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Review

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]

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 takes place 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.

Trends

Behavioral, computational, and neuropsychological studies have provided a detailed picture of the processes involved in sensorimotor adaptation tasks.

Performance changes in response to perturbations are typically attributed to learning mechanisms that recalibrate a sensorimotor map based on the difference between predicted and observed feedback.

A growing body of research points to the operation of additional learning processes, including the use of strategies and heuristics that support flexible, goal-oriented behavior.

Theoretical models must address the interplay of these processes, specifying the algorithms and error signals used by different learning mechanisms.

Investigations of the neural substrates engaged during sensorimotor adaptation tasks should cast a wider net, looking beyond the cerebellum and motor cortex to regions involved in action selection.

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 crucial for the survival of our ancestors [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 human ancestors' 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]. Although 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, and the results help us to 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

[1]Department of Psychology, Princeton University, Princeton, NJ 08544, USA
[2]Princeton Neuroscience Institute, Princeton University, Princeton, NJ 08544, USA
[3]Department of Psychology, University of California, Berkeley, CA 94720, USA

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

*Correspondence: ivry@berkeley.edu (R.B. Ivry).

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 particular 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, and experimental instructions are 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 achieve functional performance 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 (Figure 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 'after-effect' is observed, taken as the signature of a recalibrated sensorimotor mapping. Over time, the after-effect 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 faced by the participants in such experiments. While throwing darts one evening, imagine that you don a pair of prism glasses and then 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.