UC Berkeley
UC Berkeley Previously Published Works

Title

Taking Aim at the Cognitive Side of Learning in Sensorimotor Adaptation Tasks

Permalink

Journal

ISSN

Authors

McDougle, Samuel D
Ivry, Richard B
Taylor, Jordan A

Publication Date

2016-07-01

DOI

Peer reviewed

Taking Aim at the Cognitive Side of Learning in Sensorimotor Adaptation Tasks

Samuel D. McDougle[1,2], **Richard B. Ivry**[3,4], and **Jordan A. Taylor**[1,2]

[1]Department of Psychology, Princeton University, Princeton, New Jersey 08544

[2]Princeton Neuroscience Institute, Princeton University, Princeton, New Jersey 08544

[3]Department of Psychology, University of California, Berkeley, California 94720

[4]Helen Wills Neuroscience Institute, University of California, Berkeley, California 94720

Abstract

Sensorimotor adaptation tasks have been used to characterize processes responsible for calibrating the mapping between desired outcomes and motor commands. Research has focused on how this form of error-based learning occurs in an implicit and automatic manner. However, recent work has revealed the operation of multiple learning processes, even in this simple form of learning. This review focuses on the contribution of cognitive strategies and heuristics to sensorimotor learning, and how these processes enable humans to rapidly explore and evaluate novel solutions to enable flexible, goal-oriented behavior. This new work points to limitations in current computational models, and how these must be updated to describe the conjoint impact of multiple processes in sensorimotor learning.

The Versatility of Human Motor Control

Flexible use of the upper limbs is fundamental to our species. The ability to manipulate objects with our hands, coupled with an expanding capacity to plan future states, was critical to our ancestors' survival [1]. Dexterous arm movements confer a tremendous advantage for efficiently harvesting foods in varied environments, as well as for manufacturing and manipulating tools. Indeed, Darwin argued that humans' use of thrown projectiles may have been an adaptation brought about by the pressure to hunt, and suggested that this distinctive behavior may be linked to the emergence of bipedalism [2,3]. Though other primates have occasionally been shown to perform analogous upper limb behaviors, these actions are rarely observed and lack much of the precision of human throwing [4–6].

Many classic studies of sensorimotor learning have been based on reaching and throwing movements, with the results helping us gain fundamental insights into foundational ideas such as the trade-off of speed and accuracy [7–10] and the representation of sensorimotor

dynamics [11]. One important subfield of motor learning research employs adaptation tasks to ask how an internal model, a representation of body-environment interactions, is calibrated to support feedback and feedforward control [12]. The internal model concept has provided a useful theoretical tool to understand how people adjust their behavior when moving in atypical force fields or when the visuomotor mapping is altered. These paradigms capture computational problems that enable us to skillfully manipulate objects when dynamics fluctuate (e.g., the changing weight of a bottle as we consume its contents) or when environmental factors require that we adjust our movements (e.g., throwing a frisbee on a windy day). Building on a rich body of neurophysiological and neuropsychological evidence, [13–17] and articulated in sophisticated computational models [18–22], this form of incremental motor learning has provided a fundamental characterization of one important function of the cerebellum.

Models of error-based learning have provided a reasonable approximation of behavior. For example, a simple state space model [18] in which an error signal is used to recalibrate an internal model from trial to trial, captures the general shape of the learning function, one in which performance changes follow a negatively accelerating exponential (or linear in log-log coordinates, [23]). However, these models fail to capture certain features of performance such as spontaneous recovery and savings [20,24]. The inadequacy of these models reflects the complexity of human motor performance: We are flexible, generalist problem-solvers, and, as shown in studies of learning across diverse task domains [25–27], readily employ multiple learning systems to solve the problem at hand. In studies of sensorimotor adaptation, this means that the learner, when presented with an unexpected and salient perturbation, is likely to generate a compensatory strategy or heuristic. Much as the spear fisher adjusts his aim to account for the refraction of light in water, a participant might opt to aim to the side of a target if an opposing force unexpectedly displaces the limb or a visuomotor perturbation results in a large reaching error.

Until recently, strategy use has been considered a nuisance [13] in studies of sensorimotor adaptation, with the experimental instructions often designed to actively discourage this behavior [14,28]. Moreover, the use of heuristics, such as an explicit change in aiming, has been ignored in computational models of the learning process. However, the flexibility of the human motor system allows us to supplement the calibration process. Strategies can allow us to use our planning abilities to rapidly find "good-enough" solutions, ones that might get performance in the right ballpark as the calibration process slowly and subtly homes in on the precise dynamics. In this paper, we review recent developments in studies of sensorimotor adaptation, highlighting work that has provided a richer picture of the operation of multiple learning processes and new insights into how these processes support skilled motor behaviors.

Using Multiple Learning Processes in Response to Sensorimotor Perturbations

The physics of the body and environment are in a continuous state of flux: Not only do long-term changes arise from growth, development, and injury, but, in the short-term, muscles

fatigue and sensory conditions fluctuate. The motor system must rapidly adjust to these variable conditions, and the ease with which we maintain calibration belies its computational complexity [29].

To study this calibration process, researchers have employed a variety of learning tasks — including prism adaptation [14,28,30,31], visuomotor rotations [32,33], and force field learning [11] — in which a perturbation is introduced to alter the relationship between a movement and the resulting sensory feedback. Across a range of contexts, performance typically follows a stereotypical learning function (Fig 1A) driven by a gradient descent process in which the error is reduced in a continuous, monotonic manner. When the perturbation is removed a persistent "aftereffect" is observed, taken as the signature of a recalibrated sensorimotor mapping. Over time, the aftereffect diminishes at roughly the same rate as that observed during the initial acquisition phase, eventually returning to the baseline, non-adapted state.

