

46 Visuomotor Adaptation Tasks as a Window into the Interplay between Explicit and Implicit Cognitive Processes

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ABSTRACT Motor learning is traditionally characterized as a function of *procedural memory*, distinct from episodic, semantic, and other forms of memory. Motor adaptation, in particular, describes the process of maintaining the calibration between motor commands and their desired sensory outcomes and has been characterized as a purely implicit, error-based learning process. Increasingly, however, evidence supports the idea that this common conception of motor adaptation is just one piece of the puzzle and should be expanded. Here we review recent evidence showing that when humans adapt visuomotor behaviors, they rely on multiple learning processes, with deliberate action selection helping to bootstrap the learning curve and flexibly maintain performance. We discuss the implications of these discoveries in short- and long-term motor learning.

Motor learning is often discussed in terms of the optimization of motor execution—that is, the specification of movement parameters that minimize noise and maximize accuracy, or the “how to do it” aspects of movement. This conception is the foundation of sensorimotor adaptation tasks, which are considered models for studying how the execution of actions is calibrated to align with desired goal states. But adaptive motor behavior needs to contend with another optimization problem: the intelligent selection of rewarding, attainable goals in the first place, or the “what to do” aspect of movement. This selection process is fundamental to the flexibility that is characteristic of a learned motor skill, though it is not known if or how it interacts with the calibration process. Recent research suggests that even in cases of learning very simple motor tasks, humans apply controlled, often explicit, reasoning processes to rapidly and flexibly select and adjust actions to improve motor performance. In this light, behavior in sensorimotor adaptation tasks involves improvements in action selection processes in addition to improvements in calibration processes.

Here we review recent psychophysical, neuropsychological, and neurophysiological evidence pertaining to how explicit selection processes are recruited throughout motor learning and how these processes may or may not interact with traditional implicit learning systems. Much of this evidence has come from sensorimotor adaptation tasks, which involve a perturbed relationship between motor commands and sensory feedback.

Although cognitive strategies were once central to theories of sensorimotor skill acquisition (Fitts & Posner, 1967), their role in motor learning has largely been overlooked in recent years. As Stanley and Krakauer (2013) have pointed out, one likely reason may be the seminal findings from patient H. M., which led to the distinction between explicit (declarative) and implicit (procedural) memory systems (Milner, Corkin, & Teuber, 1968). H. M. lacked the neural structures that support explicit memory formation, although he could apparently learn a new sensorimotor skill (e.g., mirror drawing). Thus, it would appear that explicit processes are unnecessary to sensorimotor learning. In the following sections, we hope to modify this interpretation.

The Sensorimotor Learning Curve

A number of behavioral tasks have been developed to study motor adaptation, including prism adaptation (Martin et al., 1996b), force field learning (Shadmehr & Mussa-Ivaldi, 1994), and visuomotor rotation (Krakauer et al., 2000; figure 46.1A). Regardless of the particular type of task, they all show similar learning curves (figure 46.1B) and have primarily been used as model tasks to study supervised, implicit error-based learning.

The canonical learning curve proceeds as follows (figure 46.1A, B): After a baseline phase, participants

