

Dual-process decomposition in human sensorimotor adaptation

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Multiple distinct learning processes are known to contribute to sensorimotor adaptation in humans. It is challenging to identify and characterize these multiple processes, however, because only their summed contribution can typically be observed. A general strategy for decomposing adaptation into its constituent components is to exploit their differential susceptibility to specific experimental manipulations. Several such approaches have recently emerged which, taken together, suggest that two fundamental systems operate together to achieve the adapted state: one system learns slowly, is implicit, is temporally stable over short breaks, is expressible at low reaction times, and its properties do not change based on experience. The second learns rapidly, is explicit, requires a long preparation time to be expressed, and exhibits long-term memory for prior learning.

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Introduction

A common experimental approach to studying human motor learning is to impose a systematic perturbation while subjects perform a simple movement such as a point-to-point reach. For example, a force field may be applied to the hand [1] or visual feedback might be rotated about the origin of the movement [2]. Human subjects readily eliminate the errors induced by such perturbations, usually regaining near-baseline levels of performance within 50 trials or so. Although a seemingly straightforward behavior, a wealth of evidence now suggests that the capacity to adapt to perturbations is

supported by multiple distinct processes acting in parallel. Early theories posited the existence of multiple processes underlying learning [3,4]. However, whereas these early theories assumed that these processes were qualitatively similar (for instance, all depending on the same error signal), growing evidence now suggests that they are in fact qualitatively distinct.

A clear understanding of the multi-faceted nature of adaptation is critical both for investigations into the neural basis of learning and in order to best leverage adaptation for therapeutic purposes. In practice, however, identifying and characterizing the many processes that contribute to sensorimotor adaptation is challenging since only the summed contribution of all components can typically be measured. A general strategy for solving this problem is to dissociate learning into sub-components on the basis of their having particular contrasting properties that can be independently measured and/or render them susceptible to manipulation.

Empirical decomposition of motor adaptation into component processes has significantly improved our understanding but has also raised new questions. Do component processes compete or cooperate during a learning task? Can task conditions favor some components over others? Do empirical decompositions align with theoretical distinctions between potential learning rules (e.g. supervised learning versus reinforcement learning)? Here, with a focus on sensorimotor adaptation for reaching movements, we will attempt to address some of these questions. Specifically, we will discuss three recent experimental approaches that have isolated components of visuomotor adaptation through exploitation of differences in their dependence on explicit awareness, their need for preparation time, and their capacity for retention. We also consider how components isolated by these experimental manipulations relate to previous theoretical and empirical dissections of adaptation.

Empirical decompositions of motor adaptation

Awareness: explicit versus implicit

Most motor adaptation experiments to some degree engage subjects at an explicit level. The effects of a perturbation are often very obvious and frustrating and subjects will attempt to eliminate the errors by any means possible. Yet much of the compensation that occurs in such paradigms occurs through implicit mechanisms that

operate outside of subjects' awareness and cannot seemingly be modulated by explicit knowledge. The relative contributions of explicit and implicit processes becomes apparent when a perturbation is removed: subjects perform significantly better in the first trial after a perturbation is removed if they are aware that the perturbation will be removed, compared to if it is removed unexpectedly [5,6,7^{••},8]. Measuring the effect of such explicit instructions allows behavior to be decomposed into two components: one explicit component that can be easily disengaged in the light of knowledge, and one component that cannot and is therefore presumed to be implicit. This basic approach can be employed at various time points during learning to track the relative contributions of implicit and explicit components [6,9].

A more direct determination of the relative contributions of explicit and implicit processes to adaptation was recently achieved in an experiment by Taylor and colleagues [7^{••}]. Subjects were exposed to a 45° visuomotor rotation. They were also asked to declare, prior to each reach, which direction they intended to aim their movement. These aiming locations served as a direct measurement of the explicit component of learning, while the amount their actual reach deviated from the declared aiming location revealed the contribution of the implicit component. These dual measurements of subjects' behavior revealed that explicit and implicit processes operate in parallel throughout adaptation. Explicit contributions were large and exploratory early in learning. With further exposure to the perturbation, explicit contributions reduced in amplitude as the implicit contribution increased. Although asking subjects to choose and declare an explicit strategy for solving the perturbation might seem somewhat unnatural, net learning rates and aftereffects exhibited by these subjects were very similar to those seen in subjects who had no aiming targets or instruction. Thus probing explicit contributions on each trial did not qualitatively alter the canonical time course for adaptation, suggesting that these findings may be representative of learning in more conventional paradigms.

The ability to simultaneously measure both implicit and explicit components builds on previous work that isolated the implicit component of learning by instructing subjects explicitly how to counter an imposed visuomotor rotation [10,11,12[•]]. This approach has established that implicit learning is driven by sensory prediction errors and is indifferent to task success. Furthermore, it is known to be cerebellum-dependent [13] and can be abolished if feedback about movement kinematics is provided only after the movement has ended [12[•]].