However, this formulation misses a common-sense approach to the problem participants face in such experiments. While throwing darts one evening, imagine, after donning a pair of prism glasses, that you see a dart land far to the right of the target. It would be reasonable to suppose that an intelligent agent would take steps to volitionally compensate for the perturbation. For example, you might aim to the left of the target on the next trial. Indeed, such compensatory strategies are essential on windy days for golfers and placekickers.

In one oft-cited prism adaptation example, several individuals displayed extremely rapid learning, completely reducing their error on a throwing task after a single trial [28] (Fig. 1B). When queried, these individuals reported using an explicit strategy, estimating the error induced by the glasses and purposively aiming in the opposite direction to negate the perturbation. Interestingly, this strategy proved to be unstable, with successive movements increasingly overcompensating for the prismatic distortion. When instructed to throw "where the target appeared," their performance again took the form of the stereotypical learning function, indicating that performance may reflect the combined effects of strategy use and an implicit form of recalibration.

One clever way to directly examine this hypothesis involved a variant on the standard visuomotor rotation task, one in which participants were given explicit information about the perturbation and instructed to use a compensatory strategy [34]. Vision of the hand was occluded and feedback was limited to the display of a circle that indicated the position of the hand at the end of the movement. After an initial block of trials with veridical feedback, a 45° counterclockwise perturbation was imposed. Critically, after two reaches in this altered environment the experimenter intervened, describing the perturbation and instructing the participants to aim in the clockwise direction. To facilitate the use of this strategy, landmarks were positioned at 45° intervals around the target. Thus, by aiming to the landmark 45° clockwise from the target, the perturbation could be fully negated.

As would be expected, participants performed perfectly on the subsequent trial: Using an aiming strategy enabled one-trial learning (Fig. 1C). However, over the next 80 trials, the participants' movements began to "drift" in the direction opposite the perturbation. This

paradoxical behavior — where performance worsened with practice — suggests that the motor system continued to calibrate the motor commands based on the mismatch between the intended reach location (the aiming landmark) and visual feedback, while ignoring feedback about task accuracy (the difference between the target location and observed feedback). In a subsequent experiment, it was shown that the drift reversed with extended training, an effect attributed to an adjustment in the aiming strategy (Fig. 1D, [35]). This non-monotonicity, together with evidence using various other methods, has made clear that strategy use and implicit recalibration constitute dissociable and relatively independent learning processes, with their dynamic integration resulting in the observed task performance [24,34–45].

The instructed-strategy procedure [34] has provided important insights into the computational constraints on these two processes. However, it doesn't address how or whether people develop and modify strategies in a more spontaneous manner; that is, when the experimenter does not intervene and provide explicit instructions. To address this issue, we developed a task that provides a trial-by-trial measure of the contributions of explicit aiming and implicit recalibration [24,37–39,45]. To assay strategic aiming, participants verbally report their aim direction prior to each reach, providing these reports both before the perturbation and over the course of learning (Figs. 2A,B). Using a simple subtractive procedure (reach angle minus aiming angle), we can estimate the precise state of implicit recalibration in a continuous manner. Interestingly, the lion's share of early learning, especially with large perturbations, is associated with aiming and not recalibration [38]. Furthermore, and perhaps more surprising, aiming remains prevalent even in the late stages of learning, a result that challenges the standard belief that asymptotic performance only reflects the state of a recalibrated sensorimotor mapping [37–39]. Various control conditions indicate that these results are not an artifact of the aiming report task [37,39]. The learning curves and aftereffects in this task are similar to that observed in standard visuomotor rotation tasks, suggesting that strategic processes operate even when the task context (e.g., instructions, landmarks) does not prime their use.

Implications for Computational Models of Sensorimotor Learning

The field of sensorimotor learning has benefitted from the development of rigorous computational models that not only account for observed behavioral results in healthy and neurologically impaired populations, but also generate many testable predictions [18,20,46,47]. As noted in the introductory section, prevailing models of the canonical learning curve use algorithms that capture a gradient descent reduction of error. The most prominent of such models is the two-parameter "state-space" model [18], where a Markovian learning rule is used to update the motor state and account for performance errors on a trial-by-trial basis. One parameter describes a fixed learning rate, the other corresponds to a retention, or memory term.

An important extension of this model was motivated by the idea that performance changes may reflect the operation of multiple learning processes that operate at different time scales [20]; for example, one process might learn quickly with a short retention constant, whereas a second learns more slowly with longer retention. Various puzzling phenomena observed in

motor adaptation tasks, including spontaneous recovery [20,48] and savings [24,49–51] can be explained by this multiple-rate model. Moreover, this work inspired new ways of placing constraints on computational and neural mechanisms of sensorimotor learning. For example, whereas different environments may demand rapid changes (e.g., walking on granite or walking on sand), the body is generally stable. It would be advantageous to use error signals that operate at different rates depending on the nature of the representations [52]. In terms of neural systems, it has been proposed that fast cerebellar learning allows for the rapid reduction of error when learning a new skill or mapping, whereas slower learning within the motor cortex is essential for retention [53].

However, it is not clear how processes such as strategic planning fit into the picture, especially in the case of one-trial learning. One solution is to associate explicit processes with the fast process of the two-rate model, and implicit recalibration with the slow process [39] (Figure 2C). This framing is in accord with results showing that explicit, fast learning is more flexible than sensorimotor recalibration, enabling generalization to new target locations, perturbation sizes, and other variations in task demands [38]. Indeed, many markers of human sensorimotor learning, including savings [24] and structural learning [54], are likely products of our flexible ability to quickly select an appropriate movement plan.