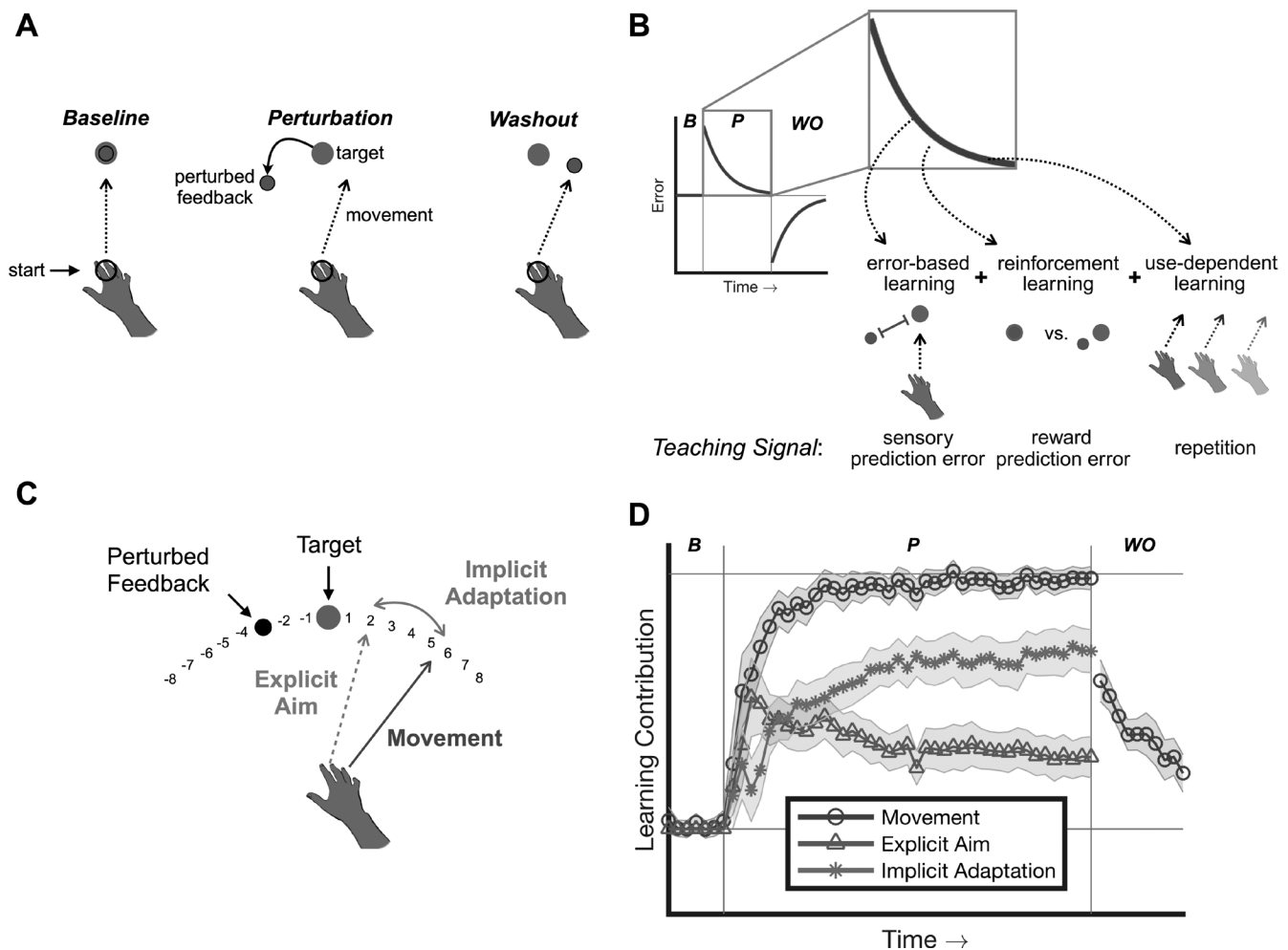


FIGURE 46.1 A, Standard adaptation task procedure (visuo-motor rotation task is shown). Participants attempt to land a cursor (red circle) on a target (green circle), with vision of their limb occluded. B, Canonical adaptation learning curve over the baseline (B), perturbation (P), and washout (WO) phases depicted in panel (A), with a schematic of multiple learning processes making up the learning curve. Inspired by Huang

et al. (2011) and Izawa and Shadmehr (2011). Learning processes rely on distinct teaching signals. C, Schematic of explicit report method used by Taylor, Krakauer, and Ivry (2014) and others, which separates explicit and implicit learning. D, Explicit and implicit learning contributions revealed by the reporting method depicted in (C). Adapted with permission from Taylor, Krakauer, and Ivry (2014).

experience large errors upon the introduction of a perturbation. Over time they adapt to these errors in a manner resembling a power function, eventually approaching a learning asymptote. Finally, in a washout phase, even though the perturbation is removed, adapted movements do not rapidly disappear—participants often show pronounced *aftereffects*, which are unlearned at a comparable rate to initial learning. Aftereffects are the gold standard of implicit adaptation, reflecting a new association between a goal (e.g., hitting a target at 90°) and a movement command (e.g., reaching at an angle of 120° instead of 90°). The dynamics of this learning function can be approximated by a Markovian *state-space* model of adaptation, where an internal state is updated trial by trial (Thoroughman &

Shadmehr, 2000). Identifying the underlying processes and neural systems that give rise to this learning function has been a primary focus of research in the motor control field.

