 1964; Kahneman and Beatty, 1966), cardiovascular responses such as elevated heart rate and blood pressure, as well as heightened muscle sympathetic nerve activity (Anderson et al., 1987; Callister et al., 1992). These ANS responses tend to scale with the (presumably subjective) difficulty of the task, suggesting that they covary with cognitive effort (van der Wel and van Steenbergen, 2018).

Autonomic indices also respond to unexpected or unfamiliar events, reflecting their involvement in novelty detection and attentional or vigilance processes, often described as orienting responses (Sara and Bouret, 2012; Sokolov, 1990). For example, in oddball paradigms, where participants respond to or passively observe sequences of frequent and infrequent stimuli, pupil diameter and skin conductance responses (SCR) increase more strongly in response to infrequent (i.e., rare) stimuli (Bach et al., 2008; Friedman et al., 1973; Graham and Clifton, 1966; Hirano et al., 1994; Qiuyan et al., 1985), while heart rate shows deceleration. These effects often habituate with repeated stimulus presentation, highlighting the role of the ANS as an indicator of novelty detection. Particularly, the locus coeruleus (LC), one of subcortical autonomic centers, shows typical responses to novel stimuli/situations and also habituation in animals (Hervé-Minvielle and Sara, 1995; Vankov et al., 1995) and humans (Meissner et al., 2024; Murphy et al., 2014).

Related to stimulus unexpectedness, similar orienting-like ANS responses are also observed after participants made an error during various cognitive tasks, including increased pupil diameter, heightened skin conductance, and transient heart rate deceleration (Danev and de Winter, 1971; Di Gregorio et al., 2024; Hajcak et al., 2003; Maier et al., 2019; Murphy et al., 2016; Nassar et al., 2012; Preuschoff et al., 2011; Wessel et al., 2011). The post-error slowing (PES), an increase in response time after an error (Botvinick et al., 2001), and subsequent behavioral adjustments have been associated with these ANS responses, such that the magnitude of pupil dilation following an error correlates positively with PES and improved accuracy on subsequent trials (Maier et al., 2019; Murphy et al., 2016). Although this positive association between PES and post-error performance is not always observed (Wessel, 2017), error-related ANS responses likely form part of a broader performance monitoring system that coordinates post-error adjustments and behavioral control (Botvinick et al., 2001; Ullsperger et al., 2014; Wessel, 2017). An interesting topic in this context is that whether the ANS indices also respond to errors that does not reach conscious awareness. Although evidence is mixed, several studies have reported the modulation of ANS response by whether or not the participants were aware of the error (O'Connell et al., 2007; Wessel et al., 2011). Correspondingly, activity in the anterior insular cortex (AIC), one of cortical regions influencing autonomic regulation (Beissner et al., 2013), is known to be modulated by the error awareness (Klein et al., 2007; Ullsperger et al., 2010). Another recent report demonstrated that the pupil responds to novel stimulus transition pattern that participants were not aware of (Alamia et al., 2019). Although one needs to carefully interpret these results, as the definition of error (or surprise) varies across the studies, these results suggest the potential of ANS indices to probe into implicit error processing.

Building on prior work linking ANS indices to cognitive effort and orienting, more recent studies have interpreted ANS activity, particularly pupil dilation, through the lens of information theory (Zénon, 2019) and Bayesian inference frameworks that estimate hidden task or environmental states (De Berker et al., 2016; Nassar et al., 2012; O'Reilly et al., 2013; Preuschoff et al., 2011; Urai et al., 2017). For example, in decision-making and choice tasks, cue-evoked pupil dilation increases in response to both stimulus uncertainty (De Berker et al., 2016; Satterthwaite et al., 2007; Urai et al., 2017) and response uncertainty (Muller et al., 2019; Richer and Beatty, 1987), indicating that ANS activity may also reflect subjective uncertainty (Dayan and Yu, 2006; De Berker et al., 2016). Furthermore, the link between ANS indices (pupil diameter) and learning during value-based inference tasks has also been suggested. For example, Nassar et al. (2012) recorded pupil diameter while participants performed a predictive inference task in which they estimated the mean of noisy stimuli sampled from distributions that switched unpredictably. The authors developed a normative Bayesian model of belief updating that included two key latent variables: change-point probability and belief uncertainty. They found that tonic (baseline) pupil diameter correlated with belief uncertainty, while phasic outcome-evoked pupil dilation tracked the change-point probability. Notably, the learning rate (defined as the ratio of estimate update to prediction error) was jointly predicted by these two latent variables, and thus, by pupil measures. In short, large prediction errors indicate a likely change in the generative environment (i.e., distribution switch), leading

to increases in both change-point probability (indexed by phasic pupil dilation) and belief uncertainty (indexed by baseline pupil diameter), which together drive an adaptive increase in learning rate. Other studies have similarly suggested that ANS activity tracks hierarchical Bayesian inference processes in volatile environments (De Berker et al., 2016; Vincent et al., 2019).

Crucially, brain regions implicated in performance and conflict monitoring, cognitive flexibility, and hierarchical Bayesian inference, such as the anterior cingulate cortex (ACC) and anterior insula cortex (AIC), also exert strong regulatory influence on ANS activity (Beissner et al., 2013; Botvinick et al., 2001; Critchley, 2005; Critchley et al., 2003; Soltani and Izquierdo, 2019; Ullsperger et al., 2014). These cortical regions, including several subcortical structures like the amygdala and LC, are called the central autonomic network (CAN) (Beissner et al., 2013). These regions have been shown to encode unsigned prediction errors and uncertainty (or volatility) of task environment in human fMRI studies (Behrens et al., 2007; Critchley et al., 2001; Loued-Khenissi et al., 2020; Preuschoff et al., 2008; Singer et al., 2009). Thus, as a result, the peripheral ANS indices, such as pupil diameter, skin conductance and heart rate, can also reflect these variables. Of these ANS indices, pupil diameter is attracting increasing attention as an established peripheral indicator of central noradrenergic activity in the LC (Joshi et al., 2016; Joshi and Gold, 2020; Rajkowski et al., 1993). The LC–noradrenaline (NA) system has been extensively studied in relation to prefrontal attention (Arnsten et al., 2012; Sara, 2009), cognitive flexibility (Aston-Jones et al., 1994; Bouret and Sara, 2004; McBurney-Lin et al., 2022), novelty detection (Bouret and Sara, 2005; Hervé-Minvielle and Sara, 1995; Vankov et al., 1995), and memory formation and consolidation (Clewett et al., 2020, 2025; Clewett et al., 2018; Sara et al., 1999; Sara and Devauges, 1988; Strange et al., 2003; Strange and Dolan, 2004; Takeuchi et al., 2016). For instance, LC neurons increase their firing rates, mirroring increases in reaction time, when animals (re-)adapt to cue–reward contingency in reversal learning tasks (Aston-Jones et al., 1997). Similarly, increases in baseline pupil diameter have been shown to precede exploratory behavior in humans performing analogous tasks (Gilzenrat et al., 2010; Jepma and Nieuwenhuis, 2011). These body of evidence, thus, suggest the involvement of CAN in various cognitive functions.

Cognitive contribution during motor learning tasks

In the context of motor skill learning, such as sequential finger tapping, the relationship between explicit and implicit aspects of learning (e.g., declarative knowledge of the sequence versus implicit motor memory of finger transitions) has been extensively studied and debated (Abrahamse et al., 2013; Robertson, 2007; Verwey et al., 2010; Willingham et al., 1989). However, the role of explicit cognitive processes has received comparatively less attention in the domain of motor adaptation, such as goal-directed reaching movements (Shadmehr et al., 2010; Shadmehr and Krakauer, 2008; Wolpert, 2015; Wolpert et al., 2011). Although earlier work had suggested a contribution of cognitive factors in motor adaptation (Fernandez-Ruiz et al., 2011; Kagerer et al., 1997; Saijo and Gomi, 2010; Sakaguchi et al., 2001; Slachevsky et al., 2001, 2003; Taylor and

Ivry, 2012; Taylor and Thoroughman, 2007, 2008), it is only recently that the field has begun to explicitly isolate and characterize the role of explicit cognitive processes in adaptation paradigms (Bond and Taylor, 2015; McDougle et al., 2015; Taylor et al., 2014).

