Implicit and Explicit Processes in Motor Learning

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Introduction

Executing a movement requires two distinct stages: 1) determining the goal or the desired consequence of the movement and 2) specifying the parameters of the movement. Playing billiards requires selecting which ball is to be pocketed, and how to approach the cue ball to achieve this goal. The person may plan to strike the cue ball such that it directly hits the target ball into the pocket, or may opt to bank the target ball off a bumper. Once the approach is selected, great skill is required to properly manipulate the pool cue such that the cue ball is struck at the proper angle and with the right force.

As demonstrated in this example, motor skills require the integrated operation of planning and execution. To begin to understand how the various processes associated with these phases interact to yield successful motor behavior, it is useful to consider their respective optimization functions. Planning processes must be sensitive to outcome variables defined in terms of goals, allowing the system to generate and explore novel strategies that may produce long-term gains, even at the expense of short-term costs. While these factors may also influence execution processes, various lines of research indicate that movement optimization is more focused on minimizing factors such as energy expenditure or motor noise.

Planning and execution processes also tend to differ in terms of awareness. Planning processes are frequently explicit—in our pool example, the player might announce an intention to put the eight ball in the corner pocket. Execution processes are generally more implicit—it may be difficult to teach a novice how to balance the cue stick with the postural hand. This distinction is far from absolute: It seems clear that many processes involved in planning operate implicitly (e.g., biases) and we can certainly be aware of how our execution failed, even without external feedback. Nonetheless, it is useful to keep in mind the planning/execution distinction when considering the role of awareness in the study of skill acquisition.

In this chapter, we focus on two model tasks: the serial reaction time task (SRT) and visuomotor adaptation. An appealing feature of each of these tasks is that they have goal-selection and movement-execution stages, but with emphasis on different stages as most relevant to the task. In the SRT, goal selection is critical to success, while simple motor execution is less important. In visuomotor adaptation, movement execution is critical to task performance and goal selection is less emphasized. Researchers have probed and/or manipulated awareness in experiments with both tasks. We review this literature here, focusing on how these two experimental paradigms offer insight into understanding the functional role of explicit and implicit processes in the acquisition and refinement of goal-directed motor behavior. A key theme in this chapter is to ask whether the manner in which a skill is represented varies as a function of learning under implicit or explicit conditions. Indeed, we conclude the chapter with an integrative model of the role of implicit and explicit processes in visuomotor adaptation.

Goal-driven Learning: Insights from the SRT task.

Sequence learning has proven to be an invaluable tool in examining the contribution of explicit and implicit processes in motor learning. In the SRT task, the participant performs a sequential choice reaction-time task. In the standard task, the stimuli appear at one of four locations and the participant makes a key press with one of four fingers to indicate the cued location (Nissen and Bullemer, 1987), responding as quickly as possible (Figure 1A). The key manipulation is whether the series of spatial locations are selected randomly or follow a specified sequence. Learning is inferred by the difference in reaction time (RT) on trials or blocks in which the stimuli follow a sequence compared to when they are selected at random. Over time, the participants become faster at responding to predictable events and show a cost in RT when these predictions are violated (Figure 1B).

An appealing feature of the SRT task is its simplicity, making it appropriate for studies with both normal and neurologically impaired individuals. Participants need not be instructed that they are to learn a sequence; rather, the RT data provide a measure of the degree of sequence learning. Nonetheless, participants may develop partial awareness of the sequence, and in the extreme, reach the point where their RTs anticipate the onset of the stimuli. The degree to which participants gain awareness of the underlying sequence can also be experimentally manipulated. Awareness of the sequence may be abolished or attenuated when participants are required to simultaneously perform the SRT task and a demanding secondary task (e.g., discriminate high and low pitch tones that are presented during the response-to-stimulus time interval). Assessing awareness can be tricky (Willingham et al., 1989; Perruchet and Amorim, 1992; Curran and Keele, 1993): Post-experimental interviews, in which the participants are asked to either recall the sequence or perform a forced-choice task (e.g., "Press a key indicating where the next stimulus would occur."), are generally used. Even when awareness by these measures is near chance level, sequence learning is evident, although to a lesser degree than under single-task training (Nissen and Bullemer, 1987). The degree of dual-task attenuation (Figure 1B) is related to a variety of factors such as sequence complexity (Cohen et al., 1990) or the temporal relationship between the SRT stimuli and the secondary stimuli (Hsiao and Reber, 2001).

A key debate in the SRT literature concerns the overlap of implicit and explicit learning. Behaviorally, one might suppose that implicit learning reflects the formation of relatively weak stimulus-response associations; gaining explicit awareness of the sequence provides a means to rapidly strengthen these associations. Alternatively, implicit and explicit learning may involve relatively independent processes. Curran and Keele (1993) explored this question by providing a group of participants with knowledge of the sequence prior to the start of SRT training. As expected, RTs were very fast. However, when a secondary task was introduced after training, performance became similar to a group trained under dual-task conditions from the start (Figure 1C). This result suggests the parallel operation of explicit and implicit learning systems: While learning occurred within both systems during training for the informed group, only the implicit system could continue to operate when the secondary task was introduced. Conversely, participants that initially learned under dual-task conditions showed marked improvements when the secondary task was removed; Indeed, they performed similarly to participants trained under single task conditions.

The parallel operation of explicit and implicit learning is also borne out at the neural level. Grafton and colleagues (Grafton et al., 1995; Hazeltine et al., 1997) used PET while participants performed the SRT task with and without a secondary task. When attention was distracted, awareness was minimal and learning related changes were prominent in intraparietal cortex, supplementary motor cortex, and motor cortex. In contrast, during single-task training, learning-related changes were correlated with increased activity in prefrontal cortex (PFC), premotor, and the temporal lobe. Within this condition, some participants developed awareness of the sequence. Interestingly, there were minimal activation differences in learning-related areas between the aware and unaware participants. Other neuroimaging studies of sequence learning without distraction have identified learning effects in similar networks (Rauch et al., 1995; Doyon et al., 1996; Seidler et al., 2005). These results suggest that, whereas, implicit sequence learning involves an increase in activation in motor regions, explicit sequence learning involves the recruitment of a network associated with a range of attention-demanding tasks.