A second major issue concerns the nature of the error signals used for learning. Current versions of multi-rate models assume that different learning mechanisms operate on the same error signal. However, it is increasingly clear that implicit and explicit forms of learning respond to distinct error signals (Figure 3A): Implicit recalibration is driven by the difference between the expected and observed outcome, what is referred to as sensory prediction error [29]. In contrast, strategy learning is sensitive to the difference between the goal and observed outcome, or what is refer to as performance error [35]. Note that in most experimental contexts, and in the natural world, these two types of errors are confounded: We usually aim at the target of our movements, so the expected outcome is the same as the goal. However, experimental manipulations such as the instructed-strategy task [34] or aiming report task [24,37–39,45] decouple these error signals. Thus, in the strategy task, the drift phenomenon described above occurs because the recalibration system is presented with a large error signal — the difference between the aiming location and the rotated cursor, even when performance error is negligible (as in the first aiming trials). Indeed, when these error signals are decoupled, it appears that implicit recalibration is completely insensitive to task success [34,35]. The non-monotonic shape of the performance curve in the strategy task reflects the fact that participants have to "re-aim" to offset the consequences of a modular implicit learning process driven by sensory prediction errors [24,35] (Figure 3A).

This new conceptualization will require revisiting our computational models. Not only is it necessary to incorporate distinct error terms for explicit and implicit processes, but it may also be necessary to reconsider whether these processes utilize different learning algorithms. Recent work suggests that the gradient descent algorithm may be an inappropriate characterization of implicit learning: The learning function and asymptotic state of recalibration does not appear to be proportional to error size [38,55–57], and when isolated from task performance, recalibration appears to proceed in fixed, discrete-like steps [57]. Likewise, explicit learning appears to be highly non-monotonic, producing behaviors more

consistent with active exploration and/or hypothesis testing [37]. Thus, the stereotypical learning curve may not reliably reflect individual learning curves, but may instead be an artifact that arises from the averaging of data across individuals [58]. A more accurate account of the performance function will require models that reflect the combined operation of explicit and implicit learning processes and their respective error signals (Figure 3B).

Neural Systems for Explicit Aiming and Implicit Recalibration

The notion that learning reflects the conjoint operation of multiple learning systems is prevalent in many cognitive domains such as category learning, recognition memory, and reinforcement learning [25,26,59]. The work of Milner and colleagues with amnesic patient HM was, of course, highly influential in the development of memory taxonomies, and in particular, the striking distinction between explicit, or declarative memory and implicit, procedural memory [60,61]. Although the initial demonstration of spared implicit learning in HM came from motor tasks such as mirror drawing, subsequent work revealed varying capacities for implicit learning on a range of perceptual tasks [60]. This work has inspired a half-century of research on the neural correlates of different memory processes, with the insight that learning, even within a taxonomic branch, is likely to be highly distributed.

Neuroimaging studies have shown that areas including, but not limited to, prefrontal cortex, premotor and primary motor cortices, parietal cortex, basal ganglia, and cerebellum are recruited during sensorimotor adaptation tasks [62–69]. Of particular interest here has been the cerebellum. Dating back to the 19th century, this structure has been recognized as essential for motor coordination and learning [70]. Inspired by its unique anatomy and physiology, detailed models of cerebellar learning [71–74] have been developed and refined, using tasks that involve adaptation of eye movement reflexes [51,75]. In terms of reaching studies, patients with cerebellar degeneration consistently show attenuated adaptation in response to sensory perturbations [14,15,36,47,76]. Furthermore, cerebellar activity is correlated with sensory prediction errors, the putative signal for sensorimotor recalibration [77]. Taken together, there is general consensus that the cerebellum is essential for keeping the motor and sensory systems calibrated across a range of contexts.

What are the putative neural substrates for the more cognitive contributions to motor learning? In terms of explicit processes such as strategy use, it is noteworthy that frontal lobe regions, including lateral and medial aspects of prefrontal cortex, as well as premotor cortex, often exhibit increased activity during the early phases of sensorimotor learning [62,64,78]. Although the functional role of the prefrontal activations have typically been described in terms of meta-cognitive control processes such as planning, working memory, or monitoring [67,68,78], it would also be reasonable to suppose that these regions are essential for strategic changes in aiming, consistent with a more general view of the frontal lobes being essential for action selection when the sensory-motor mapping is novel or arbitrary [79]. Aiming, at least when invoked to hasten learning in response to a perturbation, requires an indirect mapping with the direction of the action displaced from the target, similar to the spear fisher accounting for the refraction of light in water.

The instructed-strategy task [34] has revealed intriguing differences between the effects of cerebellar and frontal lobe damage: Patients with cerebellar degeneration actually perform more accurately than matched controls on this task, showing attenuated drift after implementing an aiming strategy [36]. Their impaired sensitivity to sensory prediction errors confers a form of "immunity" to maladaptive recalibration in this task. In contrast, patients with prefrontal lesions from stroke tend to show greater drift than their matched controls [80]. We assume this pattern reflects a deficit in being able to adjust their aiming strategy, even when intact recalibration has led to a gradual increase in performance error. In line with this hypothesis, older adults, assumed to have mild forms of frontal lobe dysfunction, show intact implicit learning but reduced explicit learning in visuomotor adaptation tasks [44].

We speculate that these results suggest a key role for the frontal lobe in aiming. However, there are reasonable alternative hypotheses to consider. For example, the excessive drift in our study with PFC patients [80] could reflect an insensitivity to performance error, perseveration, or even a "hyper-sensitive" calibration system (e.g., a cerebellum unchecked by the cortex). Future work that directly manipulates and measures different markers of implicit and explicit processes will be required to advance our understanding of the functional contributions of different neural systems to sensorimotor learning.