Error-Based Learning, Reinforcement Learning, and Use-Dependent Plasticity in Adaptation Tasks

One demonstration of the various processes underlying motor adaptation came from Huang et al. (2011), who dissociated multiple factors that appeared to drive different aspects of learning (figure 46.1B): sensory prediction error (e.g., a visual cursor's deviation from a movement direction), task success (e.g., a cursor hitting a target or not), and the direction of movement (e.g.,

the path of the hand). The authors were able to dissociate three distinct forms of learning that appeared to respond, respectively, to these different signals: (1) error-based adaptation, which responds to discrepancies between movement and feedback, (2) reinforcement learning, which reinforces movements that result in task success (i.e., reward), and (3) use-dependent learning, which merely reinforces repeated movement directions (figure 46.1B).

In another study, Izawa and Shadmehr (2011) showed how sensory prediction errors (the difference between expected and observed sensory feedback) and reward prediction errors (the difference between expected and observed reward feedback) drive different learning processes: the former was linked to a proprioceptive illusion, where at the end of learning participants misjudge the position of their hand in space. Moreover, while error-based learning led to broad generalization of the learned mapping to novel target locations, learning with reward prediction errors generalized more narrowly (and did not cause sensory recalibration). Taken together, these two studies showed how learning in a sensorimotor adaptation task is clearly multifaceted (figure 46.1B).

The cerebellum has been singled out as the primary locus of error-based recalibration via sensory prediction error (Tseng et al., 2007). The cerebellum is known to be vital for the learning and execution of coordinated movements (Thach, Goodkin, & Keating, 1992), and this learning is thought to rely on plasticity at the parallel fiber-Purkinje cell synapse (Albus, 1971; Marr, 1969): Parallel fibers carry a state representation that includes sensory context and current outgoing motor commands (e.g., efference copy) to the cerebellar cortex, while the second primary input to the Purkinje cells, the climbing fibers, provide a teaching signal when an unexpected sensory event occurs (i.e., a sensory prediction error). Long-term depression at the parallel fiber-Purkinje cell synapse induced by these teaching signals is thought to eventually lead to adapted motor behaviors that reduce error over time (Ito, 2006).

Consistent with a role for the cerebellum in error-based reach adaptation, cerebellar damage in humans leads to attenuated aftereffects in prism adaptation (Martin et al., 1996a; Weiner, Hallett, & Funkenstein, 1983). Similarly, patients with cerebellar damage show significant deficits in force field learning (Izawa, Criscimagna-Hemminger, & Shadmehr, 2012) and visuomotor rotation adaptation (Morehead et al., 2017; Tseng et al., 2007).

Positron emission topography (PET) and functional magnetic resonance imaging (fMRI) studies have revealed that a wide network of areas, including the

cerebellum, prefrontal cortex, premotor and primary motor cortices, parietal cortex, and basal ganglia, are active during sensorimotor adaptation tasks (Krakauer et al., 2004; Seidler, Noll, & Chintalapati, 2006). As mentioned above, another process involved in sensorimotor learning is reward-based reinforcement: This process is thought to be homologous to standard model-free reinforcement learning (Daw et al., 2011), which involves reinforcing actions that directly lead to reward (e.g., hitting a target). This learning process is dubbed *model-free* because it does not require planning to future reward states but merely associates a running average of rewards with certain actions (Sutton & Barto, 1998).