Studies of patient populations provide a direct assessment of the neural regions associated with implicit and explicit learning. The classic work with H.M. (Corkin, 1968), a patient who underwent a bilateral temporal lobectomy, demonstrated that skill learning is preserved in the face of a severe disruption of declarative memory. This dissociation has been confirmed in subsequent work involving amnesic patients suffering from a range of disorders and pathologies affecting the medial temporal lobe (MTL) region (Corkin, 1968; Weiner et al., 1983) or pharmacological studies that induce transient amnesia (Nissen et al., 1987). These individuals may exhibit retention of sequence learning over extended periods of time, despite having no episodic memory of ever performing the task (Nissen and Bullemer, 1987; Nissen et al., 1988). Thus, SRT learning does not require declarative knowledge or awareness of the sequence, nor does it require the involvement of neural regions associated with the formation of declarative memories.

Conversely, impairments in SRT learning have been observed in patients with lesions of subcortical structures associated with implicit skill learning and automatization (Phillips and Carr, 1987; Saint-Cyr et al., 1988; Pascual-Leone et al., 1993; Doyon et al., 1997). Patients with Parkinson's disease or focal basal ganglia lesions exhibit a range of performance on the SRT task, with some studies suggesting a severe impairment (Jackson et al., 1995) and other studies reporting modest degrees of learning (Pascual-Leone et al., 1993; Doyon et al., 1997). The effects of cerebellar pathology are more pronounced. These individuals have been shown to exhibit essentially no evidence of sequence learning (Pascual-Leone et al., 1993; Doyon et al., 1997; Shin and Ivry, 2003).

However, one recent study suggests that the cerebellum may not be related to sequence learning *per se*, but may be involved with the maintenance of the S-R associations (Spencer and Ivry, 2009). In most sequence learning paradigms, the participant is presented with a stimulus on a computer screen and responds on a keyboard. This translation process, from the screen to a keyboard may engage working memory processes, with the indirect relationship between stimulus and response space constituting a form of symbolic transformation (Ivry et al., 2004). When the demands on this transformation are minimized by aligning S-R space (i.e., responses are made directly at the stimulus locations), patients with cerebellar degeneration showed normal learning (Spencer and Ivry, 2009). In contrast, the same individuals exhibited no evidence of learning when the cues were indirect, even though the responses were identical to those required with the direct cues. This dissociation argues against a direct cerebellar role in sequence learning.

The dichotomy between explicit and implicit processes has proven extremely useful for developing a taxonomic description of memory, as well as identifying critical neural systems associated with different memory tasks. As noted above, the MTL appears to be essential for the formation of declarative memories. However, given that patients with lesions of this region do not have overt impairments of awareness, it remains a challenge to characterize the unique associative processes of this network. Models of MTL function have emphasized the importance of this system in the formation of contextual representations, associations that bind information across different sensory modalities or dimensions (Rudy and Sutherland, 1995; O'Reilly and Rudy, 2001). Keele and colleagues (Keele et al., 2003) extended this idea to the SRT task, arguing that the attenuation of SRT learning under dual-task conditions arises because the secondary task introduces noise into a cross-dimensional associative mechanism. Indeed, if the secondary stimuli are correlated with the SRT stimuli, learning is enhanced (Schmidtke and Heuer, 1997).

Error-driven learning: Insights from studies of visuomotor adaptation.

Another paradigm used to study motor learning centers around tasks in which the participant must adapt movements to overcome an experimentally-induced perturbation. Here, we focus mainly on tasks in which the mapping between visual and proprioceptive space is altered. Such perturbations can be achieved by introducing prismatic eyeglasses (Figure 2A) that impose a translational shift of the visual input (Redding and Wallace, 1988, 1993, 1997) or, with virtual reality systems, a visuomotor rotation (Figure 2B) in which the visual input is shifted in an angular manner (Cunningham, 1989; Imamizu and Shimojo, 1995; Krakauer et al., 2000). These types of perturbations are akin to using a computer mouse, but with a distortion of the mapping between the movement of the mouse and the movement of the cursor. In visuomotor adaptation experiments, rotations typically take on values ranging between 30-60°, with vision of the hand occluded to disguise the perturbation. For this chapter, we will focus mainly on the findings from visuomotor adaptation tasks.

Visuomotor distortions may be overcome by recalibrating an internal model of motor system. An internal model represents a mapping between a desired goal and the motor response necessary to achieve that goal. An error signal is used to recalibrate the mapping between desired goals and motor responses. This signal might be available on-line, allowing the person to make adjustments to the movement so as to achieve the desired location. Alternatively, the experimenter may only provide knowledge of results, ensuring that learning can only occur from trial-to-trial. Participants readily adapt to these visual perturbations, showing a reduction in target errors with training (Figure 2C). Learning to accommodate a visuomotor transformation could occur because of the implementation of an appropriate, volitional strategy -- for example, consciously reaching in the opposite direction of the rotation. However, a pronounced aftereffect is observed when the rotation is removed and the original environment is reinstated: Participants now produce an error opposite to the initial distortion. The presence of an aftereffect provides strong evidence that the motor system has truly been recalibrated.