Preparation time: rapidly-expressible versus time-consuming

Another means by which adaptation can be decomposed is according to the amount of preparation time each

component might require. Reaction times are known to increase during adaptation to a visuomotor rotation [14,15^{••}]. Fernandez-Ruiz and colleagues [15^{••}] showed that this increase in reaction time is causally related to the rate of learning; subjects who were forced to move at very low reaction times showed significantly slower learning relative to control subjects. The critical role of preparation time appears to be specific to some components of learning but not others. In an experiment by Haith and colleagues [16^{••}], preparation time was varied on a trial-by-trial basis during adaptation to a 30° visuomotor rotation by unexpectedly switching the target location shortly before movement initiation in a subset of trials. Early in learning, subjects exhibited larger errors in trials in which preparation time was limited, compared to normal trials immediately before or after. This transient reversion towards baseline during trials with limited preparation time suggests that some component of learning could not be expressed when preparation time was short. After further practice, subjects performed comparably well in both trial types, suggesting that the component requiring little preparation time accounted for most of the observed adaptation later in learning. Importantly, the effect that limiting preparation time has on expression of learning does not appear to be specific to adaptation to a visuomotor rotation; reducing reaction time through startle has a similar effect on expression of adaptation to either visuomotor [17] or force-field [18] perturbations.

Decomposition according to preparation time requirements suggests parallels with the decomposition obtained on the basis of an explicit/implicit duality. One component (the high RT and the explicit) dominates early in learning, while the other component (the low RT and the implicit) learns more slowly but dominates later in adaptation. It is therefore tempting to conclude that a prolonged preparation time is required in order to apply an explicit strategy [15^{••}]. One cannot, however, rule out the possibility of a component of learning that is implicit yet requires a prolonged preparation time, or an explicit component of learning that can be expressed rapidly. More direct comparisons between the effects of awareness and preparation time will be necessary to determine whether they are dissociable.

Retention: stable versus decaying over time

Adaptation occurs very rapidly, but is also forgotten rapidly. If errors are removed during adaptation — either by withholding feedback, or by artificially constraining errors to zero — behavior begins to revert or decay towards baseline [19,20,21[•],22–24]. Earlier theories of adaptation posit that it is comprised of two or more components that are qualitatively similar (driven by the same error signal) but which have different rates of learning and decay [3,4]. More recent work, however, has established that adaptation can decay in two distinct ways: either as a function of the number of movements made [24,25], or with the passage of time [22,24,26,27].

It has been suggested that these contrasting modes of decay might relate to distinct components of learning. Patterns of retention seen 24 hours after initial learning of a force field are consistent with only a single component of learning being partially retained [26]. More recent studies have shown that adaptation decays over far shorter timescales than 24 hours; most of the decay in fact occurs within just 1 minute [27]. The amount of residual learning after such breaks gradually increases with practice, suggesting that it corresponds to a separate slower component of learning that has greater temporal stability. These findings therefore support the existence of two distinct components of learning that can be dissociated based on their differential susceptibility to decay with the passage of time.

The two components identified here resemble those discussed above in that one component seems to dominate early on (in this case the one which is not retained over time) but gives way to the other component later in learning (the temporally stable component). Notably, prior learning does not appear to be completely forgotten after a one-minute break; subjects are able to regain their prior level of performance within just two to three trials after the break [27]. Therefore, the apparent decay in learning over time is perhaps better interpreted as a transient failure to express this component of learning—paralleling the expression failure seen when reaction time is limited and consistent with the flexible engagement of the explicit component of learning. It seems plausible that the reason for the drop in performance is that subjects forget to apply a previously successful explicit strategy until reminded to do so when they experience an error in the first trial after the break.

Mapping global properties of adaptation onto subcomponents

The three approaches described above each offer a means to empirically decompose overall behavior into different sub-components based on either differences in conscious awareness associated with each component, differences in the amount of preparation time required to express each component, or differences in the retention properties of each component across short breaks. Taken together, these findings demonstrate the existence of at least two components of learning that differ qualitatively. A consequent challenge is to understand how these component processes contribute to or are responsible for features of learning that have so far only been characterized at the level of overall learning. We discuss two specific aspects of behavior in adaptation experiments that highlight how our understanding can be enriched by coupling existing insights with a decomposition approach: the role of different learning mechanisms and experience-dependent changes in learning rate.