Beyond Adaptation: Towards a Broader View of Motor Learning

Tools from statistical decision theory and Bayesian statistics may prove useful in developing descriptive models, as well as offering new ways to characterize mechanisms of motor learning [81,82]. Aiming locations could be thought of as (indirect) spatial goals, cached motor commands as action options, and the planning and execution of a specific command as an enacted decision. The honing of a true motor skill, as opposed to adaptation to an external perturbation, has been theorized to entail a model-free reinforcement learning process [83]. Thus, learning in a reaching task can be characterized by a trade-off between exploration and exploitation [84], where strategic processes initially explore the manifold of actions that may yield task success, and, once a solution is found, the rewarded movement is reinforced over time. This approach helps shed light on the relationship between motor variability and learning [85]: The operation of cognitive strategies, especially prominent during early learning, may confer rapid dimensionality reduction (i.e., reducing the space of possible solutions).

Insights gained from the study of strategy use point to other aspects of cognition that are likely to be relevant for the study of sensorimotor learning. For example, there can be costs in motor performance from cognitive control [86], an idea captured by the folk psychology notion that experts are wise to not "think", but just "do," and reflected in the venerable model of Fitts and Posner on the stages of skill acquisition [87]. However, we cannot assume that the reduction in cognitive contributions to performance implies that all learning has shifted to the implicit calibration system. There appear to be multiple forms of implicit learning: In addition to error-based remapping, the evidence suggests that changes in performance also reflect contributions from associative processes such as use-dependent learning and operant conditioning [50,88,89].

Moreover, it is unclear if this explicit component ever really "disappears." For instance, professional riflemen adeptly use "Kentucky Windage" to adjust their aim to correct for the direction of the wind. In this and other cases, cognitive strategizing is the mark of an expert, not an amateur. Indeed, the kinds of cognitive strategies discussed here are not limited to motor tasks: A generalized capability for one-trial learning has obvious implications for learning writ large.

Ultimately, it is critical to incorporate the influence of cognitive planning into any realistic and comprehensive model of human sensorimotor learning. High-level motor planning is not just relevant to spearfishing, darts, or shooting: The ability to execute aimed movements — to rapidly, accurately, and flexibly perform planned, multi-joint movements to interact with the environment — is a hallmark of human behavior.

Acknowledgments

References Cited

1. Stout D, et al. Neural correlates of Early Stone Age toolmaking: technology, language and cognition in human evolution. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 2008; 363:1939–1949. [PubMed: 18292067]

2. Roach NT, et al. Elastic energy storage in the shoulder and the evolution of high-speed throwing in Homo. Nature. 2013; 498:483–486. [PubMed: 23803849]

3. Darwin, C. The descent of man, and selection in relation to sex. New York: D. Appleton and company; 1871.

4. Goodall J. Tool-Using and aimed throwing in a community of free-living chimpanzees. Nature. 1964; 201:1264–1266. [PubMed: 14151401]

5. Westergaard GC, et al. A comparative study of aimed throwing by monkeys and humans. Neuropsychologia. 2000; 38:1511–1517. [PubMed: 10906376]

6. Hopkins WD, et al. The neural and cognitive correlates of aimed throwing in chimpanzees: a magnetic resonance image and behavioural study on a unique form of social tool use. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 2012; 367:37–47. [PubMed: 22106425]

7. Woodworth RS. Accuracy of voluntary movement. The Psychological Review: Monograph Supplements. 1899; 3:100–114.

8. Fitts PM. The information capacity of the human motor system in controlling the amplitude of movement. J. Exp. Psych. 1954; 47:381–391.

9. Schmidt RA, et al. Motor-output variability: a theory for the accuracy of rapid motor acts. Psychol. Rev. 1979; 47:415–451. [PubMed: 504536]

10. Elliott D, et al. A century later: Woodworth's (1899) two-component model of goal-directed aiming. Psychol. Bull. 2001; 127:342–357. [PubMed: 11393300]

11. Shadmehr R, Mussa-Ivaldi FA. Adaptive representation of dynamics during learning of a motor task. J. Neurosci. 1994; 14:3208–3224. [PubMed: 8182467]

12. Wolpert DM, et al. An internal model for sensorimotor integration. Science. 1995; 269:1880–1882. [PubMed: 7569931]

13. Weiner MJ, et al. Adaptation to lateral displacement of vision in patients with lesions of the central nervous system. Neurology. 1983; 33:766–772. [PubMed: 6682520]

14. Martin TA, et al. Throwing while looking through prisms. I. Focal olivocerebellar lesions impair adaptation. Brain. 1996; 119:1183–1198. [PubMed: 8813282]

15. Tseng YW, et al. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. J. Neurophysiol. 2007; 98:54–62. [PubMed: 17507504]

16. Izawa J, et al. Cerebellar contributions to reach adaptation and learning sensory consequences of action. J. Neurosci. 2012; 32:4230–4239. [PubMed: 22442085]

17. Rabe K, et al. Adaptation to Visuomotor Rotation and Force Field Perturbation Is Correlated to Different Brain Areas in Patients With Cerebellar Degeneration. J. Neurophysiol. 2009; 101:1961–1971. [PubMed: 19176608]

18. Thoroughman KA, Shadmehr R. Learning of action through adaptive combination of motor primitives. Nature. 2000; 407:742–747. [PubMed: 11048720]

19. Lee J-Y, Schweighofer N. Dual adaptation supports a parallel architecture of motor memory. J. Neurosci. 2009; 29:10396–10404. [PubMed: 19692614]

20. Smith MA, et al. Interacting adaptive processes with different timescales underlie short-term motor learning. PLoS Biol. 2006; 4:e179. [PubMed: 16700627]

21. Herzfeld DJ, et al. A memory of errors in sensorimotor learning. Science. 2014; 345:1349–1353. [PubMed: 25123484]

22. Cheng, Sen; Sabes, PN. Modeling sensorimotor learning with linear dynamical systems. Neural Comput. 2006; 25:1693–1731.

23. Newell A, Rosenbloom PS, Anderson JR. Cognitive skills and their acquisition. Mechanisms of skill acquisition and the law of practice. 1981:1–51.