The core idea is that behavioral changes in response to novel environments, such as force fields or visuomotor rotations, cannot be fully explained by implicit adaptation (sensorimotor recalibration) alone, but instead include a sizable contribution from explicit processes, such as deliberately altering the aiming direction to counteract perceived errors (Jakobson and Goodale, 1989; Redding and Wallace, 2006). This perspective led researchers to directly ask participants to report their intended aiming location on each trial. The reported aim was then subtracted from the observed reach direction to estimate the contribution of implicit adaptation (Bond and Taylor, 2015; McDougle et al., 2015; Taylor et al., 2014). These studies revealed a characteristic pattern: an initial, transient rise and fall in deliberate aiming responses, followed by a gradual, sustained increase in implicit adaptation across repeated trials with perturbed feedback (Bond and Taylor, 2015; McDougle et al., 2015; Taylor et al., 2014).

A very similar pattern of transient rise and fall has also been observed in reaction time (RT) following the onset of a perturbation (Benson et al., 2011; Fernandez-Ruiz et al., 2011; Haith et al., 2015; Huberdeau et al., 2015). Importantly, such transient increases in RT are positively correlated with the use of deliberate strategies in motor adaptation tasks (Fernandez-Ruiz et al., 2011; McDougle et al., 2015). Furthermore, when participants are forced to initiate movements under strict time constraints, the explicit component of adaptation is diminished (Fernandez-Ruiz et al., 2011; Haith et al., 2015), supporting the link between RT increase and strategic involvement. Also, as described in the previous section, such increase in RT following an error reminds us of the PES (Botvinick et al., 2001; Hajcak et al., 2003; Murphy et al., 2016; Ullsperger et al., 2014), which possibly implies the involvement of similar cognitive control processes triggered by sudden increase in movement error.

Computationally, the trial-by-trial trajectory of explicit strategy use closely resembles the memory dynamics predicted by two-state state-space models of learning, which posit the coexistence of fast and slow learning systems with distinct learning and forgetting rates (Smith et al., 2006). Accordingly, the fast and slow processes have been mapped onto explicit strategy use and implicit learning, respectively (McDougle et al., 2015). Intriguingly, experimental manipulations that interfere cognitive processes, such as limiting reaction time or introducing dual-task interference resulted in selective impairment of the fast component (Haith et al., 2015; Keisler and Shadmehr, 2010), strengthening the view that fast cognitive learning system and slow implicit learning system coexist in motor adaptation. These results are in line with the observation that the patients with prefrontal damage show deficit in the strategy use and correctly describe (or notice) perturbations during visuomotor adaptation (Slachevsky et al., 2001, 2003), indicating the critical contribution of performance monitoring and cognitive control systems in motor adaptation tasks.

In terms of the interaction between the explicit and implicit motor learning systems, evidence suggests something like competitive cooperation. Although the two processes work together to compensate the error produced by perturbation (McDougle et al., 2015; Miyamoto et al., 2020; Taylor et al., 2014), a number of studies have suggested the suppression of the implicit

learning by the explicit process (Albert et al., 2022). For instance, a high reliance on explicit strategies may reduce the extent of implicit adaptation, as error-driven learning is attenuated when behavioral errors are actively corrected by cognitive means (Benson et al., 2011; Fernandez-Ruiz et al., 2011). Conversely, several studies have shown that implicit adaptation is enhanced when participants are unaware of the error or environmental change, for instance, when the perturbation is introduced gradually (Benson et al., 2011; Kagerer et al., 1997; Neville and Cressman, 2018; Sakaguchi et al., 2001). The exact mechanism behind such reciprocal interaction is still unclear.

Although directly asking participants to report their aiming direction on each trial initially appeared to be a simple yet effective approach for quantifying explicit learning process, recent work has raised concerns that such explicit commitment to reports may themselves influence the learning process. Indeed, several studies have demonstrated that the act of reporting can significantly bias the contribution of the explicit process (Maresch et al., 2021a; Maresch et al., 2021b), and that the standard subtraction method used to isolate implicit learning may not accurately capture the learning process (t Hart et al., 2024). In addition, it is not clear *a priori* that how much of cognitive processes contributing to motor behavioral change is accessible for conscious report. It is likely that the strategic re-aiming is one of many forms for explicit cognitive contribution in motor adaptation that work on top of the implicit sensorimotor recalibration. Some of them could be difficult to verbalize and other may express even without conscious awareness. Under such circumstances, there is the growing need for less biased, more ecologically valid methods to assess the cognitive contributions to motor learning (de Brouwer et al., 2018).

How can ANS be useful for motor learning research and what does it capture?

As discussed, a common trigger for both the ANS-indexed cognitive processes and the use of cognitive strategies in motor adaptation is presumably (un)conscious¹ detection of an error and its unexpectedness (surprise). Therefore, conceivably, the ANS responses to movement errors can provide informative markers of explicit cognitive processes during motor learning. Several recent studies have begun to test this hypothesis directly by measuring ANS indices during motor learning tasks (Nogami et al., 2025; O'Bryan and Song, 2025; Pfalz et al., 2025; Yokoi and Weiler, 2022). Consistent with the findings from cognitive inference tasks (e.g., Nassar et al., 2012), these studies suggest that phasic pupil dilation in response to movement errors reflects sensory surprise, while tonic (baseline) pupil diameter likely

1 As discussed in the previous section, several studies have reported ANS responses to errors show modulation by whether the participants were aware of the error. For LC and pupil, clear responses to noxious stimuli (e.g., foot shock) have been reported in anesthetized animals (Ohsawa et al., 1997; Sugiyama et al., 2012), suggesting that conscious detection may not always be required for some ANS responses. Therefore, there might be a continuum of this process between conscious and unconscious error detection. Nevertheless, it is certain that a large error elicits both of ANS responses and conscious awareness.

track subjective uncertainty about the task environment (Pfalz et al., 2025; Yokoi and Weiler, 2022). The study also suggested that the tonic pupil diameter may explain the degree to which individuals were aware of environmental change (Yokoi and Weiler, 2022). Additionally, a clear dose-dependency of phasic ANS responses (pupil dilation, skin conductance change, and heart rate deceleration) to different magnitudes of unexpected motor errors were demonstrated (Nogami et al., 2025). These observations strongly suggest that the large deviation from the expected sensory outcome leads to strong activation of ANS and implies the involvement of cognitive control process, possibly mediated by CAN, during motor learning tasks. Taken together, although still much research is needed, these findings underscore the potential of ANS measurements as non-invasive information source to study cognitive processes in human motor learning research.

What would be the “common cognitive processes” indexed by ANS activity for cognitive and motor learning tasks? In the rest of this perspective, we suggest that the contextual inference (Heald et al., 2023a; Heald et al., 2023b) would be one candidate for such cognitive computations. Contextual inference has gained increasing attention as a unifying computational principle that enables flexible behavior across domains. Rather than relying on fixed mappings between stimuli and responses, the brain appears to infer latent “contexts,” or hidden states of the environment, to appropriately guide perception and decision-making (Mante et al., 2013; Okazawa and Kiani, 2023), memory updating (Gershman et al., 2014), and motor control and learning (Heald et al., 2021). In the domain of motor learning, recent work by Heald et al. (2018, 2021) demonstrated that humans can learn and express multiple motor memories by inferring which context is currently active. This framework is powerful enough to account for a wide range of motor learning phenomena, including spontaneous recovery, interference, savings, dynamic learning rates, and the use of explicit strategies, that have been previously treated as distinct features (Heald et al., 2021). The creation and switching between multiple internal models based on the current context estimate is somewhat consistent with the reciprocal relationship between explicit strategy and implicit learning component, as well as the rapid disengagement of explicit strategy when instructed. Assuming the implicit learning system, presumably in the cerebellum, as a “base model” within this array of models (Oh and Schweighofer, 2019; Taylor and Ivry, 2014), could also explain the suppression of the implicit learning by explicit strategy (i.e., other model) through the process of context-dependent expression/suppression of specific internal model.