In contrast to learning in the SRT task, a key feature in visuomotor adaptation is that it is error driven. Adaptation proceeds in a gradual manner, with the learning function typically conforming to an exponentially-decaying function. This suggests that an error is used to continuously adjust the visuomotor mapping, with the magnitude of the change proportional to the error. Recent experiments have suggested that this trial-by-trial process of error reduction may occur over multiple time scales. There appears to be a temporally labile process of learning that learns quickly but with poor retention, as well as a slower process that exhibits better retention (Smith et al., 2006). It remains unclear whether these processes reflect the operation of a single learning system with different time constants, or instead, the contributions of distinct neural systems.

An extensive literature points to a critical role of the cerebellum in error-based learning (Marr, 1969; Gilbert and Thach, 1977). Patients with cerebellar lesions have difficulty on a range of motor adaptation tasks (Rabe et al., 2009), including prism adaptation (Martin et al., 1996a), visuomotor adaptation (Tseng et al., 2007; Werner et al., 2009), and force field learning (Smith, 2005). Neuroimaging studies of visuomotor adaptation report activation changes in a broadly distributed network, including the cerebellum. In general, there is a reduction in cerebellar activity over time, perhaps reflecting the reduction in error. However, one study (Imamizu et al., 2000) reported that this broad decrease in cerebellar activation was accompanied by a focal region showing an increase in activation during visuomotor learning, consistent with the hypothesis that the latter reflects the development of a new internal model.

Activation increases are also observed in various cortical areas. During the initial stages of learning when error signals are large, activation increases are most prominent in frontal areas including dorsolateral PFC and anterior cingulate cortex (Jueptner et al., 1997; Shadmehr and Holcomb, 1997; Floyer-Lea and Matthews, 2004). Areas showing prominent changes over the latter part of training include premotor and motor cortex, and posterior parietal cortex (Shadmehr and Holcomb, 1997; Sakai et al., 1998; Krakauer, 2003; Floyer-Lea and Matthews, 2004). Thus, with training, learning-related activation changes in the cortex shift from frontal areas to motor structures, a pattern consistent with the idea that learning may initially engage areas involved in goal-selection and planning, and then shift to areas involved in movement specification and execution. This shift in activation may reflect the automatization of the skill.

The activation of frontal areas during visuomotor adaptation suggest that explicit processes may be engaged, an assumption consistent with the observation that people are usually aware that the environment has been perturbed even if they cannot explicitly describe the change. Recall that a key component of visuomotor adaptation involves changes in motor execution. The sensorimotor system must be modified such that the action associated with a particular goal incorporates the effects of the altered environment. Thus, while explicit knowledge may not produce a benefit for motor execution, it is possible that explicit processes influence visuomotor adaptation.

As in SRT learning, a demanding secondary task can reduce performance gains during adaptation tasks (Taylor and Thoroughman, 2007, 2008; Galea et al., 2010). The cost is not generic, but maximal when the secondary task stimuli occur simultaneously with movement errors (Taylor and Thoroughman, 2007). Interestingly, the effects of dual-task interference are not limited to conditions in which the participants are aware of the sensorimotor perturbation. Galea et al. (2010) reported similar reductions from a secondary task on the rate of visuomotor adaptation, regardless of whether the participants were aware or unaware of the manipulations. This suggests that implicit processes underlying adaptation entail some degree of overlap with those involved in secondary task processing. Thus, the interference may be unrelated to explicit processes used for adaptation. For example, the interference may result from an overload in sensory processing requirements for the primary and secondary tasks.

A different approach involves participants performing the two tasks in a sequential manner and observing whether they exhibit retrograde interference on the memory of the first task after performing the second (Ebbinghaus, 1885). Keisler and Shadmehr (2010) adopted this approach and found that a word-list learning task following motor adaptation selectively disrupted the most recent motor memories, while leaving older memories intact. This effect was not observed when the secondary task did not involve learning (i.e., vowel counting), suggesting that the point of overlap was within processes associated with learning *per se*. This direct involvement of explicit learning processes may reflect strategy development at a verbal level ("On the next trial, I will push to the left."). The effects of a verbal secondary learning task may disrupt the use of such strategies (Keisler and Shadmehr, 2010).

Finally, a more direct approach for comparing implicit and explicit processes in visuomotor adaptation is to manipulate the manner in which the environmental perturbation is introduced. In the standard paradigm, a rotation is introduced in a single step: the participant is performing a reaching task and a large rotation is abruptly imposed. With the abrupt introduction of the rotation, there is a large error between the cursor and hand, a change participants are generally aware of. An alternative approach is to introduce the rotation in a gradual manner. For example, the rotation may be increased by a few degrees every few trials (e.g., Kagerer et al., 1997). In the gradual condition, the added error with each increment falls within the bounds of motor noise and adaptation occurs without awareness.

Performance is generally more variable when the rotation is introduced abruptly compared to when it is imposed gradually. This variability may reflect the contribution of explicit processes. Some participants may opt to test strategies when they experience the large error following the onset of the rotation; other participants may simply rely on implicit processes (Martin et al., 1996b). Strategic processes have also been proposed to account for individual differences in adaptation rates. Participants with higher spatial working memory capacity show faster adaptation, presumably because they are able to use their mental rotation abilities to compensate for the rotation (Anguera et al., 2009). Moreover, while older adults learn at a slower rate compared to younger individuals (Fernández-Ruiz et al., 2000; Bock, 2005), this difference is attenuated for older adults who are able to explicitly describe the perturbation (Heuer and Hegele, 2008). Interestingly, older adults, despite having slower adaptation rates, show comparable and even larger aftereffects (Fernández-Ruiz et al., 2000; Bock, 2005; Heuer and Hegele, 2008). Thus, explicit knowledge may provide a means to bootstrap adaptation, allowing for the generation of a strategy to facilitate learning, even if this does not directly impact implicit learning within the motor system.