Learning through exploration as a signature of early learning

An important distinction in theories of learning is between supervised learning from vector errors versus reinforcement learning from scalar costs and rewards [28,29]. Most theories of learning have suggested that adaptation represents a form of supervised learning based on vector performance errors [10,30]. Even when multiple components are posited, they are often assumed to operate in a qualitatively similar manner [3]. It is clear, however, that learning can occur even in the absence of vector errors—if subjects are given only binary [29] or scalar [31] feedback about performance, for example. Learning from scalar or binary outcomes is much more challenging than learning from vector errors, since vector errors provide critical directional information that is not available with only scalar feedback. Consequently, with scalar feedback, a more exploratory trial-and-error approach is necessary to identify better motor commands [32–35]. Therefore, if trial-to-trial variability could be shown to be directly related to learning (rather than simply reflecting unrelated noise), it could potentially serve as a hallmark of learning from scalar outcomes rather than vector error.

In a recent study by Wu and colleagues [36^{*}], subjects whose movements were more variable during an initial baseline phase could more rapidly adapt to a perturbation than those whose baseline movements were less variable. Furthermore, the precise within-movement structure of baseline variability was predictive of the rate of learning for different types of perturbation that required different temporal patterns of force compensation. A similar relationship between variability and learning rate has also been noted during adaptation to a visuomotor rotation [15^{**}], as well as in more abstract motor learning tasks in which only scalar feedback is provided to the subject [36^{*},37]. These findings appear to recapitulate classic observations relating learning rate and response variability in discrete action selection settings [38,39]. Although consistent with the notion of exploratory learning, the exact mechanism by which variability might aid adaptation is as yet unclear. In particular, it is not known whether variability reflects a very deliberate attempt to identify better motor commands, or whether the motor system is simply good at exploiting improvements stumbled on through variability that is present for other reasons. Either way, the ability to retain successful outcomes and ignore bad ones is suggestive of a learning process that is sensitive to scalar outcomes rather than vector errors.

The type of error signal used for learning may differ across components of learning. The existence of an implicit, cerebellum-dependent learning process that learns from vector errors is now well established [13,40,41]. A relationship between learning rate and trial-to-trial variability during adaptation appears to be specific to components of

learning that can be expressed at high preparation times [15**]. Explicit components of learning also appear to exhibit more exploratory behavior than implicit ones [7**]. The presence of this apparent exploratory behavior therefore suggests that some components of learning (those characterized as explicit or as preparation-time-dependent) are sensitive to scalar reward, in contrast to other (e.g. implicit) components of learning that are driven by vector error and appear to be indifferent to success or failure [10]. Reward-sensitive components of learning may also account for the differential effects of reward and punishment on adaptation rate [42].

Savings and recall in adaptation paradigms

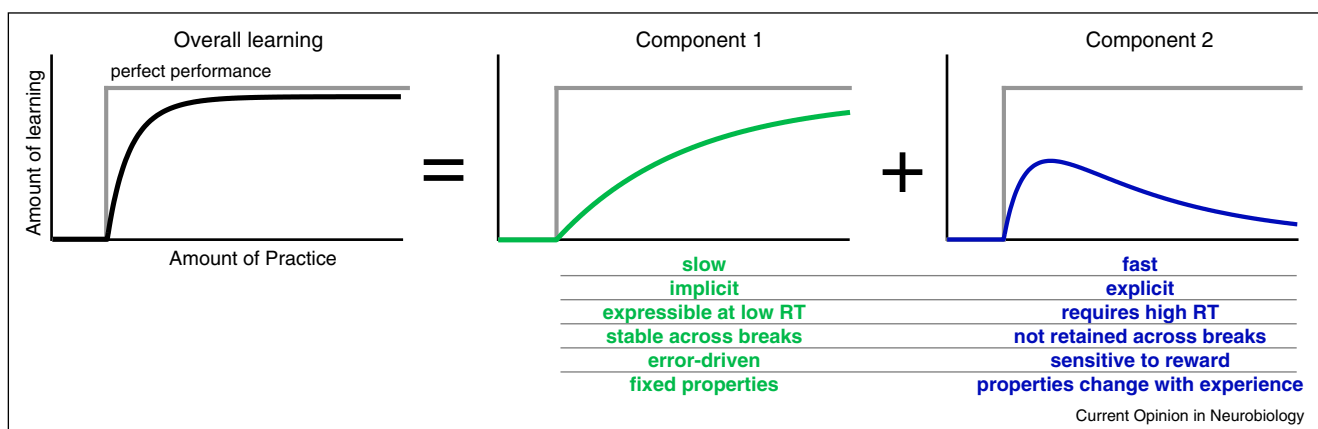
An important characteristic of behavior in adaptation paradigms is that subjects exhibit long-term memory. One form of memory already discussed is retention of a fraction of learning from one day to the next [22,26]. Another, more flexible and longer-term form of memory is exhibited through *savings*, whereby adaptation is faster the second time a perturbation is encountered [43,44], even weeks later [43]. While savings typically applies to a single learn/re-learn episode, repeated experience with a specific perturbation type can influence learning rates more strongly [36*,45–47]. One way to quantify learning rates is by examining the amount a subject learns from a single exposure to a perturbation. This single-trial learning rate is found to increase after experience in environments where imposed perturbations tend to persist from one trial to the next [46,47]. Single-trial learning rates even decrease following experience with perturbations that are transient, or which tend to reverse direction from one trial to the next [46,47]. These changes in learning rate appear to be specific to particular error magnitudes [47] and to the particular

type of perturbation encountered (e.g. velocity-dependent or position-dependent force fields) [36*].