Similar principles apply in cognition, where behavior depends on integrating current sensory input with beliefs about hidden environmental states and their transitions (Heald et al., 2023a). Computational models such as the Hierarchical Gaussian Filter (HGF) (Mathys et al., 2011, 2014), the Volatile Kalman Filter (VKF) (Piray and Daw, 2020), and the Dirichlet Process Kalman Filter (DP-KF) (Gershman et al., 2014) formalize this process by representing beliefs not only about the current state but also about the latent state as well as its volatility, enabling dynamic modulation of learning rates and behavioral flexibility. Despite differences in implementation across these models, the problems of hierarchical inference they aim to solve are highly similar, making the contextual inference framework a potential candidate for a domain-general computational principle in the brain. Also important is that in

the absence of *a priori* sensory cues that indicate specific context, the (large) prediction error is the critical cue for context change, making room for ANS to take part in this process.

Crucially, as discussed in the previous section, several key regions of the central autonomic network (CAN) (Beissner et al., 2013), including the ACC, AIC, orbitofrontal cortex (OFC), and the LC, are consistently implicated in higher-order processes such as the computation of prediction errors (i.e., surprise), uncertainty, and state transitions (Aston-Jones and Cohen, 2005; Behrens et al., 2007; Chan et al., 2021; Critchley et al., 2001; Preuschoff et al., 2008; Schuck et al., 2016; Singer et al., 2009; Soltani and Izquierdo, 2019). As repeatedly proposed (Bouret and Sara, 2005; Sara, 2009; Sara and Bouret, 2012), the LC is well-positioned to receive surprise and uncertainty signals from CAN areas and broadcast interrupt signals to multiple systems across the brain, including the hippocampus and cerebellum. The LC receives input from medial prefrontal regions such as the ACC and subcortical structures like the amygdala, and projects broadly, including to the hippocampus (Joshi and Gold, 2020; Szabadi, 2013), making it a core node for complex hidden-state learning, such as estimating environmental changes (De Berker et al., 2016; Nassar et al., 2012) or identifying episodic memory boundaries, through the hippocampus (Clewett et al., 2020, 2025). While several researchers have studied the effect of LC projection (NA) on motor learning in rodents (Heron et al., 1996; Tan et al., 1991; Watson and McElligott, 1984), a clear mechanistic view of how LC-NA system affects motor learning is still missing (Waterhouse et al., 2022).

Taken together, these bodies of evidence suggest that the CAN may support computations essential for contextual inference across cognitive and motor domains. By continuously integrating external sensory input with internal belief states, these regions enable the brain to form predictions about latent environmental structures and adjust behavior accordingly. Thus, ANS indices may offer an informative window into latent computational variables relevant to the contextual inference process in both cognitive and motor learning. In this context, revisiting prior ANS findings through the lens of the Bayesian contextual inference framework may be fruitful (Zénon, 2019).

Conclusion and future directions

In this perspective, we have provided a brief overview of studies investigating ANS-tagged internal states during cognitive tasks and suggested their possible link to recent evidence for cognitive contributions to motor adaptation. While the proposed similarity may initially appear superficial, the concurrent rise of hierarchical inference models in both cognitive and motor neuroscience suggests that similar computational processes operate across these domains. As one of such cognitive computational processes, we further suggested that the framework of contextual inference may provide a unifying perspective to understand learning in both fields, which emphasizes conscious error detection, inference about latent task states, and selection of appropriate actions based on inferred context. The overlap between CAN and brain regions involved in hierarchical inference process further highlights the importance of ANS signals to probe these processes. Thus, we propose that the ANS can be useful for motor learning study to look closer into such process.

Box 1 Experimental paradigms to probe autonomic contributions to context formation in motor learning.

The autonomic nervous system (ANS) may serve as a key interface linking cognitive and motor learning processes. We propose that *the formation of context boundaries and the creation of new motor memories depend on ANS-tagged novelty or surprise signals*. To test this “ANS–context–motor” hypothesis, coordinated efforts across human and animal studies are essential.

Human paradigms

Although invasive neural manipulation in humans is limited, behavioral flexibility enables systematic examination of how autonomic arousal relates to context transitions during motor learning. Forward- and back-translation of paradigms, such as reach adaptation involving contextual inference, and reversal learning, allow quantification of how trial-by-trial changes in ANS activity accompany the emergence of new internal models. Causal manipulations of autonomic state are accessible through physiological means (e.g., cold pressor test (Antov et al., 2015), isometric handgrip), pharmacological modulation of adrenergic or cholinergic tone (Jepma et al., 2016, 2018), transcutaneous vagus nerve stimulation (tVNS) (Kilgard et al., 2025), or voluntary biofeedback (e.g., pupil-size training) (Meissner et al., 2024). When combined with simultaneous ANS monitoring and non-invasive neural recordings (EEG, MEG, fMRI), these approaches can test whether autonomic activation precedes or gates neural signatures of context re-encoding.

Animal paradigms

In animal models, circuit-specific manipulation techniques (optogenetics, chemogenetics) allow causal probing of ANS–context interactions at cellular resolution. Motor learning tasks such as reach adaptation in rodents (Mathis et al., 2017) or marmosets (Ebina et al., 2018, 2024) provide quantitative readouts of boundary formation. AI-based kinematic tracking, such as the DeepLabCut (Nath et al., 2019) enables simultaneous assessment of movement adaptation and peripheral ANS signals, including contactless indices such as nasal temperature (Kuraoka and Nakamura, 2022; Nakayama et al., 2005). Direct autonomic manipulations, including pharmacological, implanted vagus nerve stimulation (Collins et al., 2021; Mridha et al., 2021), or locus coeruleus photostimulation (Glennon et al., 2019; Grimm et al., 2024; McBurney-Lin et al., 2022), can determine whether perturbing ANS-linked arousal circuits alters the delineation of motor contexts.

Cross-species integration

Aligning task structures and ANS metrics across species will reveal whether autonomic signals merely co-vary with, or actively define, the cognitive boundaries that segment motor memories.

As already mentioned, to what degree the consciously unperceived error and corresponding ANS responses have an impact on the above inference process is still elusive. Although, clearly, the size of prediction error is an essential factor for hierarchical inference, regardless of the awareness to the error (Gershman et al., 2014; Heald et al., 2021; Mathys et al., 2011; Piray and Daw, 2020), the role of conscious awareness and ANS states in the hierarchical inference about task environment needs to be tested in the future.

Another important future question is whether the ANS is mere a leaking signal of “higher” cognitive computational processes, or it has a bidirectional influence on the cognitive processes. Converging evidence suggests that within ANS the LC-NA system is “causally” involved in task performance. Rodent studies have shown that optogenetic LC activation can shift global cortical excitability in a stimulation specific manner (i.e., tonic or phasic) (Grimm et al., 2024) and improve cognitive flexibility (Glennon et al., 2019; McBurney-Lin et al., 2022). In parallel, human studies have also demonstrated that manipulation of pupil-linked arousal by task-unrelated surprisal stimuli influenced the learning rate in an inverted-U manner (Nassar et al., 2012) and that self-regulation of pupil-linked arousal through biofeedback affected oddball detection (Meissner et al., 2024). This line of evidence supports the idea that LC-NA system (and ANS) is functionally engaged in regulating cognitive functions, such as cognitive flexibility and novelty detection, rather than a simple readout of the control process. This is also critical to the question of how we can test the hypothetical relationship between cognitive contribution in motor learning (e.g., contextual inference) and ANS in more direct way (see Box 1). Also, although we did not cover the possibility of ANS directly affecting the implicit learning in the current manuscript, direct modulation of the cerebellar complex spike rate possibly through the noradrenergic input from the LC has been reported (Carey and Regehr, 2009; Sun et al., 2019). This topic is open for future research.

In summary, on top of its bodily functions, ANS signals could allow us to better understand flexible, adaptive human behavior in an uncertain world.

Data availability statement

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

Author contributions

AY: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing.

Funding

The author(s) declare financial support was received for the research and/or publication of this article. This work was supported by JSPS KAKENHI (JP22H03501 and JP23K24758) and JST FOREST Program (JPMJFR234Z) awarded to AY.

