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# Human sensorimotor learning: adaptation, skill, and beyond

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Recent studies of upper limb movements have provided insights into the computations, mechanisms, and taxonomy of human sensorimotor learning. Motor tasks differ with respect to how they weight different learning processes. These include adaptation, an internal-model based process that reduces sensory-prediction errors in order to return performance to pre-perturbation levels, use-dependent plasticity, and operant reinforcement. Visuomotor rotation and force-field tasks impose systematic errors and thereby emphasize adaptation. In skill learning tasks, which for the most part do not involve a perturbation, improved performance is manifest as reduced motor variability and probably depends less on adaptation and more on success-based exploration. Explicit awareness and declarative memory contribute, to varying degrees, to motor learning. The modularity of motor learning processes maps, at least to some extent, onto distinct brain structures.

## Addresses

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## Introduction

Sensorimotor learning refers to improvement, through practice, in the performance of sensory-guided motor behavior. Here we will focus primarily on learning studies of the hand and arm in humans. Based on our own scientific leanings and limited space for this review, we chose to neglect learning with eyes and legs. It is worthwhile to admit to this effector chauvinism as it raises a question that almost never gets explicitly mentioned in the field of motor learning: how to choose which animal, body part, or task to study? Reductionism applies in motor control as much as in the rest of science; we need reduced systems in order to build up from the simple to the complex. Sherrington's studies of reflexes across single joints in cats and dogs were predicated on just this kind of reasoning [1]. Thus the sheer richness and variety

of learned real-world motor behaviors has been reduced to a small repertoire of laboratory-based learning tasks using different body parts. The crucial question is how interchangeable are these tasks with respect to general insights? It is fairly typical to read a paper where the methods section is task-specific but the discussion assumes the results are about motor learning in general. Thus we would argue that there is a tendency in the field to prematurely lump, and that we should be splitting instead. We focus on goal-directed arm movements because, in our view, they represent an intermediate level of behavior that embodies both low-level motor execution and higher-level cognition.

Psychophysical studies, in which learning is recorded through quantitative movement analysis, reveal regularities and performance patterns at the behavioral level, which suggest organizational principles for learning. Computational modeling offers normative principles, such as optimal Bayesian estimation and minimization of costs, to explain and predict behavioral data. Lesions in patients and stimulation techniques, such as transcranial magnetic (TMS) and direct current stimulation (tDCS), can be used to test the causal role of anatomical structures.

This review, necessarily selective, will describe recent noteworthy studies of goal-directed arm movements, and is organized around the principles of modularity and hierarchy. The text is structured on the premise that motor learning (as a blanket term) consists of multiple component processes, each of which has been studied with particular experimental paradigms. We have divided the sections into what we view as roughly separable components of learning. The order of the sections proceeds from adaptation, to skills, and then to the role of explicit cognitive processes.

## Adaptation

### Learning rates

Error-based paradigms (prisms, rotations, force fields) have been used extensively to investigate motor learning [2<sup>\*</sup>]. In these paradigms, subjects experience a perturbation of their hand during reaching or pointing movements: lateral displacement by prisms, rotation of movement direction, or lateral forces applied by a robot arm. Specifically, these paradigms have focused on adaptation, a form of learning characterized by gradual improvement in performance in response to altered conditions. Recent studies of motor adaptation have shown this type of learning to consist of incremental reduction in sensory prediction errors caused by a per-

## 2 Sensory and Motor Systems

turbation in the world through trial-by-trial modification of a motor-to-sensory mapping (forward model) [3]. The update in the forward model is then somehow translated into an update of motor commands [2\*].

Adaptation is well captured by linear time-invariant (LTI) (multi-) state-space models, which have sensory errors or perturbations as inputs, sensorimotor mappings as hidden variables, and the learned or adapted response as the output. These models have identifiable learning and retention parameters [4], whose origin has been of great interest: are they fixed by evolution or can some or all of them vary in some non-arbitrary way within the lifetime of a single individual? One normative Bayesian hypothesis is that these parameters can indeed change and do so optimally based on our ability to alter our estimates of both the stochastic behavior of the world and the noise in our sensory observations [5,6]. Given this hypothesis, the optimization algorithm that has been most investigated is the Kalman filter [7]. This filter can be understood heuristically as computing a learning rate (Kalman gain) at each trial that depends on the variance of the prior estimate of the world relative to the variance of sensory observations of the world. The Kalman filter becomes an LTI-state space model when the Kalman gain converges. Thus in interpreting adaptation data, one can either be agnostic about the values of parameter estimates from fits to adaptation data and go on to make predictions with these parameters, or one can ask whether adaptation is optimal in a Bayesian sense. Recent studies have taken both approaches.