This type of learning is likely reliant on dopamine-dependent reward prediction errors, which are computed in the midbrain and broadcast to a wide network that includes the basal ganglia and frontal cortex (Schultz, 1998). Patients with damage to the basal ganglia generally show a normal ability to adapt to sensory prediction errors (Smith & Shadmehr, 2005; Weiner, Hallett, & Funkenstein, 1983) but show diminished abilities, relative to controls, to rapidly relearn a perturbation days after initial training (Marinelli et al., 2009), suggesting a role for reinforcement learning in savings and relearning (Huang et al., 2011).

A third procedural process, use-dependent learning, is characterized as an “attractor” toward movements that are repeated (figure 46.1B; Huang et al., 2011): As a particular movement is repeated, similar movement commands are “pulled” toward the repeated direction (Verstynen & Sabes, 2011). This bias is primarily thought to result from plastic changes in primary motor cortex (Mawase et al., 2017), and the stimulation of motor cortex with transcranial magnetic stimulation (TMS) has been shown to enhance the effects of use-dependent learning (Bütefisch et al., 2004). This form of learning is essentially an acquired bias, described as a form of unsupervised learning (Doya, 2000).

We have just outlined three learning processes that are generally put under the “procedural” umbrella. Given the classic results of patient H.M. and the concomitant declarative/procedural divide, it has often been assumed that procedural processes fully account for motor learning. Do any nonprocedural processes subservise motor learning?

Deliberate Action Selection in Sensorimotor Adaptation

Various lines of evidence from prism adaptation studies suggest that *strategic control* plays a role in the rapid reduction of performance errors (Redding & Wallace, 1996). For instance, in a prism adaptation study by

Martin et al. (1996b), one individual appeared to immediately counteract the prism-induced shift after a single trial. Indeed, this individual reported using a deliberate “aiming” strategy. Upon explicit instruction to inhibit that strategy, the participant returned to an incremental learning function. How common are such deliberate strategies, and do they represent a fundamental aspect of motor learning?

Several studies in visuomotor rotation learning have provided indirect evidence for the concurrent operation of deliberate selection strategies and procedural learning. Benson et al. (2011) showed that explicitly describing a rotational perturbation to participants speeds their learning. Heuer and Hegele (2008) used verbal posttests to show that participants could provide a relatively accurate explicit spatial description of the perturbation at the end of learning, suggesting that they could have leveraged this knowledge during learning.

To directly probe explicit learning, Taylor, Krakauer, and Ivry (2014) developed a task in which participants explicitly reported their deliberate aiming strategy before every trial (figure 46.1C). This was accomplished by tiling the learning environment with numbered landmarks that corresponded to possible aiming directions. Participants’ verbal reports could be converted to angular coordinates and subtracted from their actual movement directions on each trial, revealing the time course of implicit adaptation (figure 46.1D). Indeed, both explicit and implicit processes seemed to be active during learning, with the explicit selection of movements rapidly bootstrapping the learning curve and implicit learning slowly calibrating movements over time. Critically, the implicit learning curve was contiguous with observed aftereffects.

A follow-up study (McDougle, Bond, & Taylor, 2015) linked these two processes with a popular model of motor adaptation, the *two-state* model (Smith, Ghazizadeh, & Shadmehr, 2006). In this model, motor adaptation is shown to be parsimoniously explained by the concurrent operation of two subcomponents with different time constants: a “fast” process, which is fast and flexible, and a “slow” process, which is rigid and robust. Importantly, the assumption was that these two processes are qualitatively the same but quantitatively different. Results from McDougle, Bond, and Taylor (2015), however, suggest that the two proposed subcomponents of adaptation represent two fundamentally different learning systems: error-based implicit learning, which appears to map on to the slow process, and explicit action selection, which appears to map on to the fast process.

Explicit learning likely functions in force field adaptation as well: adding a cognitive load through a dual

task causes decreased trial-by-trial adaptation to force perturbations (Taylor & Thoroughman, 2007), and this decrement is mediated by the difficulty of the secondary task (Taylor & Thoroughman, 2008). Awareness and instruction about force perturbations correlates with improved force adaptation (Hwang, Smith, & Shadmehr, 2006), and the fast process of force field learning appears to require access to declarative memory resources (Keisler & Shadmehr, 2010). Lastly, participants can verbally report using explicit strategies during force field adaptation, and the time course of these reports closely matches that seen in rotation tasks (McDougle, Bond, & Taylor, 2015).