Acknowledgments

I thank Nobuhiro Hagura and Kagari Yamada for comments on the manuscript.

Conflict of interest

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

Generative AI statement

The author declares that Generative AI was used in the creation of this manuscript. Generative AI used exclusively for language editing. The output was reviewed by the author to ensure that it accurately convey the author's original intention.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of

artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

References

- Abrahamse, E. L., Ruitenberg, M. F. L., de Kleine, E., and Verwey, W. B. (2013). Control of automated behavior: Insights from the discrete sequence production task. *Front. Hum. Neurosci.* 7:82. doi: 10.3389/fnhum.2013.00082
- Ahern, S., and Beatty, J. (1979). Pupillary responses during information processing vary with scholastic aptitude test scores. *Science* 205, 1289–1292. doi: 10.1126/science.472746
- Alamia, A., VanRullen, R., Pasqualotto, E., Mouraux, A., and Zénon, A. (2019). Pupil-linked arousal responds to unconscious surprisal. *J. Neurosci.* 39, 5369–5376. doi: 10.1523/JNEUROSCI.3010-18.2019
- Albert, S. T., Jang, J., Haith, A. M., Lerner, G., Della-Maggiore, V., Shadmehr, R., et al. (2022). Competition between parallel sensorimotor learning systems. *eLife* 11:e65361. doi: 10.7554/eLife.65361
- Anderson, E. A., Gunnar Wallin, B., and Mark, A. L. (1987). Dissociation of sympathetic nerve activity in arm and leg muscle during mental stress. *Hypertension* 9, III114–III119. doi: 10.1161/01.hyp.9.6_pt_2.iii114
- Antov, M. I., Melicherová, U., and Stockhorst, U. (2015). Cold pressor test improves fear extinction in healthy men. *Psychoneuroendocrinology* 54, 54–59. doi: 10.1016/j.psyneuen.2015.01.009
- Arnsten, A. F. T., Wang, M. J., and Paspalas, C. D. (2012). Neuromodulation of thought: Flexibilities and vulnerabilities in prefrontal cortical network synapses. *Neuron* 76, 223–239. doi: 10.1016/j.neuron.2012.08.038
- Aston-Jones, G., and Cohen, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. *Annu. Rev. Neurosci.* 28, 403–450. doi: 10.1146/annurev.neuro.28.061604.135709
- Aston-Jones, G., Rajkowski, J., and Kubiak, P. (1997). Conditioned responses of monkey locus coeruleus neurons anticipate acquisition of discriminative behavior in a vigilance task. *Neuroscience* 80, 697–715. doi: 10.1016/s0306-4522(97)00060-2
- Aston-Jones, G., Rajkowski, J., Kubiak, P., and Alexinsky, T. (1994). Locus coeruleus neurons in monkey are selectively activated by attended cues in a vigilance task. *J. Neurosci.* 14, 4467–4480. doi: 10.1523/jneurosci.14-07-04467.1994
- Bach, D. R., Schächinger, H., Neuhoﬀ, J. G., Esposito, F., Salle, F. D., Lehmann, C., et al. (2008). Rising sound intensity: An intrinsic warning cue activating the amygdala. *Cereb. Cortex* 18, 145–150. doi: 10.1093/cercor/bhm040
- Beatty, J. (1982). Task-evoked pupillary responses, processing load, and the structure of processing resources. *Psychol. Bull.* 91, 276–292. doi: 10.1037/0033-2909.91.2.276
- Behrens, T. E. J., Woolrich, M. W., Walton, M. E., and Rushworth, M. F. S. (2007). Learning the value of information in an uncertain world. *Nat. Neurosci.* 10, 1214–1221. doi: 10.1038/nn1954
- Beissner, F., Meissner, K., Bär, K. J., and Napadow, V. (2013). The autonomic brain: An activation likelihood estimation meta-analysis for central processing of autonomic function. *J. Neurosci.* 33, 10503–10511. doi: 10.1523/JNEUROSCI.1103-13.2013
- Benson, B. L., Anguera, J. A., and Seidler, R. D. (2011). A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *J. Neurophysiol.* 105, 2843–2851. doi: 10.1152/jn.00002.2011
- Bond, K. M., and Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *J. Neurophysiol.* 113, 3836–3849. doi: 10.1152/JN.00009.2015
- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., and Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychol. Rev.* 108, 624–652. doi: 10.1037/0033-295x.108.3.624
- Bouret, S., and Sara, S. J. (2004). Reward expectation, orientation of attention and locus coeruleus-medial frontal cortex interplay during learning. *Eur. J. Neurosci.* 20, 791–802. doi: 10.1111/j.1460-9568.2004.03526.x
- Bouret, S., and Sara, S. J. (2005). Network reset: A simplified overarching theory of locus coeruleus noradrenaline function. *Trends Neurosci.* 28, 574–582. doi: 10.1016/j.tins.2005.09.002
- Brooks, D. N., and Baddeley, A. D. (1976). What can amnesic patients learn? *Neuropsychologia* 14, 111–122. doi: 10.1016/0028-3932(76)90012-9
- Callister, B. Y. R., Suwarno, N. O., and Seals, D. R. (1992). Sympathetic activity is influenced by task difficulty and stress perception during mental challenge in humans. *J. Physiol.* 454, 373–387. doi: 10.1113/jphysiol.1992.sp019269
- Canon, W. B. (1915). *Bodily changes in pain, hunger, fear and rage: An account of recent researches into the function of emotional excitement*. Boston, MA: D Appleton & Company. doi: 10.7326/0003-4819-39-2-383_1
- Carey, M. R., and Regehr, W. G. (2009). Noradrenergic control of associative synaptic plasticity by selective modulation of instructive signals. *Neuron* 62, 112–122. doi: 10.1016/j.neuron.2009.02.022
- Chan, S. C. Y., Schuck, N. W., Lopatina, N., Schoenbaum, G., and Niv, Y. (2021). Orbitofrontal cortex and learning predictions of state transitions. *Behav. Neurosci.* 135, 487–497. doi: 10.1037/bne0000461
- Clewett, D. V., Huang, R., Velasco, R., Lee, T. H., and Mather, M. (2018). Locus coeruleus activity strengthens prioritized memories under arousal. *J. Neurosci.* 38, 1558–1574. doi: 10.1523/JNEUROSCI.2097-17.2017
- Clewett, D., Gasser, C., and Davachi, L. (2020). Pupil-linked arousal signals track the temporal organization of events in memory. *Nat. Commun.* 11, 1–13. doi: 10.1038/s41467-020-17851-9
- Clewett, D., Huang, R., and Davachi, L. (2025). Locus coeruleus activation “resets” hippocampal event representations and separates adjacent memories. *Neuron* 113:2521–2535.e8. doi: 10.1016/j.neuron.2025.05.013
- Collins, L., Boddington, L., Steffan, P. J., and McCormick, D. (2021). Vagus nerve stimulation induces widespread cortical and behavioral activation. *Curr. Biol.* 31:2088–2098.e3. doi: 10.1016/j.cub.2021.02.049
- Critchley, H. D. (2005). Neural mechanisms of autonomic, affective, and cognitive integration. *J. Comp. Neurol.* 493, 154–166. doi: 10.1002/CNE.20749
- Critchley, H. D., Mathias, C. J., and Dolan, R. J. (2001). Neural activity in the human brain relating to uncertainty and arousal during anticipation. *Neuron* 29, 537–545. doi: 10.1016/S0896-6273(01)00225-2
- Critchley, H. D., Mathias, C. J., Josephs, O., O'Doherty, J., Zanini, S., Dewar, B. K., et al. (2003). Human cingulate cortex and autonomic control: Converging neuroimaging and clinical evidence. *Brain* 126, 2139–2152. doi: 10.1093/brain/awg216
- Danev, S. G., and de Winter, C. R. (1971). Heart rate deceleration after erroneous responses. *Psychol. Forschung* 35, 27–34. doi: 10.1007/bf00424472