Smith *et al.* originally introduced a two-rate state-space model description of force-field adaptation, which posits that adaptation is driven by a fast error reduction process with poor retention and a slow process with good retention [4]. They have recently studied important ramifications of this model. In one study [8\*] these authors investigated anterograde interference – the ability of a previously learned force field (Task A) to reduce the rate of subsequent learning of an opposite force field (Task B). Empirically, the amount of anterograde interference observed in the learning of Task B increased with the duration of Task A but then reached asymptote. The authors show that the 2-state model, using parameter values obtained from previous data, accurately predicted the observed anterograde interference effects. Critically, the degree of anterograde interference was not determined only by the final level of initial adaptation to A, but also by the duration of practice in Task A. This result is predicted if net adaptation is weighted more towards the slow system as adaptation proceeds. These results join previous successful predictions by the two-state model of savings, spontaneous recovery, and long-term retention [4,9]. The deep implication of being able to almost fully capture the results of initial force-field adaptation and

subsequent phenomena with a simple fixed parameter 2-state state-space model is that these experiments and the model successfully isolate a distinct learning mechanism. This kind of learning may be what the cerebellum is specialized to implement (see Box 1).

### Box 1 Where does sensorimotor learning take place? Evidence from neurologic patients and brain stimulation

*Adaptation and the cerebellum:* Recent studies add to the growing evidence for a crucial role for the cerebellum in adaptation [47–50]. Mazzoni and Krakauer [3] showed that, in adaptation to visuomotor rotation, implicit adaptation to a prediction error overrides an alternative explicit cognitive strategy to reduce target error. Taylor and Ivry [51\*] recently used the same task design to test a complementary prediction: if the cerebellum computes prediction error, cerebellar patients should be able to implement the cognitive strategy without interference from adaptation, which is what they found. Rabe *et al.* [52] found a double dissociation between two cerebellar regions and their contribution to different types of adaptation. Atrophy of the intermediate and lateral anterior lobe correlated with impairment of adaptation to a laterally displacing force field, while atrophy of the intermediate zone of the posterior lobe correlated with impairment of adaptation to a visuomotor rotation. Finally, a brain stimulation study [53\*\*] recently confirmed the cerebellum's importance in adaptation, not by causing a reversible lesion, but through enhancement of function. The authors reasoned that, if the cerebellum adjusts forward models in incremental steps on a trial-by-trial basis, enhancement of cerebellar activity via transcranial direct current stimulation (tDCS) might result in faster adaptation. This is precisely what they found, reinforcing the crucial role of the cerebellum in adaptation and suggesting that the rate of adaptation can be manipulated directly rather than through changing uncertainties.

*Skill and the motor cortex:* What is the structural anatomical basis for a high level of motor skill? One approach has been to use transcranial magnetic stimulation (TMS) to probe the variety of finger postures elicited by stimulation at various scalp positions over the motor cortex. Gentner and Classen [54] initially demonstrated that TMS elicits a range of finger postures that can be summarized by a small number of mathematical building blocks (principal components), and that these building blocks can be used to accurately reconstruct finger postures assumed by the hand during normal grasping movements. These findings suggested that finger postures are embedded in a modular fashion in the circuitry of the motor cortex. In a subsequent study [55\*\*], the authors then compared this cortical organization between musicians and non-musicians. The hypothesis was that the motor cortex of musicians may have elicitable representations specialized for playing their particular instrument. Musicians' and non-musicians' finger postures were recorded while they played a musical instrument. While the musicians' principal components, obtained from stimulation, could be used to accurately reconstruct these skilled movements, those of non-musicians could not. In other words, the musicians' ability to play the instrument was reflected in an instrument-specific specialized motor cortical organization that was not present in non-musicians. That motor cortex maintains representations of motor skills was brought one step further in a study [29\*] that used tDCS over the motor cortex of healthy subjects while they practiced a difficult visuomotor task. Task performance was limited by a speed-accuracy trade-off function (SAF), and motor skill learning was measured as daily improvements in the SAF. Motor cortex stimulation enhanced skill learning through an effect on overnight retention, consistent with the idea that motor cortex can store task-specific representations of motor skill.