24. Morehead JR, et al. Savings upon re-aiming in visuomotor adaptation. J. Neurosci. 2015; 35:14386–14396. [PubMed: 26490874]

25. Ashby FG, et al. A neuropsychological theory of multiple systems in category learning. Psychol. Rev. 1998; 105:442–481. [PubMed: 9697427]

26. Jacoby LL. A process dissociation framework: Separating automatic from intentional uses of memory. J. Mem. Lang. 1991; 30:513–541.

27. Willingham DB. A neuropsychological theory of motor skill learning. Psychol. Rev. 1998; 105:558–584. [PubMed: 9697430]

28. Martin TA, et al. Throwing while looking through prisms. II. Specificity and storage of multiple gaze-throw calibrations. Brain. 1996; 119:1199–1211. [PubMed: 8813283]

29. Shadmehr R, et al. Error correction, sensory prediction, and adaptation in motor control. Annu. Rev. Neurosci. 2010; 33:89–108. [PubMed: 20367317]

30. Helmholtz, HV.; Southall, JPC. Helmholtz's treatise on physiological optics. Rochester: The Optical Society of America; 1924.

31. Redding GM, et al. Applications of prism adaptation: a tutorial in theory and method. Neurosci. Biobehav. Rev. 2005; 29:431–444. [PubMed: 15820548]

32. Cunningham HA. Aiming error under transformed spatial mappings suggests a structure for visual-motor maps. J. Exp. Psychol. Hum. Percept. Perform. 1989; 15:493–506. [PubMed: 2527958]

33. Krakauer JW, et al. Learning of visuomotor transformations for vectorial planning of reaching trajectories. J. Neurosci. 2000; 20:8916–8924. [PubMed: 11102502]

34. Mazzoni P, Krakauer JW. An implicit plan overrides an explicit strategy during visuomotor adaptation. J. Neurosci. 2006; 26:3642–3645. [PubMed: 16597717]

35. Taylor JA, Ivry RB. Flexible cognitive strategies during motor learning. PLoS Comp. Biol. 2011; 7:e1001096.

36. Taylor JA, et al. An explicit strategy prevails when the cerebellum fails to compute movement errors. Cerebellum. 2010; 9:580–586. [PubMed: 20697860]

37. Taylor JA, et al. Explicit and implicit contributions to learning in a sensorimotor adaptation task. J. Neurosci. 2014; 34:3023–3032. [PubMed: 24553942]

38. Bond KM, Taylor JA. Flexible explicit but rigid implicit learning in a visuomotor adaptation task. J. Neurophysiol. 2015; 113:3836–3849. [PubMed: 25855690]

39. McDougle SD, et al. Explicit and implicit processes constitute the fast and slow processes of sensorimotor learning. J. Neurosci. 2015; 35:9568–9579. [PubMed: 26134640]

40. Haith AM, et al. The influence of movement preparation time on the expression of visuomotor learning and savings. J. Neurosci. 2015; 35:5109–5117. [PubMed: 25834038]

41. Huberdeau DM, et al. Dual-process decomposition in human sensorimotor adaptation. Curr. Opin. Neurobiol. 2015; 33:71–77. [PubMed: 25827272]

42. Sulzenbruck S, Heuer H. Functional independence of explicit and implicit motor adjustments. Conscious. Cogn. 2009; 18:145–159. [PubMed: 19136279]

43. Benson BL, et al. A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. J. Neurophysiol. 2011; 105:2843–2851. [PubMed: 21451054]

44. Heuer H, Hegele M. Generalization of implicit and explicit adjustments to visuomotor rotations across the workspace in younger and older adults. J. Neurophysiol. 2011; 106:2078–2085. [PubMed: 21775724]

45. Day KA, et al. Visuomotor learning generalizes around the intended movement. eneuro. 2016 ENEURO-0005.

46. Trewartha KM, et al. Fast but fleeting adaptive motor learning processes associated with aging and cognitive decline. J. Neurosci. 2014; 34:13411–13421. [PubMed: 25274819]

47. Schlerf JE, et al. Individuals with cerebellar degeneration show similar adaptation deficits with large and small visuomotor errors. J. Neurophysiol. 2013; 109:1164–1173. [PubMed: 23197450]

48. Pekny SE, et al. Protection and expression of human motor memories. J. Neurosci. 2011; 31:13829–13839. [PubMed: 21957245]

49. Ebbinghaus H. Memory: a contribution to experimental psychology. Ann. Neurosci. 2013; 20:155–156. [PubMed: 25206041]

50. Huang VS, et al. Rethinking motor learning and savings in adaptation paradigms: model-free memory for successful actions combines with internal models. Neuron. 2011; 70:787–801. [PubMed: 21609832]

51. Medina JF, et al. A mechanism for savings in the cerebellum. J. Neurosci. 2001; 21:4081–4089. [PubMed: 11356896]

52. Berniker M, Kording KP. Estimating the relevance of world disturbances to explain savings, interference and long-term motor adaptation effects. PLoS Comput. Biol. 2011; 7:e1002210. [PubMed: 21998574]

53. Galea JM, et al. Dissociating the roles of the cerebellum and motor cortex during adaptive learning: the motor cortex retains what the cerebellum learns. Cereb. Cortex. 2011; 21:1761–1770. [PubMed: 21139077]

54. Braun DA, et al. Motor task variation induces structural learning. Curr. Biol. 2009; 19:352–357. [PubMed: 19217296]

55. Wei K, Körding K. Relevance of error: what drives motor adaptation? J. Neurophysiol. 2009; 101:655–664. [PubMed: 19019979]

56. Fine MS, Thoroughman KA. Trial-by-trial transformation of error into sensorimotor adaptation changes with environmental dynamics. J. Neurophysiol. 2007; 3:1392–1404. [PubMed: 17615136]

57. Morehead, JR., et al. Translational and computational motor control. Washington DC: 2014. Implicit adaptation via visual error clamp.