- Dayan, P., and Yu, A. J. (2006). Phasic norepinephrine: A neural interrupt signal for unexpected events. *Netw. Comput. Neural Syst.* 17, 335–350. doi: 10.1080/0954880601004024
- De Berker, A. O., Rutledge, R. B., Mathys, C., Marshall, L., Cross, G. F., Dolan, R. J., et al. (2016). Computations of uncertainty mediate acute stress responses in humans. *Nat. Commun.* 7, 1–11. doi: 10.1038/ncomms10996
- de Brouwer, A. J., Albaghdadi, M., Flanagan, J. R., and Gallivan, J. P. (2018). Using gaze behavior to parcellate the explicit and implicit contributions to visuomotor learning. *J. Neurophysiol.* 120, 1602–1615. doi: 10.1152/jn.00113.2018
- Di Gregorio, F., Steinhäuser, M., Maier, M. E., Thayer, J. F., and Battaglia, S. (2024). Error-related cardiac deceleration: Functional interplay between error-related brain activity and autonomic nervous system in performance monitoring. *Neurosci. Biobehav. Rev.* 157, 105542–105542. doi: 10.1016/j.neubiorev.2024.105542
- Ebina, T., Masamizu, Y., Tanaka, Y. R., Watakabe, A., Hirakawa, R., Hirayama, Y., et al. (2018). Two-photon imaging of neuronal activity in motor cortex of marmosets during upper-limb movement tasks. *Nat. Commun.* 9:1879. doi: 10.1038/s41467-018-04286-6
- Ebina, T., Sasagawa, A., Hong, D., Setsuie, R., Obara, K., Masamizu, Y., et al. (2024). Dynamics of directional motor tuning in the primate premotor and primary motor cortices during sensorimotor learning. *Nat. Commun.* 15:7127. doi: 10.1038/s41467-024-51425-3
- Fernandez-Ruiz, J., Wong, W., Armstrong, I. T., and Flanagan, J. R. (2011). Relation between reaction time and reach errors during visuomotor adaptation. *Behav. Brain Res.* 219, 8–14. doi: 10.1016/j.bbr.2010.11.060
- Friedman, D., Hakerem, G., Sutton, S., and Fleiss, J. L. (1973). Effect of stimulus uncertainty on the pupillary dilation response and the vertex evoked potential. *Electroencephalogr. Clin. Neurophysiol.* 34, 475–484. doi: 10.1016/0013-4694(73)90065-5
- Gershman, S. J., Radulescu, A., Norman, K. A., and Niv, Y. (2014). Statistical computations underlying the dynamics of memory updating. *PLoS Comput. Biol.* 10:e1003939. doi: 10.1371/journal.pcbi.1003939
- Gilzenrat, M. S., Nieuwenhuis, S., Jepma, M., Cohen, J. D., and State, R. C. (2010). Pupil diameter tracks changes in control state predicted by the adaptive gain theory of locus coeruleus function. *Cogn. Affect. Behav. Neurosci.* 10, 252–269. doi: 10.3758/CABN.10.2.252
- Glennon, E., Carcea, I., Martins, A. R. O., Multani, J., Shehu, I., Svirsky, M. A., et al. (2019). Locus coeruleus activation accelerates perceptual learning. *Brain Res.* 1709, 39–49. doi: 10.1016/j.brainres.2018.05.048
- Graham, F. K., and Clifton, R. K. (1966). Heart-rate change as a component of the orienting response. *Psychol. Bull.* 65, 305–320. doi: 10.1037/h0023258
- Grimm, C., Duss, S. N., Privitera, M., Munn, B. R., Karalis, N., Frässle, S., et al. (2024). Tonic and burst-like locus coeruleus stimulation distinctly shift network activity across the cortical hierarchy. *Nat. Neurosci.* 2024, 1–11. doi: 10.1038/s41593-024-01755-8
- Haith, A. M., Huberdeau, D. M., and Krakauer, J. W. (2015). The influence of movement preparation time on the expression of visuomotor learning and savings. *J. Neurosci.* 35, 5109–5117. doi: 10.1523/JNEUROSCI.3869-14.2015
- Hajcak, G., McDonald, N., and Simons, R. F. (2003). To err is autonomic: Error-related brain potentials, ANS activity, and post-error compensatory behavior. *Psychophysiology* 40, 895–903. doi: 10.1111/1469-8986.00107
- Heald, J. B., Ingram, J. N., Flanagan, J. R., and Wolpert, D. M. (2018). Multiple motor memories are learned to control different points on a tool. *Nat. Hum. Behav.* 2, 300–311. doi: 10.1038/s41562-018-0324-5
- Heald, J. B., Lengyel, M., and Wolpert, D. M. (2021). Contextual inference underlies the learning of sensorimotor repertoires. *Nature* 600, 489–493. doi: 10.1038/s41586-021-04129-3
- Heald, J. B., Lengyel, M., and Wolpert, D. M. (2023a). Contextual inference in learning and memory. *Trends Cogn. Sci.* 27, 43–64. doi: 10.1016/j.tics.2022.10.004
- Heald, J. B., Wolpert, D. M., and Lengyel, M. (2023b). The computational and neural bases of context-dependent learning. *Annu. Rev. Neurosci.* 46, 233–258. doi: 10.1146/annurev-neuro-092322-100402
- Heron, C., Gould, T. J., and Bickford, P. (1996). Acquisition of a runway motor learning task is impaired by a beta adrenergic antagonist in F344 rats. *Behav. Brain Res.* 78, 235–241. doi: 10.1016/0166-4328(95)00252-9
- Hervé-Minvielle, A., and Sara, S. J. (1995). Rapid habituation of auditory responses of locus coeruleus cells in anaesthetized and awake rats. *NeuroReport* 6, 1235–1240. doi: 10.1097/00001756-199507100-00001
- Hess, E. H., and Polt, J. M. (1964). Pupil size in relation to mental activity during simple problem-solving. *Science* 143, 1190–1192. doi: 10.1126/science.143.3611.1190
- Hirano, T., Inoue, H., Uemura, T., and Matsunaga, K. (1994). Pupillary responses in normal subjects following auditory stimulation. *Eur. Arch. Oto Rhino Laryngol.* 251, 3–6. doi: 10.1007/BF02565210