The 2-state, and other LTI models, cannot, however, explain all the phenomena observed in adaptation experiments [10–12], such as savings (faster relearning on a second exposure to a perturbation). This limitation could in principle be addressed by introducing nonlinearities in the internal-model framework. Alternatively, additional learning processes besides adaptation may be at work in what appear to be relatively pure adaptation experiments [13<sup>\*</sup>], processes that are not captured by the internal-model framework.

Wei and Kording [14<sup>\*</sup>] investigated whether learning rate data can be explained within the framework of Bayesian estimation. For a Kalman filter, the learning rate should decrease as sensory noise increases and increase after a period when there is no sensory information. This is what the authors found: in a reaching task with adaptation to a visuomotor rotation, there was a reduction in learning rates when the position of a computer screen cursor, indicating hand position, was artificially blurred. The learning rate increased when it was preceded by a block of trials with no visual feedback. A note of caution needs to be raised, however, about this experiment and others that have made similar claims [15]. First of all, it is never stated what the implication is for optimality arguments if some of, but not all, the required parameters are adjusted in a direction consistent with a Kalman filter mechanism. For example, Burge *et al.* [15] also found a reduction in learning rate with increased sensory noise but not for increased output noise, and no increase when they increased variability in the motor-to-sensory mapping. To remain within the Bayesian framework it could be conjectured that some parameters are fixed (hard-wired) or that changes in, for example, state noise cannot be detected in the short time frame of a single experiment. More damaging, however, are examples where changes in rate occur when they are not predicted by a Kalman filter; for example, increases in learning rate after a period of baseline trials with normal feedback (washout) [10,11]. Such results suggest that there are alternative and likely more potent influences on adaptation rates than uncertainty.

### Representation of adapted mappings

Several recent studies have probed the constraints on adaptation to test hypotheses about neural representations of new sensorimotor mappings.

Sing *et al.* [16<sup>\*\*</sup>] measured the lateral forces that subjects expect during force-field adaptation by introducing intermittent ‘force-channel’ trials, in which a robot arm only allows subjects to make straight movements. These trials reveal the lateral forces subjects plan before each movement in order to counter the expected lateral velocity-dependent forces imposed in previous and subsequent trials. Sing *et al.* made the interesting observation that early on in adaptation to viscous force-fields there are not only the expected transient lateral forces midway through the

movement but also sustained lateral forces at the end of the movement. This is surprising – why apply a lateral force at the endpoint (static force tail) when there is no opposing force (velocity is zero)? As adaptation proceeds the force tails disappear and adaptation consists only of the transient response. The same mixture of transient and static responses is seen early on in adaptation to positional force fields but then evolves, appropriately, to only the static component. Thus subjects seem to adapt in a non-specific manner in their early responses to perturbations and become more task-specific later on. The explanation proffered by the authors is that subjects have a distribution, in position/velocity gain space, of motor primitives with correlated positional and velocity tuning. Such tuning has been found in muscle spindle afferents and primary motor cortex. A simple error-based learning rule selects those primitives best tuned to the perturbation. The authors go on to show that the model is able to predict those state-dependent force fields that subjects will find easier or more difficult to learn. The overall behavior ends up being identical to a Bayesian model having a prior that assumes that perturbations have correlated position and velocity components. Another recent study [17] has shown evidence for generic responses to perturbations of different types that are presented in single randomly interleaved trials. The interpretation offered, similar to that of Sing *et al.* [16<sup>\*\*</sup>], is that the interleaved design, analogous to early adaptation to a constant perturbation, does not allow for estimation of the specific perturbation and therefore a generic response is generated.