Mazzoni and Krakauer (2006) devised a clever way to examine the interaction of explicit and implicit processes in visuomotor adaptation. Participants were presented with a display of 8 visual landmarks, spaced 45° apart (Figure 3A). On each trial, a visual target appeared at one of the landmarks. After a series of reaches, a 45° counterclockwise rotation was introduced. The participants were then informed about the 45° counterclockwise rotation and instructed to counteract this by aiming 45° in the clockwise direction, using the neighboring landmark as an aiming target (Figure 3A). The implementation of a strategy resulted in good performance and the immediate cancellation of the visual error (Figure 3B). However, as training continued, participants spontaneously increased the angle of their aim, reaching to positions more than 45° in the clockwise direction (Figure 3B). That is, their performance became worse with practice!

To account for this effect, Mazzoni and Krakauer (2006) argued that implicit processes for visuomotor adaptation operate on an error signal representing the difference between the aiming location (predicted endpoint) and the feedback location. Although the participants choose to aim 45° clockwise from the target (so as to offset the rotation), the motor system receives an error since there is a substantial difference between the aiming location and the feedback location. To reduce this error, the aiming location is shifted in the clockwise direction. What is striking here is that the operation of this implicit adaptive process results in an increase in error as defined by the target location. Indeed, the participants were puzzled to watch their performance deteriorate as training progressed. This result points to a strong segregation of explicit and implicit processes. The implicit system does not have access to the strategy; rather, the mechanism underlying implicit learning assumes that the aiming location should coincide with the feedback location and uses this error to update an internal model.

A similar effect has been reported in a drawing experiment in which gain was adjusted such that visual feedback of a movement was either greater or lesser than the actual distance of the hand movement (Sülzenbrück and Heuer, 2009). The participants were provided with an inappropriate strategy, one that called for compensation to a larger gain shift than was actually introduced. While participants initially adopted the instructed strategy—and thus increased the endpoint error-- the motor system eventually adapted to the appropriate gain. This study further supports the segregation between implicit and explicit adaptive processes.

Studies in which participants are given a strategy to compensate for a visuomotor perturbation place explicit and implicit processes in opposition with one another. The strategy provides participants with a guide concerning where to aim their movement, influencing the planning stage of the movement. In contrast, the implicit system operates on the execution stage, realigning the sensorimotor system so that the arm moves toward the desired location. In SRT studies, instructions, when given, are also directed at the selection stage: the participant is informed of the embedded sequence. However, in SRT learning, such manipulations supplement implicit learning in that both explicit and implicit systems are designed to learn the same information, the sequence of stimuli/responses. A strong test of the degree of independence between implicit and explicit processes in SRT learning would require developing an experimental manipulation in which these two systems are put in opposition with one another.

Representation of learning as probed through transfer and generalization.

Transfer studies have been used to explore the representational changes that occur during skill acquisition. In the typical transfer study, participants are trained with one set of effectors and then tested with a different set. Aspects of skill that show strong transfer are taken to indicate components that are represented at an abstract or task-level. Aspects of skills that show weak transfer are taken to indicate components that that are represented at an effector or response-level (Imamizu and Shimojo, 1995). In sequence learning, near-perfect transfer has been observed when the task is initially performed with finger responses and transfer is tested with arm movements (Cohen et al., 1990), indicating that sequence learning is effector-independent. Perfect transfer suggests that learning is of the sequence of stimuli or the sequence of stimulus-to-response mappings. Alternatively, the response code may be represented as a spatial map of locations, or goals.

Transfer is not always perfect. There is a slight reduction in measures of learning for transfer between manual and vocal responses (Keele et al., 1995). Moreover, with extended practice, the degree of transfer in sequence learning is substantially reduced (Karni et al., 1998). A skilled pianist may be able to use her left hand to play the right-hand notes of a learned piece, but performance will not be as fluid or facile. With consolidation, skill representation likely involves some degree of learning at the response level (Grafton et al., 1998).

Researchers have also used transfer-like manipulations to examine the reference frame of a learned representation. In one SRT study, participants learned a sequence and were then asked to move to a new seat such that the left side of the keyboard was now on the right side. Training resumed in the new arrangement, with the sequence either following the same pattern as before or following a mirror-reversed pattern. Performance was best when the sequence was reversed, indicating that learning was in an egocentric frame of reference (relative to body) rather than in an allocentric frame of reference (relative to the world) (Witt et al., 2008), see also (Liu et al., 2007).

What remains unclear from this study is whether the learned representation is effector-centered. For example, if the index finger was used to start the sequence, reversing the sequence (and participant) would mean that the sequence would again start with the index finger. To address this issue, Witt et al (2008) had participants initially learn the sequence with their hand in a supine configuration (palm face up). During transfer, the posture was altered such that the hand was now in a prone configuration (palm face down). Interestingly, the participants showed a high degree of transfer, indicating that the sequence was represented in an egocentric reference frame centered on the head or body, rather than a frame based on the effector (e.g., the hand). As in the earlier transfer studies, these results indicate that a large component of learning is not linked to specific muscles or movements, but rather is situated in a space relative to the body. It should be noted that the effects of awareness in these studies are unclear. It may be that the reference frames underlying explicit versus implicit learning processes are different.

Transfer and generalization studies have been used to ask similar questions regarding sensorimotor adaptation. Learning here can be in a coordinate system that is in extrinsic space and centered on the hand (Vindras and Viviani, 1998). When participants are trained to learn a visuomotor rotation at a specific location (e.g., target in upper right quadrant), the degree of generalization to other locations drops off sharply as the angular distance between the training and test locations increases (Krakauer et al., 2000). However, a small, yet significant degree of transfer extends across the entire workspace. Moreover, specific components of adaptation transfer across hands, and these effects are in extrinsic space. That is, training with the right hand to a rotation in the upper right quadrant is associated with the largest left hand transfer in the same quadrant (Imamizu and Shimojo, 1995; Sainburg and Wang, 2002). Thus, the learned representation exhibits some degree of abstraction, both in terms of generalization to untrained locations and across effectors. In this manner, implicit learning for visuomotor adaptation and sequence learning are similar, despite the underlying task and computational differences.