How do such changes in learning rate come about? One possible explanation is that the sensitivity of error-driven learning increases or decreases based on prior experience [46,47]. There are, however, a number of results that are difficult to explain with this kind of theory. First, although savings is usually direction-specific [43], savings can be achieved across opposing perturbations if the targets are arranged such that the actions required to solve the two perturbations are the same [28,48]. This result can be explained by the idea that savings occurs through recall of a previously successful action [28], rather than an increase in sensitivity to error or recall of the perturbation. Two recent studies have provided evidence that changes in learning rate are brought about, at least in part, through recall effects. In both cases, subjects who had experienced one perturbation followed by a perturbation in the opposite direction responded to this new perturbation by directing their reach towards the action that had cancelled the first perturbation [46,9].

It seems unlikely that a single mechanism can universally account for all experience-dependent changes in learning rate. Rather, many qualitatively different effects likely all contribute to savings to varying degrees in different scenarios. Nevertheless, several recent studies have shown that savings, at least in some circumstances, is attributable to a single component of adaptation that tends to dominate early in learning. Haith and colleagues [16**] demonstrated that savings is only seen in components of learning that require a long preparation time in order to be expressed. In a similar vein, savings has recently been shown to occur in explicit but not implicit

Figure 1



Learning in adaptation paradigms reflects the summed contribution of multiple underlying components. Recent findings suggest the existence of two fundamental components of learning which possess contrasting properties in terms of their accessibility to conscious awareness, their preparation time requirements, their capacity for retention, the learning mechanisms they employ and their capacity for meta-learning.

components of learning [9]. Finally, savings seems to be attributable to components of learning that fail to be expressed following a 1 minute break [27]. Thus savings appears to be associated with explicit awareness, prolonged preparation time, and transient failure to express learning after a break. This suggests that these three forms of experimental decomposition might be exposing the same underlying single component.

Conclusions and outlook

Based on current evidence, it seems reasonable to speculate the existence of two fundamental components of learning (Figure 1). The first of these components learns slowly, is implicit, is driven by sensory prediction errors, is stable over short breaks, is expressible at low reaction times, and its properties do not change based on experience (i.e. it does not exhibit savings). The second component learns rapidly, is explicit, is sensitive to scalar outcomes (i.e. degree of success/failure), is disengaged following a brief break, requires a long preparation time to be expressed, and can exhibit latent long-term memory for prior learning, possibly through recall of previous successes.

This dualistic decomposition is likely an oversimplification. It is possible that these processes may in turn be decomposable into distinct sub-processes. Some existing findings are also difficult to explain within this particular dual-process account. For instance, in a study by Shmuelof *et al.* [21^{*}], a brief exposure during adaptation to an environment that promotes reinforcement learning was able to prevent decay back to baseline. The presence of rewards during learning is also known to promote retention better than equivalent punishment [42]. These findings suggest the existence of a third learning process, distinct from either process outlined above, that is highly stable and learns from reinforcement. Despite its limitations, we hope that the dual-process organization of motor adaptation we have outlined here can serve to highlight emerging phenomenology and stimulate a more comprehensive characterization of the constituent processes underlying adaptation.

Although our discussion has been limited to a few specific aspects of behavior in adaptation paradigms, decomposition of learning into constituent sub-components represents a very general strategy for understanding the nature of learning. Many other aspects of learning continue to offer a fruitful avenue for research, but have so far been little explored from a multi-component perspective of learning, including generalization [29,49–51] and interference [43,52^{*},53,54].

Adaptation paradigms probe a particular ability of the motor system: how to maintain accurate calibration of movement given a body and world in constant flux. Motor learning in more general settings may rely on distinct mechanisms not prominent during adaptation [55–58]. Nevertheless, we believe that many components of learning that contribute

to adaptation may serve a more general purpose. Indeed, many of the themes we have discussed here are recapitulated across a wide variety of domains, both motor and cognitive [59–63]. Although a valuable goal in its right, a thorough dissection of learning behavior in adaptation paradigms might ultimately serve a higher purpose by providing a convenient and tractable model system through which to study principles of learning in a dual-process context, together with a host of accompanying experimental innovations that may find utility beyond the domain of motor adaptation.

Conflict of interest statement

Nothing declared.

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