What determines how much adaptation to a particular perturbation generalizes across the workspace? For example, adaptation to visuomotor rotation shows limited generalization whereas adaptation of gain (amplitude scaling) generalizes broadly [18]. An upper bound on generalization function width may be the result of fixed neural tuning widths; indeed this has been argued recently as the explanation for narrow generalization of rotation adaptation [19]. Adaptation of gain (amplitude scaling), by contrast, generalizes broadly across direction for reaching movements [18], which raises the possibility of a lower bound: a coarse neural representation of movement amplitude, which would preclude learning two different gains in close proximity. Pearson *et al.* found, however, that this is not the case [20]: two gains in different directions can indeed be learned through more local generalization around each of the two training directions. Specifically, the more local gain learning could be explained by a weighted combination of single-gain generalization patterns, in which the weighting takes into account the relative angular separation between training directions. This solution is consistent with a hierarchical ‘mixture of experts’ architecture [21].

More insight into the possible reasons underlying differences in rotation and gain generalization was provided by

#### 4 Sensory and Motor Systems

Liu *et al.* [22<sup>•</sup>] The cursor position depended on experimenter-determined hand configurations recorded with a cyberglove, that is, the mapping from hand-space to cursor space was completely arbitrary and highly non-linear. The idea behind the cyberglove paradigm is that the transformations are being experienced by a naïve system and thus priors about gain (scaling) and rotation would presumably not apply. Perturbations of scaling and rotation were learned quite differently. Specifically, subjects explored and acquired a new finger coordination pattern for rotation adaptation but scaled their baseline coordination pattern for gain adaptation, thus supporting the idea that these two kinds of adaptation are computationally distinct [18]. Interestingly, however, both rotation and gain adaptation generalized narrowly. How is the narrow gain generalization seen for the cyberglove reconciled with the broad gain generalization described for arm movements? A clue comes from thinking about the Liu *et al.* [22<sup>•</sup>] and Pearson *et al.* [20] studies together. Perhaps the two-gain condition is analogous to the cyberglove: when the task space becomes complex and unfamiliar, generalization narrows to an upper, presumably neural, bound. If this is correct then it suggests an additional top-down mechanism that ‘surveys’ the task space and applies a general rule if the rule is easily applied to a familiar effector. Thus rotation might not generalize even for the arm because although the effector is familiar the rotation rule is not easily applied top-down. Note that this interpretation is speculative and quite different from the ‘mixture of experts’ argument given by Pearson *et al.* [20] and the argument provided by Liu *et al.* [22<sup>•</sup>]. The idea of a hierarchy whereby lower level building blocks generalize narrowly and higher levels generalize broadly bears conceptual similarities to the notion of reverse hierarchies in perceptual learning [23].

#### Beyond adaptation in error-based paradigms

Recent studies suggest that other learning processes are active, in addition to adaptation itself, in error-based paradigms. This is important to appreciate – the whole brain is taking part in the experiment, not just the cerebellum updating a forward model.

#### Use-dependent plasticity

It has recently been shown that repetition of a particular reaching direction leads future movements to be biased towards that direction [24<sup>•</sup>]. The term that has been used to for these repetition-induced biases is use-dependent plasticity. Diedrichsen *et al.* [25<sup>••</sup>] used a redundant task design to show that use-dependent plasticity and adaptation can occur simultaneously and in opposing directions in the task-irrelevant dimension of an adaptation task. Subjects were required to make a reach of specified amplitude but, unbeknownst to them, their arm was incrementally displaced laterally by a force channel applied by the manipulandum. Interestingly, even though the lateral movement was irrelevant to task completion, subjects

nevertheless biased their movements laterally when the manipulandum was no longer applying a lateral force and short-lived adaptation after-effects had washed out. Huang *et al.* [13<sup>•</sup>] used a modified visuomotor rotation paradigm to show that adaptation itself can act as a channel to induce directional biases in the direction of the adapted movement. Interestingly, the biases were larger in the setting of adaptation than those observed in the study by Verstynen and Sabes [24<sup>•</sup>], which suggests that use-dependent plasticity can be modified by the implicit reward of successful error reduction.