- Hirashima, M., Yamane, K., Nakamura, Y., and Ohtsuki, T. (2008). Kinetic chain of overarm throwing in terms of joint rotations revealed by induced acceleration analysis. *J. Biomech.* 41, 2874–2883. doi: 10.1016/j.jbiomech.2008.06.014
- Huberdeau, D. M., Krakauer, J. W., and Haith, A. M. (2015). Dual-process decomposition in human sensorimotor adaptation. *Curr. Opin. Neurobiol.* 33, 71–77. doi: 10.1016/j.conb.2015.03.003
- Jakobson, L. S., and Goodale, M. A. (1989). Trajectories of reaches to prismatically-displaced targets: Evidence for 'automatic' visuomotor recalibration. *Exp. Brain Res.* 78, 575–587. doi: 10.1007/BF00230245
- Jepma, M., and Nieuwenhuis, S. (2011). Pupil diameter predicts changes in the exploration-exploitation trade-off: Evidence for the adaptive gain theory. *J. Cogn. Neurosci.* 23, 1587–1596. doi: 10.1162/jocn.2010.21548
- Jepma, M., Brown, S. B. R. E., Murphy, P. R., Koelewijn, S. C., de Vries, B., van den Maagdenberg, A. M., et al. (2018). Noradrenergic and cholinergic modulation of belief updating. *J. Cogn. Neurosci.* 30, 1803–1820. doi: 10.1162/jocn
- Jepma, M., Murphy, P. R., Nassar, M. R., Rangel-Gomez, M., Meeter, M., and Nieuwenhuis, S. (2016). Catecholaminergic regulation of learning rate in a dynamic environment. *PLoS Comput. Biol.* 12:e1005171. doi: 10.1371/journal.pcbi.1005171
- Joshi, S., and Gold, J. I. (2020). Pupil size as a window on neural substrates of cognition. *Trends Cogn. Sci.* 24, 466–480. doi: 10.1016/j.tics.2020.03.005
- Joshi, S., Li, Y., Kalwani, R. M., and Gold, J. I. (2016). Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron* 89, 221–234. doi: 10.1016/j.neuron.2015.11.028
- Kagerer, F. A., Contreras-Vidal, J. L., and Stelmach, G. E. (1997). Adaptation to gradual as compared with sudden visuo-motor distortions. *Exp. Brain Res.* 115, 557–561. doi: 10.1007/PL00005727
- Kahneman, D., and Beatty, J. (1966). Pupil diameter and load on memory. *Science* 154, 1583–1585. doi: 10.1126/science.154.3756.1583
- Keisler, A., and Shadmehr, R. (2010). A shared resource between declarative memory and motor memory. *J. Neurosci.* 30, 14817–14823. doi: 10.1523/JNEUROSCI.4160-10.2010
- Kilgard, M. P., Epperson, J. D., Adehunoluwa, E. A., Swank, C., Porter, A. L., Pruitt, D. T., et al. (2025). Closed-loop vagus nerve stimulation aids recovery from spinal cord injury. *Nature* 643, 1030–1036. doi: 10.1038/s41586-025-09028-5
- Klein, T. A., Endrass, T., Kathmann, N., Neumann, J., von Cramon, D. Y., and Ullsperger, M. (2007). Neural correlates of error awareness. *Neuroimage* 34, 1774–1781. doi: 10.1016/j.neuroimage.2006.11.014
- Krakauer, J. W., Hadjiosif, A. M., Xu, J., Wong, A. L., and Haith, A. M. (2019). Motor learning. *Compr. Physiol.* 9, 613–663. doi: 10.1002/CPHY.C170043
- Kuraoka, K., and Nakamura, K. (2022). Facial temperature and pupil size as indicators of internal state in primates. *Neurosci. Res.* 175, 25–37. doi: 10.1016/j.neures.2022.01.002
- Kurtzer, I. L., Pruszynski, J. A., and Scott, S. H. (2008). Long-latency reflexes of the human arm reflect an internal model of limb dynamics. *Curr. Biol.* 18, 449–453. doi: 10.1016/j.cub.2008.02.053
- Kurtzer, I. L., Pruszynski, J. A., and Scott, S. H. (2009). Long-latency responses during reaching account for the mechanical interaction between the shoulder and elbow joints. *J. Neurophysiol.* 102, 3004–3015. doi: 10.1152/jn.00453.2009
- Loued-Khenissi, L., Pfeuffer, A., Einhäuser, W., and Preusschoff, K. (2020). Anterior insula reflects surprise in value-based decision-making and perception. *Neuroimage* 210:6549. doi: 10.1016/j.neuroimage.2020.116549
- Maier, M. E., Ernst, B., and Steinhäuser, M. (2019). Error-related pupil dilation is sensitive to the evaluation of different error types. *Biol. Psychol.* 141, 25–34. doi: 10.1016/j.biopsycho.2018.12.013
- Mante, V., Sussillo, D., Shenoy, K. V., and Newsome, W. T. (2013). Context-dependent computation by recurrent dynamics in prefrontal cortex. *Nature* 503, 78–84. doi: 10.1038/nature12742
- Maresch, J., Mudrik, L., and Donchin, O. (2021a). Measures of explicit and implicit in motor learning: What we know and what we don't. *Neurosci. Biobehav. Rev.* 128, 558–568. doi: 10.1016/j.neubiorev.2021.06.037
- Maresch, J., Werner, S., and Donchin, O. (2021b). Methods matter: Your measures of explicit and implicit processes in visuomotor adaptation affect your results. *Eur. J. Neurosci.* 53, 504–518. doi: 10.1111/ejn.14945
- Mathis, M. W., Mathis, A., and Uchida, N. (2017). Somatosensory cortex plays an essential role in forelimb motor adaptation in mice. *Neuron* 93:1493–1503.e6. doi: 10.1016/j.neuron.2017.02.049
- Mathys, C. D., Lomakina, E. I., Daunizeau, J., Iglesias, S., Brodersen, K. H., Friston, K. J., et al. (2014). Uncertainty in perception and the Hierarchical Gaussian filter. *Front. Hum. Neurosci.* 8:825. doi: 10.3389/fnhum.2014.00825
- Mathys, C., Daunizeau, J., Friston, K. J., and Stephan, K. E. (2011). A Bayesian foundation for individual learning under uncertainty. *Front. Hum. Neurosci.* 5:39. doi: 10.3389/fnhum.2011.00039
- McBurney-Lin, J., Vargova, G., Garad, M., Zagha, E., and Yang, H. (2022). The locus coeruleus mediates behavioral flexibility. *Cell Rep.* 41:111534. doi: 10.1016/j.celrep.2022.111534