The specific mechanisms driving explicit motor-learning processes are still being uncovered. Studies have shown that working-memory capacity correlates with faster rotation learning (Anguera et al., 2010), and this effect has been linked specifically to the explicit learning process (Christou et al., 2016). Eye gaze has been linked to explicit, but not implicit, learning (de Brouwer et al., 2018; Rand & Rentsch, 2014). Strategic processes are linked to high movement preparation times (Haith, Huberdeau, & Krakauer, 2015), implying the recruitment of executive control. Consistent with these behavioral results, regions in prefrontal cortex and premotor cortex are most active in the early phases of sensorimotor learning (Krakauer et al., 2004), when explicit strategies are especially important. As learning progresses, activity follows a rostrocaudal shift from frontal to parietal and subcortical areas (Krakauer et al., 2004), supporting a model where expensive computations may be slowly replaced by cached, overlearned responses (Haith & Krakauer, 2018).

The Interaction of Controlled and Automatic Motor Learning Processes

Given this multitude of learning processes, a fundamental open question concerns if and how they interact. In one clever study, Mazzoni and Krakauer (2006) found that explicit and implicit processes appear to be relatively independent: In a rotation task, after participants experienced two standard rotation trials, the experimenters intervened and instructed participants to aim at a landmark distal to the target that fully counteracted the rotation. Participants easily adopted this strategy and performed perfectly on the subsequent trial. However, after several trials participants’ movements began to overcompensate and drift in the direction opposite the rotation, paradoxically making them less accurate.

This decidedly suboptimal behavior suggested that the error-based system was not responding to performance