#### Success-based learning

Can a systematic perturbation be learned using scalar reward rather than vector error? Izawa and Shadmehr [26<sup>•</sup>] found that the answer is yes for visuomotor rotation, albeit under very specific circumstances. A rotation was introduced in 1° increments every 40 trials until it reached 8°. One group received full cursor feedback and explicit reward when they hit the target; the other group only received explicit reward. Both groups updated their commands by a similar amount and had a comparable amount of total learning. The authors argue that the two groups achieved the same performance in two qualitatively distinct ways based on two findings: only the group that received error feedback showed evidence for a change in the perceived position of their hand following a motor command (adaptation of a forward model) and showed broad generalization across directions. The group that only received scalar reward as feedback used a trial-and-error exploratory strategy, a strategy made possible by the gradual nature of the perturbation so that the required changes in movements largely occurred within the range of baseline variability. Although it is unlikely that large step perturbations could be learned with reward alone, the study by Izawa and Shadmehr shows that reinforcement learning, in some circumstances, can substitute for adaptation when there is uncertainty about, or no, sensory prediction error.

Huang *et al.* have recently suggested that even putatively pure adaptation paradigms are in fact made up of multiple distinct learning processes [13<sup>•</sup>]. Specifically, they hypothesized that hitting a target, or even getting closer to the target, is a form of implicit reward that leads to an operant reinforcement process whereby successful error reduction is associated with the commands, or movements, converged upon by adaptation. Moreover, they suggested that such model-free reinforcement is independent of internal model-based learning (adaptation) but that the two kinds of learning (model-free and model-based) combine to cause savings (faster relearning). In support of this idea, they showed that subjects could learn a 30° clockwise rotation faster after first learning a 30° counter-clockwise rotation if adaptation to the two oppositely signed rotations converged upon the same movement direction in hand space.

### Structural learning

Adaptation paradigms have also been used to provide evidence for a new framework, albeit consistent with the idea of modifiable priors, to explain learning-to-learn (meta-learning) phenomena. Braun *et al.* [27\*,28] pointed out the important distinction between *parametric* learning and *structural* learning. Parametric learning describes the adaptation processes we described in the first section: countering a perturbation through error-driven updates of a parameterized model. Structural learning can be considered learning the covariance structure among these parameters. For example, rotations and shears of a cursor's  $x,y$  position with respect to hand position can both be represented by 2 by 2 matrices. Knowing exactly how the entries of this matrix covary within each family of perturbations simplifies the decision of how to update the entries of the matrix following a given observed error; this dimensionality reduction allows an increase in learning rate. From the Bayesian point of view this would correspond to learning a new prior distribution on the parameters of the perturbation. In support of the structural learning hypothesis, Braun *et al.* [27\*] found that learning a particular rotation is facilitated after experiencing a lead-in period of random rotations, which suggests that the invariant feature during the lead-in period (the fact that all perturbations were rotations) was successfully extracted.

### Optimization and skill

We recently defined skill change operationally as a shift the speed-accuracy trade-off function (SAF) for a task when no systematic perturbation is present [29\*]. Adaptation to a perturbation, by contrast, is not a skill because subjects are knocked off their baseline SAF but at best only return to it – their performance is not better than baseline performance. The question is how is skill, that is, improved performance captured as a shift in the SAF, accomplished when there is no systematic change in the relationship between commands and their sensory consequences? Behavioral performance could be improved through better state estimation (improved forward models, or improved processing of sensory feedback), and/or through better motor execution (improved signal-to-noise ratio in motor output). Which of these processes is the rate-limiting step in skill learning is unknown. It is interesting to note that if skill could be attributed to improved state estimation by a forward model, then this would suggest that systematic changes in internal models occur much faster than improvements in the precision of these models, given that skill learning takes much longer than adaptation.