The picture becomes more complicated when considering generalization effects following adaptation in a novel force field (Shadmehr and Mussa-Ivaldi, 1994). Initially, the movements are perturbed in the direction of the force. With practice, participants learn to counteract the forces in order to move straight to the target. When the force field is unexpectedly removed, an aftereffect is observed, with the movement now shifted in the opposite direction. Thus, participants have learned the dynamics of the force field, rather than adopting a strategy that generically minimizes the perturbing effects of the forces (e.g., stiffening the limb). When participants train in a particular workspace, generalization is greatest to positions in the workspace where the mapping between joint orientation and the pattern of forces are similar to the training workspace (Shadmehr and Mussa-Ivaldi, 1994).

For the present discussion, two important points stand out. First, participants modified their motor output to produce straight trajectories. This suggests that optimization at the planning level outweighs costs related to execution factors such as torque or energetic expenditure, assuming that these are higher when producing movements that oppose the force field (Thoroughman et al., 2007; Kistemaker et al., 2010). The system appears to emphasize modifying movements to maintain a fixed goal or plan, rather than modifying the plan itself. Second, the pattern of generalization indicates that learning is in intrinsic, joint-centered coordinates (Shadmehr and Mussa-Ivaldi, 1994; Thoroughman and Shadmehr, 2000; Donchin et al., 2003). This pattern of generalization further supports the notion that implicit learning is occurring at the level of motor execution rather than movement planning.

Intermanual transfer designs have also been employed in studies of force field learning. Adaptation from training with one arm transfers to the other arm (Criscimagna-Hemminger et al., 2003). The pattern of transfer is in extrinsic space, such that if one arm learns a clockwise force field, performance with the other arm is better if the force field is unchanged, compared to when it is reversed. This pattern of transfer, however, must be qualified. Force field learning appears to be asymmetric: transfer is observed from the dominant to the non-dominant arm, but not in the reverse direction (Criscimagna-Hemminger et al., 2003).

Moreover, Malfait and Ostry (2004) suggest that intermanual transfer following force field learning may be limited to conditions in which participants are aware of the perturbation. They failed to observed transfer from the right to left arm when the force field was introduced in small, gradual steps. This null result is especially surprising given that this form of learning is frequently considered the paradigmatic example of implicit motor learning. It may be that intermanual transfer involves rather generic information—for example, that an opposing force should be generated in the clockwise direction—rather than the true adaptation of an internal model. Or it may be that awareness puts the system in a mode that enables abstract-level learning, even if the acquired representations are implicit.

The interaction and integration of explicit and implicit processes

In terms of our distinction between planning and execution, we might expect that strategic effects operate at the level of goal selection and response planning. This point is made clear when considering the Mazzoni and Krakauer (2006) study. As noted above, participants were instructed to move to an aiming location next to the target in the clockwise direction, an instruction designed to influence the planning level. This strategy produced an immediate benefit in performance, but also increased the error used by the implicit learning mechanisms. Indeed, the conflict between explicit and implicit processes is confounded with manipulations that influence planning and execution levels of performance.

We further explored this issue in a recent study (Taylor and Ivry, 2011). If the implicit adaptation system fully overrides the explicit system, one would expect performance to continue to deteriorate until the error reached 45°. This seemed highly unlikely – at some point, we expect participants would make some sort of adjustment. Indeed, when the duration of training was extended, the size of the error peaked at around 25°, and then reversed until performance was nearly perfect. To account for this non-monotonic behavior, we developed a novel state space model in which performance is the result of two processes, each modified by its unique error term (Figure 4A). First, the difference between the aiming location and feedback location defines an aiming error, a signal that is used by the implicit system to recalibrate an internal model. Second, the difference between the target and feedback location defines a target error, a signal that is used to adjust the strategy.

Our simulations show that when these two learning mechanisms operate in parallel, one observes an initial drift away from the target, with eventual correction (Figure 4B). Importantly, the model posits that the two processes are always functional. Drift is prominent during the early stages of strategy implementation because aiming error is large and target error is small; thus, changes in performance are dominated by learning within the implicit system. However, as target error becomes large, strategy changes become more prominent (Figure 4C). Even when performance stabilizes with minimal error, the two processes continue to operate, creating a stable tension (Figure 4C). Consistent with this hypothesis, the model accounts for the fact that the aftereffect observed when the rotation is turned off is larger than the maximum drift (Taylor and Ivry 2011).

This modeling enterprise raises an interesting question: Why is drift not observed in standard visuomotor rotation experiments given that participants, at least under some conditions, spontaneously develop a strategy? An important methodological difference between the task used by Mazzoni and Krakauer (2006) and the standard task is the presence of landmarks. In the former, landmarks were present every 45° to provide a reference point for the aiming strategy. In the standard task, these landmarks are absent; participants only see a stimulus at the target location. We propose that the landmarks serve as a proxy for the predicted location of a movement. When these landmarks are absent, the participant's sense of 45° is likely uncertain, and thus the weight given to the aiming error term is attenuated. We tested this idea by comparing conditions in which the landmarks were always present, disappeared at movement initiation, or were never presented. Consistent with the certainty hypothesis, the degree of drift was attenuated as uncertainty increased (Taylor and Ivry 2011). In fact, when the landmarks were never present, drift was minimal throughout the training block. These results are similar to the "target-pointing effect" on adaptation, where adaptation scales with the degree of visual error information available to the motor system (Welch and Abel 1970).