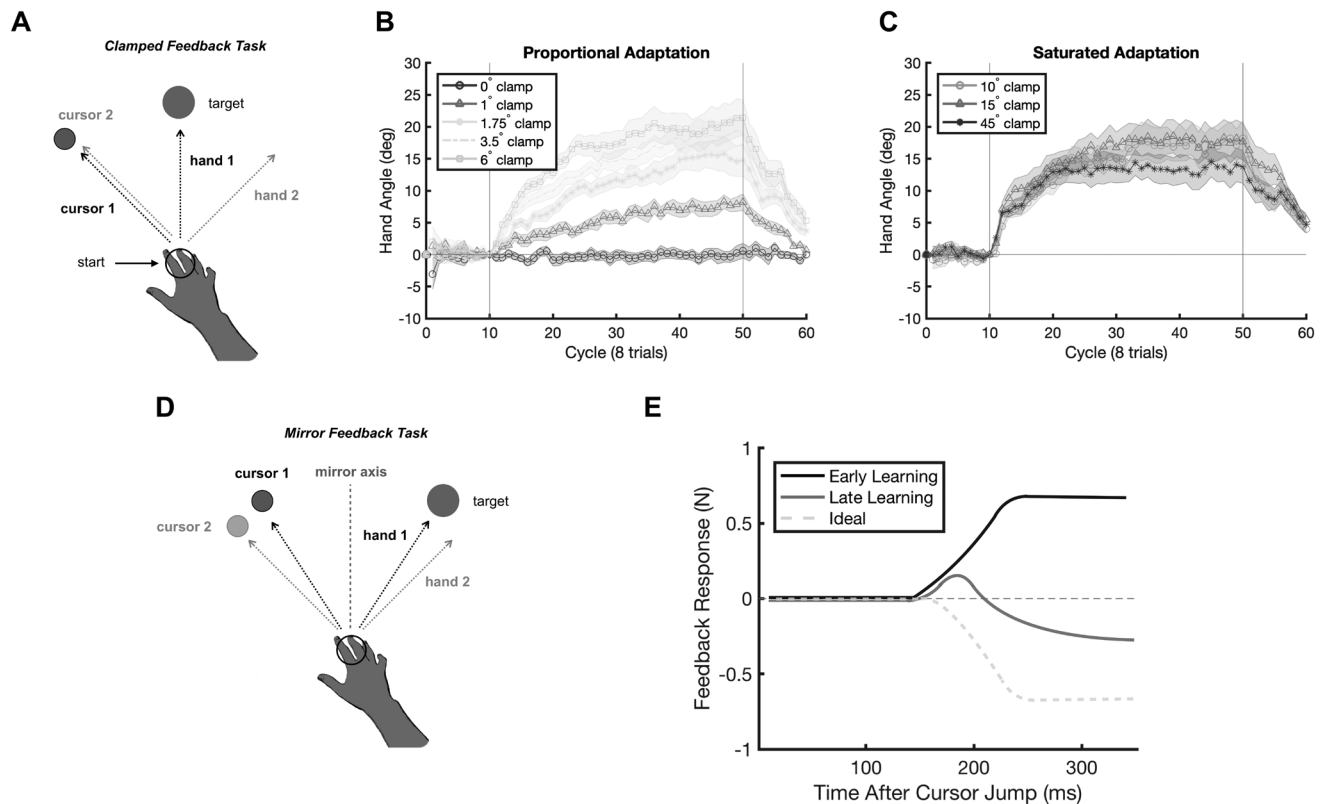


FIGURE 46.2 *A*, Clamped visual feedback used to isolate implicit learning processes. Adapted from Morehead et al. (2017). The hand will adapt in response to a sensory prediction, even though performance error is clamped. *B*, A small range of sensory prediction errors show scaling effects on the rate of learning, but *(C)* large sensory prediction errors do not scale learning rates. Adapted from Kim et al. (2018). *D*,

Schematic of mirror task used in Telgen, Parvin, and Diedrichsen (2014). Standard adaptation causes an increase in error, suggesting that the task must be learned in other ways. *E*, Short-latency feedback responses to a displaced cursor do not show ideal adaptation even after prolonged exposure to a mirror perturbation. Adapted from Telgen, Parvin, and Diedrichsen (2014). (See color plate 51.)

errors in the task (i.e., the discrepancy between the observed feedback and the target) but rather to a task-irrelevant sensory prediction error (i.e., the discrepancy between the observed feedback and the predicted feedback, given the particular motor command). The rigidity of error-based learning was further highlighted by Morehead and colleagues (2017). They developed a task in which participants are instructed to aim directly at visual targets and ignore a consistent rotational error on every trial (figure 46.2*A*). Critically, the imposed error is of the same magnitude for every trial regardless of the participant's direction of movement. This *error-clamp* paradigm produced a surprising result: adaptation proceeded even though the error had no relevance to the participant's movement direction, and movements were adapted well past where they would need to go to fully compensate for the error (e.g., 25° of adaptation for a 7.5° rotational error). These results suggest that implicit adaptation occurs at a relatively fixed rate without regard to performance error, supporting the idea that the processes may not interact directly (Mazzoni & Krakauer, 2006).

Furthermore, error-based learning is generally insensitive to the magnitude of sensory prediction errors (Bond & Taylor, 2015; Morehead et al., 2017), though it shows limited sensitivity when errors are small (figure 46.2*B, C*; Kim et al., 2018).

Given the above limitations, it is suggested that error-based cerebellar adaptation alone cannot fully solve the motor adaptation problem; rather, this process is best suited for retooling a well-trod internal model, or learned *control policy*. Consistent with this interpretation, Telgen, Parvin, and Diedrichsen (2014) further exposed the constraints on error-based learning using a mirror-reversed visuomotor transformation instead of a rotation. In mirror reversal, the solution to the task is not to adjust movements in the direction opposite the error direction but rather toward and then across the mirror axis (figure 46.2*D*). Here, a simple directionally sensitive algorithm would fail to counter the perturbation and would actually make performance worse by adapting movements away from the mirror axis. Indeed, after extensive exposure to a mirror reversal,

appropriate motor commands for countering the mirror were rarely elicited—rather, they appear to be blunted—suggesting that participants had not formed an automatic, mirror-reversed internal model (figure 46.2E; Telgen, Parvin, & Diedrichsen, 2014). After rotation learning, however, adapted motor commands were highly reliable and were easily expressed at short reaction times, consistent with the updating of an existing control policy. These results suggest that when humans are required to learn a novel, complex visuomotor mapping, error-based adaptation alone cannot forge a new automatic control policy—that process likely requires weeks of training and perhaps other neural systems, like the basal ganglia. In this sense, mirror-reversal learning is similar to learning a novel motor skill from scratch.