58. Gallistel CR, et al. The learning curve: implications of a quantitative analysis. Proc. Natl. Acad. Sci. U.S.A. 2004; 101:13124–13131. [PubMed: 15331782]

59. Daw ND, et al. Model-Based Influences on Humans' Choices and Striatal Prediction Errors. Neuron. 2011; 69:1204–1215. [PubMed: 21435563]

60. Milner B, et al. Further analysis of the hippocampal amnesic syndrome: 14-year follow-up study of H.M. Neuropsychologia. 1968; 6:215–234.

61. Milner B. Les troubles de la memoire accompagnant des lesions hippocampiques bilaterales. Physiologie de l'hippocampe. 1962:257–272.

62. Shadmehr R, Holcomb HH. Neural Correlates of Motor Memory Consolidation. Science. 1997; 277:821–825. [PubMed: 9242612]

63. Seidler, RD., et al. Neurocognitive Mechanisms of Error-Based Motor Learning. In: Richardson, MJ., et al., editors. Progress in Motor Control. Vol. 782. New York: Springer; 2013. p. 39-60.

64. Krakauer JW, et al. Differential Cortical and Subcortical Activations in Learning Rotations and Gains for Reaching: A PET Study. J. Neurophysiol. 2004; 91:924–933. [PubMed: 14523069]

65. Seidler RD, et al. Cerebellum Activation Associated with Performance Change but Not Motor Learning. Science. 2002; 296:2043–2046. [PubMed: 12065841]

66. Diedrichsen J, et al. Neural Correlates of Reach Errors. J. Neurosci. 2005; 25:9919–9931. [PubMed: 16251440]

67. Anguera JA, et al. Changes in Performance Monitoring During Sensorimotor Adaptation. Journal of Neurophysiology. 2009; 102:1868–1879. [PubMed: 19605614]

68. Anguera JA, et al. Neural correlates associated with intermanual transfer of sensorimotor adaptation. Brain Res. 2007; 1185:136–151. [PubMed: 17996854]

69. Seidler RD, et al. Bilateral basal ganglia activation associated with sensorimotor adaptation. Exp. Brain. Res. 2006; 175:544–555. [PubMed: 16794848]

70. Dow, RS.; Moruzzi, G. The physiology and pathology of the cerebellum. Minneapolis: University of Minnesota Press; 1958.

71. Eccles, JC., et al. The cerebellum as a neuronal machine. Berlin, New York etc.: Springer-Verlag; 1967.

72. Thach WT. Discharge of Purkinje and cerebellar nuclear neurons during rapidly alternating arm movements in the monkey. J. Neurophysiol. 1968; 31:785–797. [PubMed: 4974877]

73. Marr D. A theory of cerebellar cortex. J. Physiol. 1969; 202:437–470. [PubMed: 5784296]

74. Ito M. Neural design of the cerebellar motor control system. Brain Res. 1972; 40:81–84. [PubMed: 4338265]

75. Ito M. Cerebellar learning in the vestibulo–ocular reflex. Trends Cogn. Sci. 1998; 2:313–321. [PubMed: 21227227]

76. Norris SA, et al. Cerebellar inactivation impairs memory of learned prism gaze-reach calibrations. J. Neurophysiol. 2011; 105:2248–2259. [PubMed: 21389311]

77. Schlerf J, et al. Encoding of sensory prediction error in the human cerebellum. J. Neurosci. 2012; 32:4913–4922. [PubMed: 22492047]

78. Seidler RD, et al. Neurocognitive contributions to motor skill learning: the role of working memory. J. Motor Behav. 2012; 44:445–453.

79. Wise SP, et al. The premotor cortex and nonstandard sensorimotor mapping. Can. J. Physiol. Pharm. 1996; 74:468–482.

80. Taylor JA, Ivry RB. Cerebellar and prefrontal cortex contributions to adaptation, strategies, and reinforcement learning. Prog. Brain. Res. 2014; 210:217–253. [PubMed: 24916295]

81. Wolpert DM, Landy MS. Motor control is decision-making. Curr. Opin. Neurobiol. 2012; 22:996–1003. [PubMed: 22647641]

82. Trommershäuser J, et al. Decision making, movement planning and statistical decision theory. Trends Cogn. Sci. 2008; 12:291–297. [PubMed: 18614390]

83. Haith, AM.; Krakauer, JW. Model-based and model-free Mechanisms of human motor learning. In: Richardson, MJ., et al., editors. Progress in Motor Control. Vol. 782. New York: Springer; 2013. p. 1-21.

84. Wilson RC, et al. Humans use directed and random exploration to solve the explore-exploit dilemma. J. Exp. Psychol. Gen. 2014; 143:2074–2081. [PubMed: 25347535]

85. Wu HG, et al. Temporal structure of motor variability is dynamically regulated and predicts motor learning ability. Nat. Neurosci. 2014; 17:312–321. [PubMed: 24413700]

86. Beilock SL, et al. Haste does not always make waste: Expertise, direction of attention, and speed versus accuracy in performing sensorimotor skills. Psychon. B. Rev. 2004; 11:373–379.

87. Fitts, PM.; Posner, MI. Basic concepts in psychology series. Belmont: Brooks/Cole Publishing Company; 1967. Human performance.

88. Verstynen T, Sabes PN. How each movement changes the next: an experimental and theoretical study of fast adaptive priors in reaching. J. Neurosci. 2011; 31:10050–10059. [PubMed: 21734297]

89. Diedrichsen J, et al. Use-Dependent and Error-Based Learning of Motor Behaviors. J. Neurosci. 2010; 30:5159–5166. [PubMed: 20392938]

Outstanding Questions

How should aiming strategies be modeled and integrated into standard models of sensorimotor learning? How can such models be modified to include ideas from work on decision making and reinforcement learning to provide a comprehensive picture of motor performance and learning?