Our modeling efforts provide a first exploration of the interaction of strategic and implicit processes. Consistent with the conjecture of Mazzoni and Krakauer (2006), it appears that the implicit system is completely isolated from the strategy and is only involved in improving movement execution. In contrast, the strategy is adjusted with an error signal that reflects the movement goal, minimizing target errors. Learning within this system modifies a representation relevant for planning, ensuring that the outcome of the action achieves the desired goal.

This synergistic, two-process interpretation may also provide a different perspective for understanding the consequences of neural pathology on specific learning processes. Consider the effects of cerebellar damage on sensorimotor control and adaptation. One might consider the impaired performance reflective of the operation of a compromised system, one that is functioning at a suboptimal level. Alternatively, the patients' performance may reflect a compensatory process, one in which they have come to rely on alternative forms of control. Lang and Bastian (2002) observed that patients with cerebellar damage performed surprisingly well when asked to make rapid, complex drawing movements, reaching a performance level comparable to that of control participants. However, when patients were required to perform a concurrent, secondary task, their drawing performance was markedly reduced (Lang and Bastian, 2002). These results suggest that the patients may have relied on a strategy-based system, one that was taxed by the inclusion of the secondary task.

We tested this idea by instructing patients with cerebellar degeneration to use an explicit strategy to compensate for a visuomotor rotation. The patients were capable of using the strategy, to offset a visuomotor rotation. More importantly, they showed minimal maladaptive drift over the course of training (Taylor et al., 2010), consistent with the idea that the implicit adaptation system was impaired.

However, these results fail to explain why patients do not generate their own compensatory strategies? For example, in visuomotor adaptation studies, some patients will continue to produce large and consistent errors for over a hundred trials. To understand this paradoxical behavior, it is useful to consider that, while an explicit strategy does not influence implicit adaptation, the converse may not be true: Implicit processes may inform explicit strategies. Typically, visual errors in rotation studies are quite large (Weiner et al., 1983), and the patients are aware of their poor performance. However, given the complex rotational pattern of the errors, generating a successful strategy may not be entirely obvious. The error pattern would place a high demand on the attention and working memory areas required to develop the appropriate strategy.

Patients with PFC lesions have been tested to explore the importance of working memory and cognitive control processes on motor learning tasks. Disruption of PFC with TMS has been shown to selectively disrupt SRT learning (Pascual-Leone et al., 1996). More importantly, patients with PFC lesions also exhibit pronounced deficits in visuomotor adaptation (Slachevsky et al., 2001, 2003; Ivry et al., 2008), a result that challenges the notion that learning is limited to processes typically associated with implicit learning. Interestingly, these patients have difficulty describing the perturbation, or when aware of it, have difficulty reporting what action would be required to compensate for the perturbation (Slachevsky et al., 2001, 2003). Thus, their deficit may, in part, be related to difficulty with generating strategies for motor adaptation.

Concluding remarks

The terms “explicit” and “implicit” have proven useful for describing subjective states, but have also presented problems when employed as theoretical constructs. Our emphasis here has been to consider how processes associated with explicit and implicit learning may differ, and what the computational implications of these differences are for theories of motor learning. Explicit processes may best be related to the desired goals of an action. Returning to our initial billiards example, representations that are accessible to awareness are related to selecting which ball is to be pocketed, and how the cue ball will be approached to achieve this goal. On the other hand, implicit processes figure prominently in establishing the fine calibration and coordination required to execute the desired movement, defining the parameters necessary to execute the movement. Both the selected movement and the execution of that movement may result in performance errors that are used to refine future movements. Our modeling work on visuomotor adaptation makes transparent the fact that explicit and implicit processes can operate on very different error signals. Strategic planning processes are sensitive to performance errors. In contrast, motor execution processes are sensitive to prediction errors between a desired and actual outcome. The former helps define what the desired movement should be, while the latter is essential for the successful implementation of the desired movement. These processes work synergistically to produce skilled actions.

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Figure legends

Figure 1. A) Stimuli (LEDs in front of keyboard) appear at one of four locations and participant presses corresponding key. B) Single-task condition: The stimuli may be presented at random (R) or follow a repeating sequence (S). Increase in RT on random block after sequence training provides measure of learning. Dual-task condition: Addition of a secondary task (e.g., tone counting) results in slower overall RTs and reduced learning effect (compare blocks 8 and 11). C) White: Participants provided with explicit knowledge of sequence prior to the start of SRT training. Black: Participants trained under dual-task condition from start of training. During last four blocks, both groups tested under dual-task conditions. Learning, as measured by decrease in RT on Block 13, compared to surrounding blocks, is similar for the two

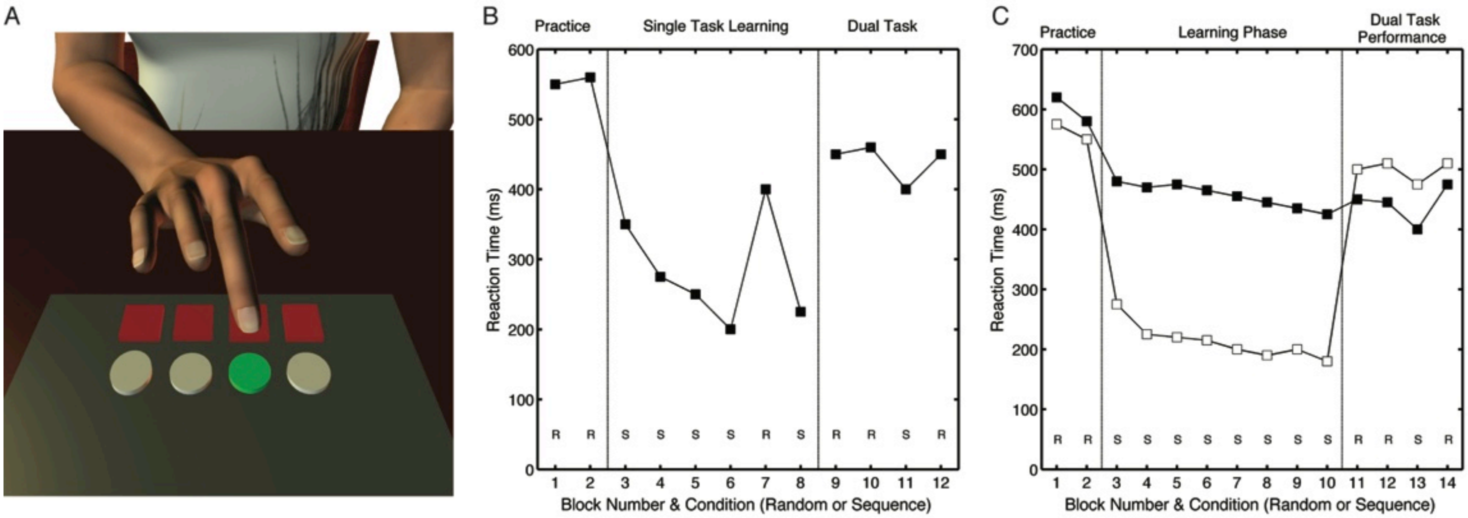
groups, suggesting parallel operation of explicit and implicit learning during single-task training. Adapted from Curran and Keele (1993).