- McDougle, S. D., Bond, K. M., and Taylor, J. A. (2015). Explicit and implicit processes constitute the fast and slow processes of sensorimotor learning. *J. Neurosci.* 35, 9568–9579. doi: 10.1523/JNEUROSCI.5061-14.2015
- McDougle, S. D., Ivry, R. B., and Taylor, J. A. (2016). Taking aim at the cognitive side of learning in sensorimotor adaptation tasks. *Trends Cogn. Sci.* 20, 535–544. doi: 10.1016/j.TICS.2016.05.002
- Meissner, S. N., Bächinger, M., Kikkert, S., Imhof, J., Missura, S., Carro Dominguez, M., et al. (2024). Self-regulating arousal via pupil-based biofeedback. *Nat. Hum. Behav.* 8, 43–62. doi: 10.1038/s41562-023-01729-z
- Miyamoto, Y. R., Wang, S., and Smith, M. A. (2020). Implicit adaptation compensates for erratic explicit strategy in human motor learning. *Nat. Neurosci.* 23, 443–455. doi: 10.1038/s41593-020-0600-3
- Morehead, J. R., Qasim, S. E., Crossley, M. J., and Ivry, R. (2015). Savings upon re-aiming in visuomotor adaptation. *J. Neurosci.* 35, 14386–14396. doi: 10.1523/JNEUROSCI.1046-15.2015
- Mridha, Z., de Gee, J. W., Shi, Y., Alkashgari, R., Williams, J., Suminski, A., et al. (2021). Graded recruitment of pupil-linked neuromodulation by parametric stimulation of the vagus nerve. *Nat. Commun.* 12, 1–14. doi: 10.1038/s41467-021-21730-2
- Muller, T. H., Mars, R. B., Behrens, T. E., and O'Reilly, J. X. (2019). Control of entropy in neural models of environmental state. *eLife* 8:e39404. doi: 10.7554/eLife.39404
- Murphy, P. R., O'Connell, R. G., O'Sullivan, M., Robertson, I. H., and Balsters, J. H. (2014). Pupil diameter covaries with BOLD activity in human locus coeruleus. *Hum. Brain Mapp.* 35, 4140–4154. doi: 10.1002/hbm.22466
- Murphy, P. R., Van Moort, M. L., and Nieuwenhuis, S. (2016). The pupillary orienting response predicts adaptive behavioral adjustment after errors. *PLoS One* 11:e0151763. doi: 10.1371/journal.pone.0151763
- Nakayama, K., Goto, S., Kuraoka, K., and Nakamura, K. (2005). Decrease in nasal temperature of rhesus monkeys (*Macaca mulatta*) in negative emotional state. *Physiol. Behav.* 84, 783–790. doi: 10.1016/j.physbeh.2005.03.009
- Nassar, M. R., Rumsey, K. M., Wilson, R. C., Parikh, K., Heasly, B., and Gold, J. I. (2012). Rational regulation of learning dynamics by pupil-linked arousal systems. *Nat. Neurosci.* 15, 1040–1046. doi: 10.1038/nn.3130
- Nath, T., Mathis, A., Chen, A. C., Patel, A., Bethge, M., and Mathis, M. W. (2019). Using DeepLabCut for 3D markerless pose estimation across species and behaviors. *Nat. Protoc.* 14, 2152–2176. doi: 10.1038/s41596-019-0176-0
- Neville, K. M., and Cressman, E. K. (2018). The influence of awareness on explicit and implicit contributions to visuomotor adaptation over time. *Exp. Brain Res.* 236, 2047–2059. doi: 10.1007/s00221-018-5282-7
- Nogami, M., Hagura, N., and Yokoi, A. (2025). Autonomic responses to proprioceptive and visual errors during single-trial reach adaptation. *bioRxiv* [Preprint]. doi: 10.1101/2025.03.31.646172
- O'Bryan, S. R., and Song, J.-H. (2025). Leveraging pupil diameter to track explicit control processes in visuomotor adaptation. *Vis. Sci. Soc. Annu. Meet. Abstract* 25:2811. doi: 10.1167/jov.25.9.2811
- O'Connell, R. G., Dockree, P. M., Bellgrove, M. A., Kelly, S. P., Hester, R., Garavan, H., et al. (2007). The role of cingulate cortex in the detection of errors with and without awareness: A high-density electrical mapping study. *Eur. J. Neurosci.* 25, 2571–2579. doi: 10.1111/j.1460-9568.2007.05477.x
- O'Reilly, J. X., Schüfflgen, U., Cuell, S. F., Behrens, T. E. J., Mars, R. B., and Rushworth, M. F. S. (2013). Dissociable effects of surprise and model update in parietal and anterior cingulate cortex. *Proc. Natl. Acad. Sci. U.S.A.* 110, E3660–E3669. doi: 10.1073/pnas.1305373110
- Oh, Y., and Schweighofer, N. (2019). Minimizing precision-weighted sensory prediction errors via memory formation and switching in motor adaptation. *J. Neurosci.* 39, 9237–9250. doi: 10.1523/JNEUROSCI.3250-18.2019
- Ohsawa, H., Yamaguchi, S., Ishimaru, H., Shimura, M., and Sato, Y. (1997). Neural mechanism of pupillary dilation elicited by electro-acupuncture stimulation in anesthetized rats. *J. Auton. Nerv. Syst.* 64, 101–106. doi: 10.1016/S0165-1838(97)00023-4
- Okazawa, G., and Kiani, R. (2023). Neural mechanisms that make perceptual decisions flexible. *Annu. Rev. Physiol.* 85, 191–215. doi: 10.1146/annurev-physiol-031722-024731
- Pfaff, L., Mu, C., and Kopiske, K. (2025). Can pupillometry reveal perturbation detection in sensorimotor adaptation during grasping? ABSTRACT – Humans adjust their motor actions to correct for errors both with and without being aware of doing so. Little is known, however, about what makes err. *bioRxiv* [Preprint]. doi: 10.1101/2025.05.15.654224
- Piray, P., and Daw, N. D. (2020). A simple model for learning in volatile environments. *PLoS Comput. Biol.* 16:e1007963. doi: 10.1371/journal.pcbi.1007963
- Preusschoff, K., Quartz, S. R., and Bossaerts, P. (2008). Human insula activation reflects risk prediction errors as well as risk. *J. Neurosci.* 28, 2745–2752. doi: 10.1523/JNEUROSCI.4286-07.2008
- Preusschoff, K., Hart, B. M., and Einhäuser, W. (2011). Pupil dilation signals surprise: Evidence for noradrenaline's role in decision making. *Front. Neurosci.* 5:115. doi: 10.3389/fnins.2011.00115
- Qiyuan, J., Richer, F., Wagoner, B. L., and Beatty, J. (1985). The pupil and stimulus probability. *Psychophysiology* 22, 530–534. doi: 10.1111/j.1469-8986.1985.tb01645.x
- Rajkowski, J., Kubiak, P., and Aston-Jones, G. (1993). Correlations between locus coeruleus (LC) neural activity, pupil diameter and behavior in monkey support a role of LC in attention. *Soc. Neurosci. Abstracts* 19:974.
- Redding, G. M., and Wallace, B. (2006). Generalization of prism adaptation. *J. Exp. Psychol. Hum. Percept. Perform.* 32, 1006–1022. doi: 10.1037/0096-1523.32.4.1006
- Richer, F., and Beatty, J. (1987). Contrasting effects of response uncertainty on the task-evoked pupillary response and reaction time. *Psychophysiology* 24, 258–262. doi: 10.1111/j.1469-8986.1987.tb00291.x
- Robertson, E. M. (2007). The serial reaction time task: Implicit motor skill learning? *J. Neurosci.* 27, 10073–10075. doi: 10.1523/JNEUROSCI.2747-07.2007
- Roelofs, K., and Dayan, P. (2022). Freezing revisited: Coordinated autonomic and central optimization of threat coping. *Nat. Rev. Neurosci.* 23, 568–580. doi: 10.1038/s41583-022-00608-2
- Saijo, N., and Gomi, H. (2010). Multiple motor learning strategies in visuomotor rotation. *PLoS One* 5:e9399. doi: 10.1371/journal.pone.0009399
- Sakaguchi, Y., Akashi, Y., and Takano, M. (2001). Visuo-motor adaptation to stepwise and gradual changes in the environment: Relationship between consciousness and adaptation. *J. Robot. Mechatron.* 13, 601–613. doi: 10.20965/jrm.2001.p0601
- Sara, S. J. (2009). The locus coeruleus and noradrenergic modulation of cognition. *Nat. Rev. Neurosci.* 10, 211–223. doi: 10.1038/nrn2573
- Sara, S. J., and Bouret, S. (2012). Orienting and reorienting: The locus coeruleus mediates cognition through arousal. *Neuron* 76, 130–141. doi: 10.1016/j.neuron.2012.09.011
- Sara, S. J., and Devaughes, V. (1988). Priming stimulation of locus coeruleus facilitates memory retrieval in the rat. *Brain Res.* 438, 299–303. doi: 10.1016/0006-8993(88)91351-0
- Sara, S. J., Roulet, P., and Przybyslawski, J. (1999). Consolidation of memory for odor-reward association: β -Adrenergic receptor involvement in the late phase. *Learn. Mem.* 6, 88–96. doi: 10.1101/lm.6.2.88
- Satterthwaite, T. D., Green, L., Myerson, J., Parker, J., Ramaratnam, M., and Buckner, R. L. (2007). Dissociable but inter-related systems of cognitive control and reward during decision making: Evidence from pupillometry and event-related fMRI. *Neuroimage* 37, 1017–1031. doi: 10.1016/j.neuroimage.2007.04.066
- Schuck, N. W., Cai, M. B., Wilson, R. C., and Niv, Y. (2016). Human orbitofrontal cortex represents a cognitive map of state space. *Neuron* 91, 1402–1412. doi: 10.1016/j.neuron.2016.08.019
- Shadmehr, R., and Krakauer, J. W. (2008). A computational neuroanatomy for motor control. *Exp. Brain Res.* 185, 359–381. doi: 10.1007/s00221-008-1280-5
- Shadmehr, R., Brandt, J., and Corkin, S. (1998). Time-dependent motor memory processes in amnesic subjects. *J. Neurophysiol.* 80, 1590–1597. doi: 10.1152/jn.1998.80.3.1590
- Shadmehr, R., Smith, M. A., and Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annu. Rev. Neurosci.* 33, 89–108. doi: 10.1146/annurev-neuro-060909-153135
- Singer, T., Critchley, H. D., and Preusschoff, K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends Cogn. Sci.* 13, 334–340. doi: 10.1016/j.tics.2009.05.001
- Slachevsky, A., Pillon, B., Fournier, P., Pradat-Diehl, P., Jeannerod, M., and Dubois, B. (2001). Preserved adjustment but impaired awareness in a sensory-motor conflict following prefrontal lesions. *J. Cogn. Neurosci.* 13, 332–340. doi: 10.1162/08989290151137386
- Slachevsky, A., Pillon, B., Fournier, P., Renié, L., Levy, R., Jeannerod, M., et al. (2003). The prefrontal cortex and conscious monitoring of action: An experimental study. *Neuropsychologia* 41, 655–665. doi: 10.1016/S0028-3932(02)00225-7
- Smith, M. A., Ghazizadeh, A., and Shadmehr, R. (2006). Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biol.* 4:e179. doi: 10.1371/journal.pbio.0040179
- Sokolov, E. N. (1990). The orienting response, and future directions of its development. *Pavlovian J. Biol. Sci.* 25, 142–150. doi: 10.1007/BF02974268
- Soltani, A., and Izquierdo, A. (2019). Adaptive learning under expected and unexpected uncertainty. *Nat. Rev. Neurosci.* 20, 635–644. doi: 10.1038/s41583-019-0180-y
- Squire, L. R. (2009). The legacy of patient H.M. for neuroscience. *Neuron* 61, 6–9. doi: 10.1016/j.neuron.2008.12.023
- Strange, B. A., and Dolan, R. J. (2004). beta-Adrenergic modulation of emotional memory-evoked human amygdala and hippocampal responses. *Proc. Natl. Acad. Sci. U.S.A.* 101, 11454–11458. doi: 10.1073/pnas.0404282101
- Strange, B. A., Hurlmann, R., and Dolan, R. J. (2003). An emotion-induced retrograde amnesia in humans is amygdala- and β -adrenergic-dependent. *Proc. Natl. Acad. Sci. U.S.A.* 100, 13626–13631. doi: 10.1073/pnas.1635116100