What are the putative neural substrates contributing to the cognitive processes underlying motor strategies and heuristics, like aiming? How much do these substrates overlap with the known neural architecture involved in planning and decision-making?

Do strategic processes and recalibration processes directly interact, or are the systems psychologically and neurally "quarantined" from each other?

Do explicit strategies become proceduralized over time as a true skill is acquired?

What aspects of "cognitive" mechanisms for motor learning are shared with other species and which, if any, are unique to humans?

TRENDS Box

Behavioral, computational, and neuropsychological studies have provided a detailed picture of the processes involved in sensorimotor adaptation tasks. This work has been based on laboratory studies in which sensorimotor feedback is perturbed, using tools such as prism glasses, force fields, and visuomotor rotations. Performance changes have been attributed to learning mechanisms that modify a sensorimotor mapping based on sensory prediction errors, the difference between predicted and observed feedback. However, a growing body of research points to the operation of additional learning processes, including the use of cognitive strategies and heuristics. In adaptation experiments, such strategies can be characterized as "aiming", one form of a flexible, goal-oriented motor plan.

Theoretical models are being revised to address the interaction of multiple learning processes, specifying computational constraints concerning the teaching signals used by different learning mechanisms. Furthermore, the search for the neural substrates of motor learning has cast a wider net, going beyond the role of the cerebellum and motor cortex, to include, for example, frontoparietal areas involved in planning and decision making.
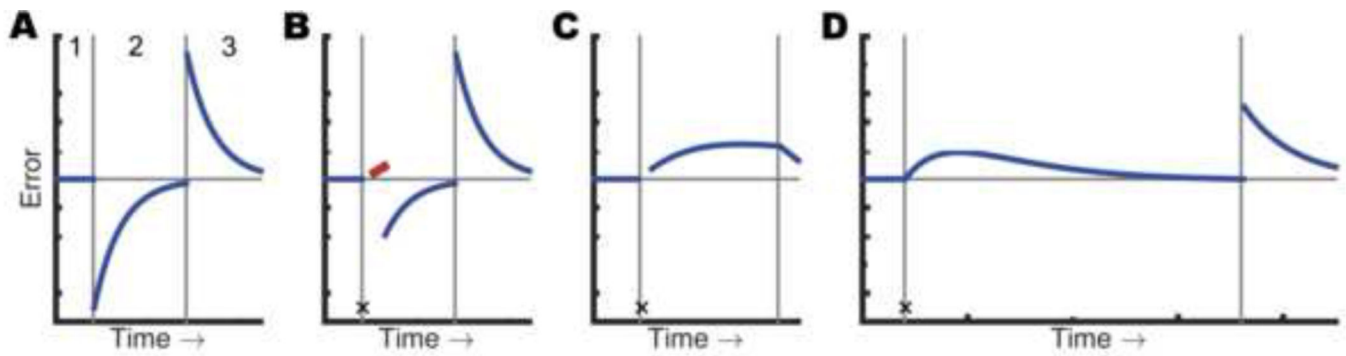
Figure 1. Explicit processes in motor learning
(**A**) The canonical human motor learning curve, with the preliminary baseline period (region 1), the learning block where a sensorimotor perturbation is applied (region 2), and a "washout" period where the motor system is re-calibrated back to baseline (region 3). (**B**) Data from a subset of participants who "cheated" in a prism adaptation study — that is, using an aiming strategy to adjust their behavior after the first perturbed trial (black X). Although this immediately eliminated the error, performance became worse over subsequent trials (red line). When instructed to stop aiming, the error became larger and reversed sign. Simulated data is modeled after reference [28]. (**C**) After the first perturbation trial in the strategy task (black