Critically, participants in the mirror-reversal study (Telgen, Parvin, & Diedrichsen, 2014) were given limited reaction time to block time-consuming explicit planning processes. It is possible that performance under mirror reversal would be much improved given ample time to deliberate on each trial; indeed, explicit knowledge of the environment does affect how simple motor skills like the serial reaction time task (SRT) are learned and which brain networks are recruited during learning (Grafton, Hazeltine, & Ivry, 1995).

Recent results have put forward a potential interaction between deliberate action selection and implicit adaptation. Evidence has been provided that adaptation is maximal at the most visited aiming direction (Day et al., 2016)—that is, the actual parameter that undergoes implicit adaptation may be tied to the volitional motor plan itself, rather than the downstream muscle commands (but see Gonzalez Castro, Monsen, & Smith, 2011). This can be tested using a generalization task, in which aftereffects are probed at various locations. The largest aftereffects are seen when, in the washout phase, participants reach in the direction they most commonly reported aiming toward during learning, not the direction they actually moved to (McDougle, Bond, & Taylor, 2017). Thus, the explicit planning stage may determine which internal representation is updated by subsequent sensory prediction errors.

This interpretation is echoed in interference studies, in which two opposing force field perturbations are induced over the same movement direction (on different trials). Sheahan, Franklin, and Wolpert (2016) showed that interfering perturbations can be learned if each is associated with a different movement plan, operationalized by different “follow-through” targets that participants would occasionally have to move toward at the end of the reach (i.e., after pushing through the force field). Without cueing distinct plans, massive

interference is observed in such tasks. These results are consistent with previous work (Hirashima & Nozaki, 2012; Krakauer et al., 2006) showing that the context of learning a specific perturbation (e.g., the effector used during learning) may act as a cue. This earlier work led to a top-down cognitive interpretation for interference effects in visuomotor adaptation experiments (Krakauer, Ghez, & Ghilardi, 2005; Krakauer et al., 2006), an interpretation that fits with the Sheahan, Franklin, and Wolpert (2016) results.

The neural interpretation is that the plan sets the initial conditions of a neural trajectory in the downstream dynamic system that directly controls motor output: recent results using a brain-machine interface (BMI) in nonhuman primates revealed that training on a visuomotor rotation “covertly” (i.e., using the BMI but not eliciting actual arm movements) transfers to overt motor behavior on that same rotation and that this transfer is linked to corresponding motor cortical activity in the planning stages of both contexts (Vyas et al., 2018). It is likely that in many settings the planning stage encompasses explicit selection of a desired action.

Explicit action selection can rapidly increase the likelihood of arriving at a rewarding state, allowing implicit, model-free reinforcement processes to then reinforce movements that maintain that state. But what if the environment changes? Learning environments are often not static, undergoing changes over time and contexts. One phenomenon in motor learning is *savings*, whereby an association that appears to have been extinguished is learned more rapidly upon a second exposure.

Huang et al. (2011) suggested that savings is attributable to reinforcement learning, though whether this effect was driven by explicit strategizing or not was unclear. In a recent study, Morehead et al. (2015) showed that savings is attributable to explicit selection processes but not implicit processes. Moreover, participants can leverage contextual cues to “re-aim” and rapidly improve their performance when the environment changes (Morehead et al., 2015), highlighting the contextual sensitivity of selection strategies. In another study Huberdeau, Haith, and Krakauer (2015) showed that even very brief exposure to a rotation (e.g., as few as five trials) leads to faster relearning of that rotation the next day. This result is not parsimoniously explained by error-based adaptation, which acts on much slower timescales (McDougle, Bond, & Taylor, 2015).