- Sugiyama, D., Hur, S. W., Pickering, A. E., Kase, D., Kim, S. J., Kawamata, M., et al. (2012). In vivo patch-clamp recording from locus coeruleus neurones in the rat brainstem. *J. Physiol.* 590, 2225–2231. doi: 10.1113/jphysiol.2011.226407
- Sun, N., Li, B. X., Hong, Y. J., Bing, Y. H., Qiu, D. L., and Chu, C. P. (2019). Noradrenaline depresses spontaneous complex spikes activity of cerebellar Purkinje cells via α 2-adrenergic receptor in vivo in mice. *Neurosci. Lett.* 703, 38–44. doi: 10.1016/j.neulet.2019.03.008
- Szabadi, E. (2013). Functional neuroanatomy of the central noradrenergic system. *J. Psychopharmacol.* 27, 659–693. doi: 10.1177/0269881113490326
- ‘t Hart, B. M., Taqvi, U., Gastrock, R. Q., Ruttle, J. E., Modchalingam, S., and Henriques, D. Y. P. (2024). Measures of implicit and explicit adaptation do not linearly add. *eNeuro* 11, 1–16. doi: 10.1523/ENEURO.0021-23.2024
- Takeuchi, T., Duszkiewicz, A. J., Sonneborn, A., Spooner, P. A., Yamasaki, M., Morris, R. G. M., et al. (2016). Locus coeruleus and dopaminergic consolidation of everyday memory. *Nature* 537, 357–362. doi: 10.1038/nature19325
- Tan, H. S., van Neerven, J., Collewin, H., and Pompeiano, O. (1991). Effects of alpha-noradrenergic substances on the optokinetic and vestibulo-ocular responses in the rabbit: A study with systemic and intraflocular injections. *Brain Res.* 562, 207–215. doi: 10.1016/0006-8993(91)90623-4
- Tanaka, H., and Sejnowski, T. J. (2013). Computing reaching dynamics in motor cortex with Cartesian spatial coordinates. *J. Neurophysiol.* 109, 1182–1201. doi: 10.1152/jn.00279.2012
- Taylor, J. A., and Ivry, R. B. (2012). The role of strategies in motor learning. *Ann. N. Y. Acad. Sci.* 1251, 1–12. doi: 10.1111/j.1749-6632.2011.06430.x
- Taylor, J. A., and Ivry, R. B. (2014). Cerebellar and prefrontal cortex contributions to adaptation, strategies, and reinforcement learning. *Prob. Brain Res.* 210, 217–253. doi: 10.1016/B978-0-444-63356-9.00009-1
- Taylor, J. A., and Thoroughman, K. A. (2007). Divided attention impairs human motor adaptation but not feedback control. *J. Neurophysiol.* 98, 317–326. doi: 10.1152/jn.01070.2006
- Taylor, J. A., and Thoroughman, K. A. (2008). Motor adaptation scaled by the difficulty of a secondary cognitive task. *PLoS One* 3:e2485. doi: 10.1371/journal.pone.0002485
- Taylor, J. A., Krakauer, J. W., and Ivry, R. B. (2014). Explicit and implicit contributions to learning in a sensorimotor adaptation task. *J. Neurosci.* 34, 3023–3032. doi: 10.1523/JNEUROSCI.3619-13.2014
- Tsay, J. S., Kim, H. E., McDougale, S. D., Taylor, J. A., Haith, A., Avraham, G., et al. (2024). Fundamental processes in sensorimotor learning: Reasoning, refinement, and retrieval. *eLife* 13:e91839. doi: 10.7554/ELIFE.91839
- Ullsperger, M., Danielmeier, C., and Jocham, G. (2014). Neurophysiology of performance monitoring and adaptive behavior. *Physiol. Rev.* 94, 35–79. doi: 10.1152/physrev.00041.2012
- Ullsperger, M., Harsay, H. A., Wessel, J. R., and Ridderinkhof, K. R. (2010). Conscious perception of errors and its relation to the anterior insula. *Brain Struct. Funct.* 214, 629–643. doi: 10.1007/s00429-010-0261-1
- Urai, A. E., Braun, A., and Donner, T. H. (2017). Pupil-linked arousal is driven by decision uncertainty and alters serial choice bias. *Nat. Commun.* 8, 1–11. doi: 10.1038/ncomms14637
- van der Wel, P., and van Steenbergen, H. (2018). Pupil dilation as an index of effort in cognitive control tasks: A review. *Psychon. Bull. Rev.* 25, 2005–2015. doi: 10.3758/s13423-018-1432-y
- Vankov, A., Hervé-Minvielle, A., and Sara, S. J. (1995). Response to novelty and its rapid habituation in locus coeruleus neurons of the freely exploring rat. *Eur. J. Neurosci.* 7, 1180–1187. doi: 10.1111/j.1460-9568.1995.tb01108.x
- Verwey, W. B., Abrahamse, E. L., and de Kleine, E. (2010). Cognitive processing in new and practiced discrete keying sequences. *Front. Psychol.* 1:32. doi: 10.3389/fpsyg.2010.00032
- Vincent, P., Parr, T., Benrimoh, D., and Friston, K. J. (2019). With an eye on uncertainty: Modelling pupillary responses to environmental volatility. *PLoS Comput. Biol.* 15:1–22. doi: 10.1371/journal.pcbi.1007126
- Waterhouse, B. D., Predale, H. K., Plummer, N. W., Jensen, P., and Chandler, D. J. (2022). Probing the structure and function of locus coeruleus projections to CNS motor centers. *Front. Neural Circuits* 16:895481. doi: 10.3389/fncir.2022.895481
- Watson, M., and McElligott, J. G. (1984). Cerebellar norepinephrine depletion and impaired acquisition of specific locomotor tasks in rats. *Brain Res.* 296, 129–138. doi: 10.1016/0006-8993(84)90518-3
- Wessel, J. R. (2017). An adaptive orienting theory of error processing. *Psychophysiology* 55:e13041. doi: 10.1111/psyp.13041
- Wessel, J. R., Danielmeier, C., and Ullsperger, M. (2011). Error awareness revisited: Accumulation of multimodal evidence from central and autonomic nervous systems. *J. Cogn. Neurosci.* 23, 3021–3036. doi: 10.1162/jocn.2011.21635
- Willingham, D. B., Nissen, M. J., and Bullemer, P. (1989). On the Development of Procedural Knowledge. *J. Exp. Psychol. Learn. Mem. Cogn.* 15, 1047–1060. doi: 10.1037/0278-7393.15.6.1047
- Wolpert, D. M. (2015). Computations in Sensorimotor Learning. *Cold Spring Harb. Symp. Q. Biol.* 79, 93–98. doi: 10.1101/sqb.2014.79.024919
- Wolpert, D. M., Diedrichsen, J., and Flanagan, J. R. (2011). Principles of sensorimotor learning. *Nat. Rev. Neurosci.* 12, 739–751. doi: 10.1038/nrn3112
- Yokoi, A., and Weiler, J. (2022). Pupil diameter tracked during motor adaptation in humans. *J. Neurophysiol.* 128, 1224–1243. doi: 10.1152/jn.00021.2022
- Zénon, A. (2019). Eye pupil signals information gain. *Proc. R. Soc. B Biol. Sci.* 286:20191593. doi: 10.1098/rspb.2019.1593