X), participants are instructed to counter the rotation by aiming towards a landmark displaced from the target. This results in immediate task success. However, performance subsequently deteriorates ("drifts") due to the operation of an implicit learning process. Simulated data is modeled after reference [34]. (**D**) If the training period is extended, the error arising from implicit drift is eventually negated by an adjustment in the strategy. An aftereffect, indicative of recalibration, is evident when the rotation is turned off and the participants are told to reach directly to the target. Simulated data is modeled after reference [35].
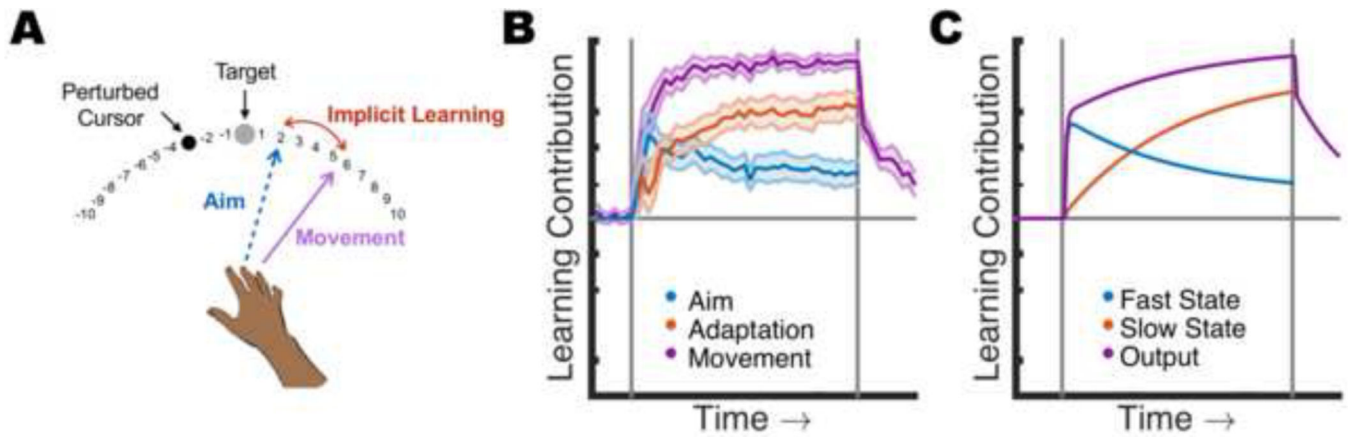
Figure 2. Measuring strategy use in a sensorimotor adaptation task
(**A**) To obtain a direct assay on aiming strategy, participants are required to explicitly report their aim location prior to each trial. The magnitude of implicit learning can be estimated by subtracting the aiming angle from the measured movement angle. (**B**) There is a large contribution from explicit re-aiming right after the perturbation, which decreases over time. In contrast, implicit learning is slower and monotonic. Note that the estimated state of remapping matches precisely the magnitude of the aftereffect at the start of the washout phase. Data adapted from reference [37]. (**C**) The fast and slow components of the two-rate state-space model [20] closely resemble, respectively, explicit and implicit learning [39].
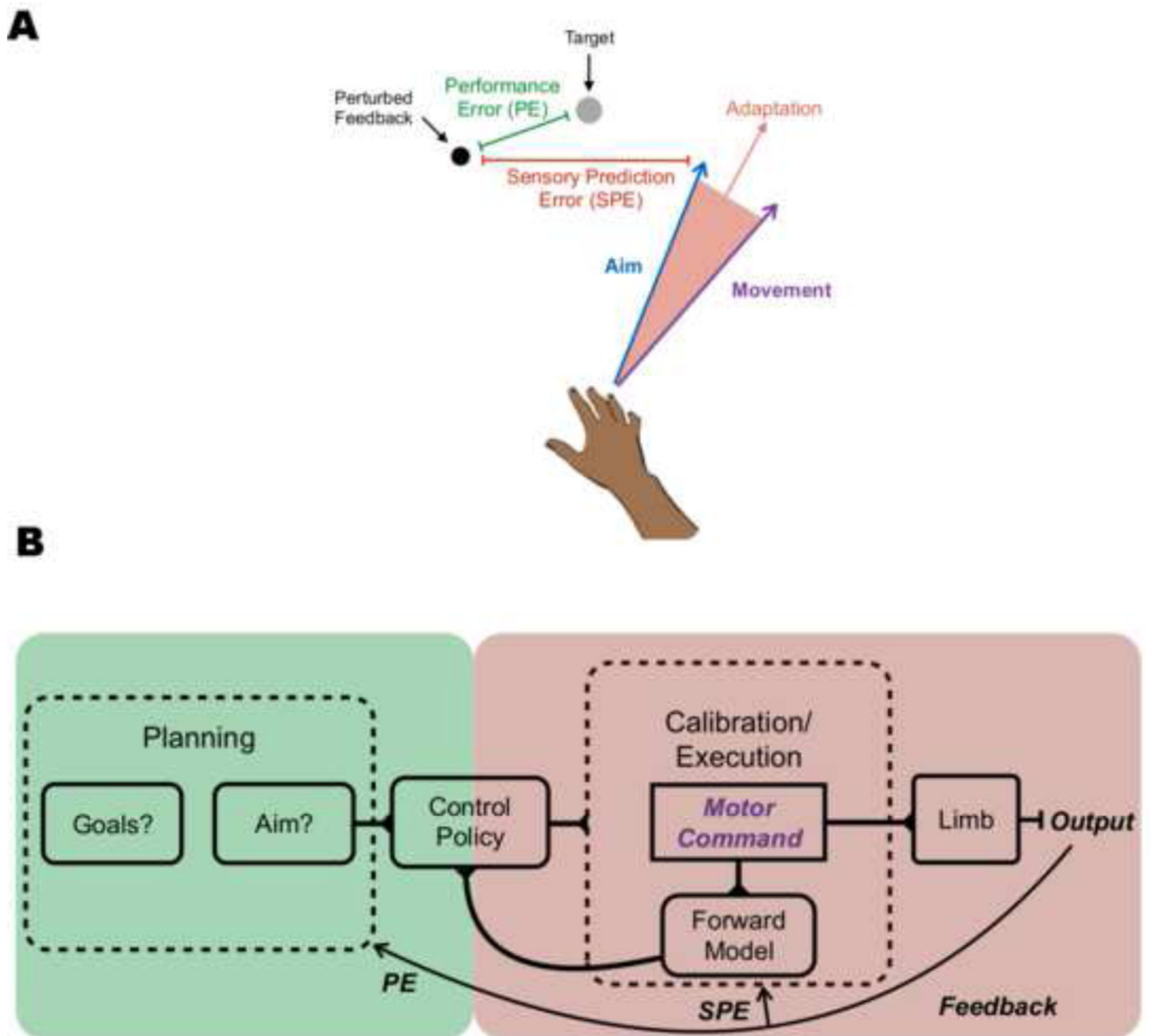
A

B

Figure 3. Multiple error signals in sensorimotor adaptation tasks

(**A**) Dissociated error signals for recalibration (sensory prediction error) and strategizing (performance error). (**B**) A simplified schematic of the primary processes thought to be involved in voluntary movement. Cognitive processes (green box) provide input to implicit motor execution processes (red box). As part of the planning process, an aim is selected based on the task goal. The control policy constitutes the precise movement plan(s) that correspond to the selected goal and results in a motor command to the limb. The motor command not only drives the movement, but is fed into a forward model to generate a sensory prediction. This prediction is compared to the feedback to define the sensory prediction error, a signal that is used to update the forward model and control policy. Performance error feedback influences the planning process, allowing for strategic

adjustment. The majority of research in motor learning has focused on details of the forward model and limb dynamics (red box). Further work should also address the computations occurring at the planning stages (green box).