Figure 2. A) Prism glasses induce a mismatch between eye-hand calibration, producing errors in throwing or reaching in the direction of the lateral prismatic shift. B) Virtual reality environments are used to impose systematic transformation between actual and projected hand position. Vision of the limb is occluded. In this example, target was the green circle and a 45° rotation clockwise led to displacement of feedback location (red). C) Hypothetical learning curve for a visuomotor rotation. A 45° rotation is presented for movements 100-300. Target errors are initially in the direction of the rotation, but with training, the person adapts. After learning, the rotation is removed (movements 301-500) and target errors are now in a direction opposite to the rotation (aftereffect).

Figure 3. A) In the baseline block, participants move towards the cued green target (could appear at one of eight locations). Red cursor indicates hand position. In the strategy-only block, participants are trained to reach to a landmark (blue circle), 45° clockwise to the target. For the two rotation probes, feedback of hand position was rotated 45° in the counter-clockwise direction. In the rotation with strategy block, participants were instructed to move to the blue landmark to compensate for the rotation. B) Rotation with Strategy: Target errors are centered around zero during the baseline block (1). Large errors are observed when the rotation is unexpectedly introduced (2). When instructed to use the strategy, movements are initially very accurate but, over time, performance deteriorates with error drifting in the direction of the strategy (3). Aftereffect is observed when participants are instructed to stop using strategy (4). Adapted from Mazzoni and Krakauer (2006).

Figure 4. A) Implicit adaptation is based on aiming error, the difference between the aiming location and feedback (blue). Strategy adjustment is based on target error, the difference between the target location and feedback (green). B) When strategy is implemented after onset of rotation, target error is small (performance is accurate), but aiming error is large and implicit adaptation produces deterioration in accuracy. As

target error becomes large, the effect of strategy adjustment becomes more prominent, leading to a reversal of the drift. System eventually stabilizes even though the two learning processes continue to operate. Aftereffect evident when the rotation is removed reveals magnitude of implicit adaptation. Circles: Observed data for one participant. Black: Model fit. C) Dynamics of learning within the implicit system (visuomotor adaptation, thin) and strategy (thick) following trial-by-trial updates with the two error signals.


A
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Practice
Single Task Learning
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Reaction Time (ms)
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Block Number & Condition (Random or Sequence)
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Practice
Learning Phase
Dual Task Performance
700
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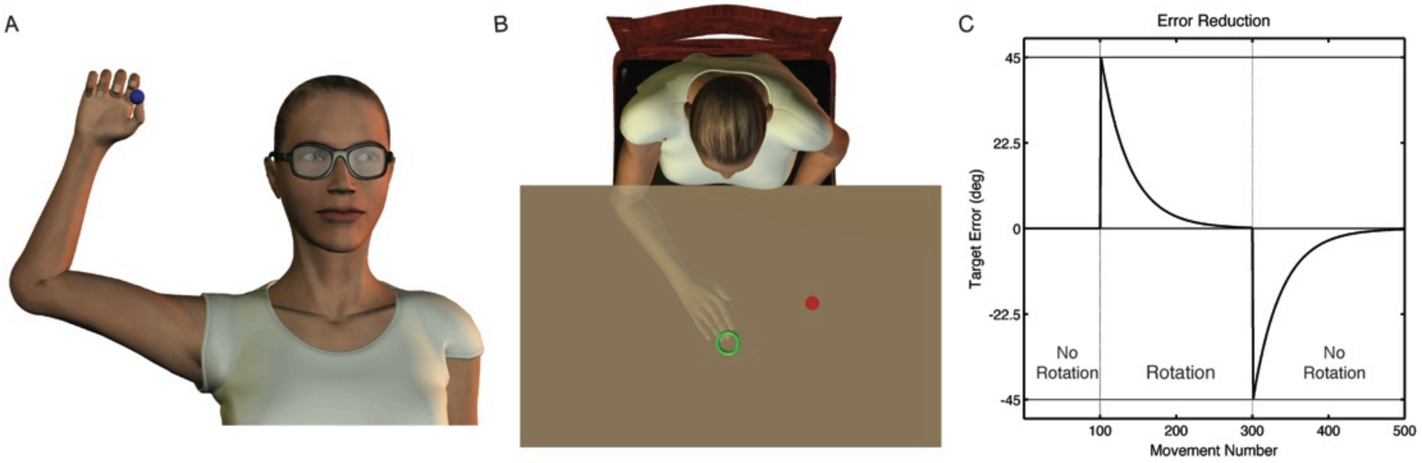
Block Number & Condition (Random or Sequence)