Haith, Huberdeau, and Krakauer (2015) used a forced-response time paradigm to dissociate explicit planning processes (which require ample preparation time) and implicit adaptation (which requires very little preparation time; Telgen, Parvin, & Diedrichsen, 2014).

Savings was attributable to the process that required high preparation time, consistent with the role of deliberative planning in savings. Surprisingly, the importance of explicit processes for savings has been corroborated in gait adaptation (Roemmich & Bastian, 2015), which is generally considered an implicit learning process.

Explicit Learning and a Role for Factual Knowledge in Motor Learning

Why have so many learning processes? Intuitively, for an optimal learner, it seems useful to have multiple processes that act on different timescales and respond to different error signals (Huberdeau, Krakauer, & Haith, 2015); different systems could be suited to different points on the learning curve or to different tasks altogether. One relevant analogy is the dissociation of model-based and model-free reinforcement learning (Daw et al., 2011; Haith & Krakauer, 2013). Model-based learning requires an explicit model of transition probabilities between responses and sensory inputs, and model-free learning merely reinforces directly rewarded responses. One speculation is that responses reflecting model-based computations (which could initially rely on working memory) are themselves made automatic (Economides et al., 2015; Huberdeau, Krakauer, & Haith, 2018). Perhaps during learning there is a transition from explicit model-based planning to an intermediate form of working memory-based stimulus-response association (S-R) and finally to habitual, model-free S-R. In this model, cognitive strategies and implicit learning work cooperatively (Collins & Frank, 2018).

While direct interactions between explicit and implicit learning processes are poorly understood, explicit learning can counter the sometimes negative effects of implicit learning (Taylor & Ivry, 2011). Moreover, as mentioned above, results from generalization (McDougle, Bond, & Taylor, 2017) and interference studies (Hirashima & Nozaki, 2012; Sheahan, Franklin, & Wolpert, 2016) suggest that volitional planning carves out the neural representations that undergo implicit adaptation. In this view, explicit selection is the fundamental first step of learning, providing the foundation on which subtle, incremental performance improvements are built. This logic could be extended to the role of reinforcement as well, where an explicit strategy guides the learner to the subset of movements that produce rewarding states, and these movements are then incrementally reinforced (Holland et al., 2018).

The sequestering of *procedural* memory in cognitive neuroscience can be attributed in part to the seminal studies on hippocampal patient H. M. (Milner, 1962). In a classic experiment, H. M. appeared to show

improvements in mirror tracing, a difficult task in which a complex shape must be traced under mirror-reversed vision of the hand. H. M. appeared to improve at this, and similar motor tasks, without explicit awareness that he had ever performed the task before (Milner, Corkin, & Teuber, 1968; Shadmehr, Brandt, & Corkin, 1998).

Critically, two facts about the studies on H. M. are relevant: First, while H. M. did show some improvements, his performance was often well below that of controls, suggesting that some aspect of performance was impeded by medial temporal lobe damage. If learning such tasks was purely procedural, why should he experience any deficits?

Second, and more importantly, for H. M. to properly perform the motor tasks each day he had to receive explicit instructions on both what the task required and how to do it (Stanley & Krakauer, 2013). Although H. M. could follow these instructions to set about doing the task, he would forget the instructions between sessions. Similar results have been found in studies of amnesiac patients learning to use novel tools: without daily explicit instruction, amnesiac patients cannot begin to solve such tasks (Roy & Park, 2010).

Access to episodic memory may play a key role in motor learning by setting the “initial state” of the learning process—that is, to rapidly reduce the dimensionality of the learning problem by selecting a manifold of correct actions to be performed. One possibility is that the medial temporal lobe helps the learner recognize the learning context and recall the appropriate subset of actions that have been useful in similar situations in the past. Indeed, *episodic control* has recently become an important concept in reinforcement learning (Gershman & Daw, 2017).

Moving forward, motor learning should be understood as recruiting a full taxonomy of memory systems, even in the context of simple adaptation tasks. That a wide network of neural systems serves motor adaptation should not be surprising; indeed, adaptive, precise movement is perhaps the most fundamental function of the central nervous system.

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