Figure 1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Movement Number

Figure 2

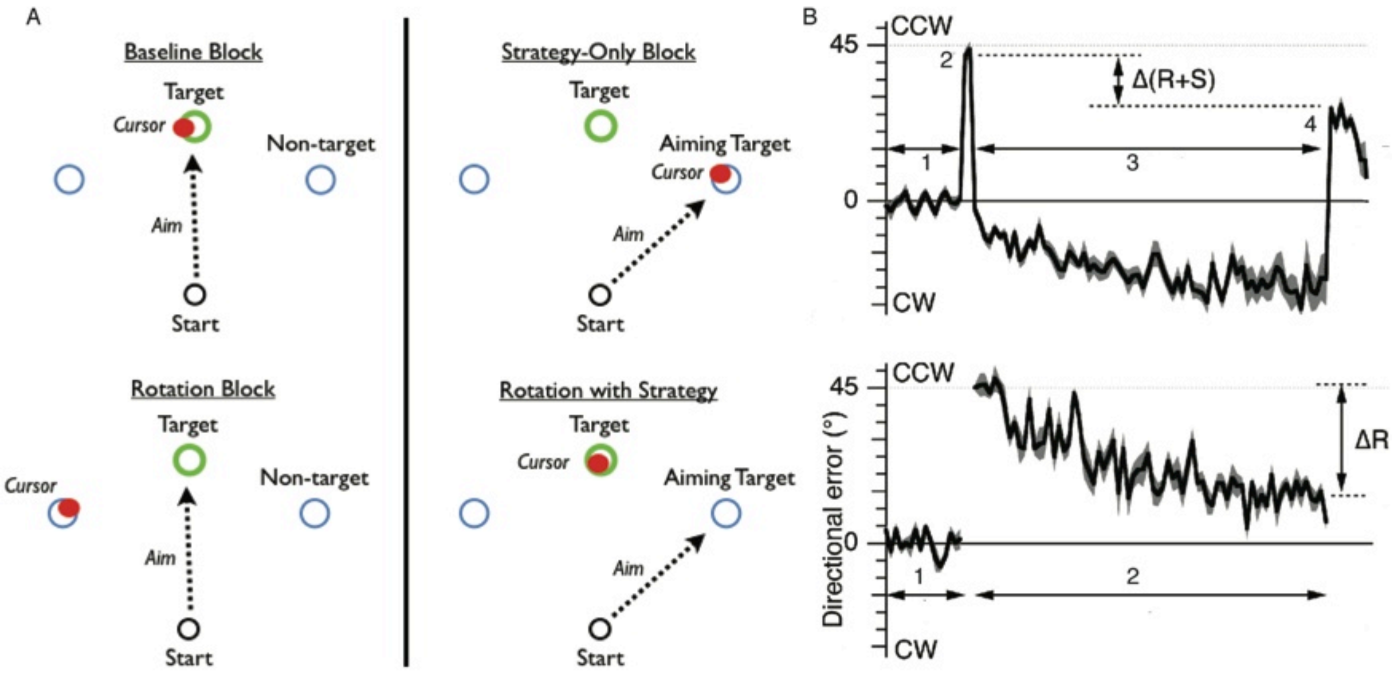
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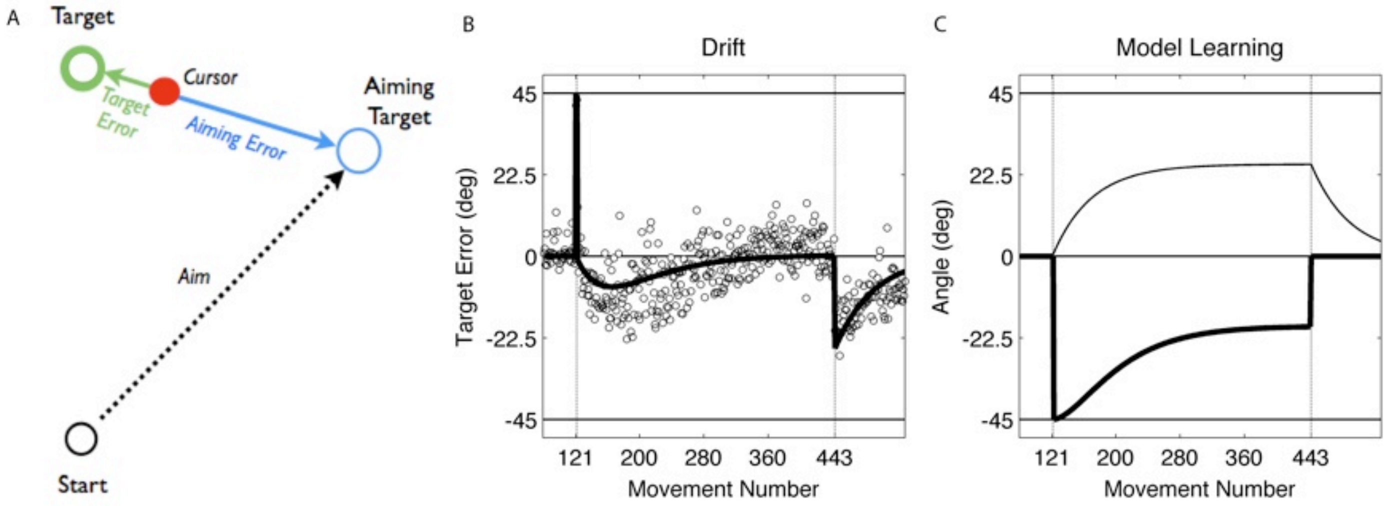
Figure 3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-45
Target Error (deg)
121
200
280
360
443
Movement Number
C
Model Learning
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22.5
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-22.5
-45
Angle (deg)
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Movement Number

Figure 4