Optimal feedback control (OFC) [30] has proven a comprehensive theory of motor coordination in redundant systems [31–33,34\*]. A cost function made up of effort and accuracy terms can be optimized, assuming

that unbiased estimates of a number of crucial parameters, including the parameters of a forward dynamic model, are available *a priori*, to derive a feedback control policy for a given task goal. How does OFC relate to skill learning? Nagengast *et al.* [35\*\*] addressed how we learn to control complex objects with internal degrees of freedom. For such objects, there is no simple one-to-one correspondence between the state of the hand and the state of the object. For example, how does a cowboy, or Wonder Woman, learn to control a lasso? In the study, subjects learned to control 6 simulated objects with complex dynamics. They were trained with these strange virtual objects and improved at meeting an accuracy criterion even though they had to move progressively faster. The main result was that at the end of learning the hand paths that subjects adopted for each object were predicted by OFC using a simple cost function. Thus the assumption was that the lead-in training comprised adaptation – subjects first learn the complex object dynamics and then model-based optimization of a cost function occurs. But the lead-in training phase was marked by an improvement in both speed and accuracy, and therefore amounted to a shift of the SAF for this task. Although this lead-in phase was not the focus of the study, the data suggest that one of two other processes must also have been occurring in the training period to lead to better performance: convergence on the optimal policy, or improved execution of the control policy itself, perhaps through an increased signal-to-noise ratio via expanded neural representations. Either of these possibilities could be the explanation for shifts in the SAF [29\*] and reductions in variability described in motor skill learning studies [36,37]. We would suggest that optimal behavior is converged upon not only through model-based mechanisms, but also through model-free processes.

### Interaction between implicit and explicit processes during motor learning

Sensorimotor learning, in the form of mirror writing (a form of adaptation), served as the prototypical instantiation of procedural or implicit learning when it was shown to be intact in the amnesic patient HM [38,39]. Having lost explicit memory, HM did not recall having practiced the motor task before but nevertheless showed motor improvement over days. This very famous result has led, however, to oversimplifications and misunderstandings. That HM could not explicitly recall having done the task does not imply that explicit processes were not used each time he performed the task, that is, explicit memory and explicit control processes are not synonymous. Adaptation can indeed proceed entirely implicitly [3] but this does not preclude the possibility that it could benefit from explicit processes. Finally, as stated in the introduction, adaptation should not stand in for all of motor learning; what is true for adaptation may not be true for other forms of motor learning.

## 6 Sensory and Motor Systems

It is very unlikely that explicit and implicit processes do not interact during motor learning; it is hard to imagine that the prefrontal cortex would just stand by as motor areas do the learning. Two ways can be envisaged for how explicit cognitive processes could help motor learning. One is the idea that an alternative explicit strategy might be found to solve the learning task. The second, hitherto less considered possibility, is that explicit cognitive processes could augment implicit processes themselves.

### Adaptation

A recent study by Taylor and Ivry [40<sup>\*</sup>] further pursued the finding that, at least initially, implicit rotation adaptation cannot be bypassed by an explicit strategy [3]. Their surprising finding was that even though an explicit aiming strategy does indeed fail initially, at a certain point, if learning is allowed to proceed for many more trials, the strategy appears to win out over the implicit adaptation process. The authors envisage two competing processes captured by a two-state model – an implicit one based on prediction error and an explicit one based on target error. The model works by updating the aiming strategy to match the implicit process. This is a very strange and intriguing result as it suggests that an explicit strategy over time can itself take on the features of an implicit adaptation process.

Keisler and Shadmehr [41<sup>\*</sup>] used an interesting approach to examine whether declarative memory contributes to force field adaptation. Subjects began by adapting to force field A, then were briefly exposed to a counter force field B, and then, after a 3-min interval, were exposed to a force channel. Movements in a force channel reveal the lateral forces that subjects have learned through adaptation. This is the same paradigm as originally used to posit the existence of a fast and a slow adaptation component [4]. The novelty was to have subjects memorize and recall 12 word pairs in the 3 min interval between the end of B and the channel trials. The result was that the channel trials only showed evidence for slow A with no competing fast B (no spontaneous recovery) – implying that the declarative memory task interfered with memory of B. This result on its face does suggest that a declarative memory task can retrogradely interfere with recall of the fast process. It is almost as if one cannot engage short-term memory and hold on to a fast-adapted state simultaneously. This is an interesting and somewhat surprising result but it is important to be clear about what it does and does not mean. What the result shows is that the fast process and working memory may compete for a retrieval resource. It does not, however, imply that the fast acquisition process is itself explicit. Thus at this point in time there is no watertight evidence that adaptation itself has an explicit component.

### Skilled sequential movements

Sequence learning tasks have also been used extensively to study motor learning. The most popular task is the

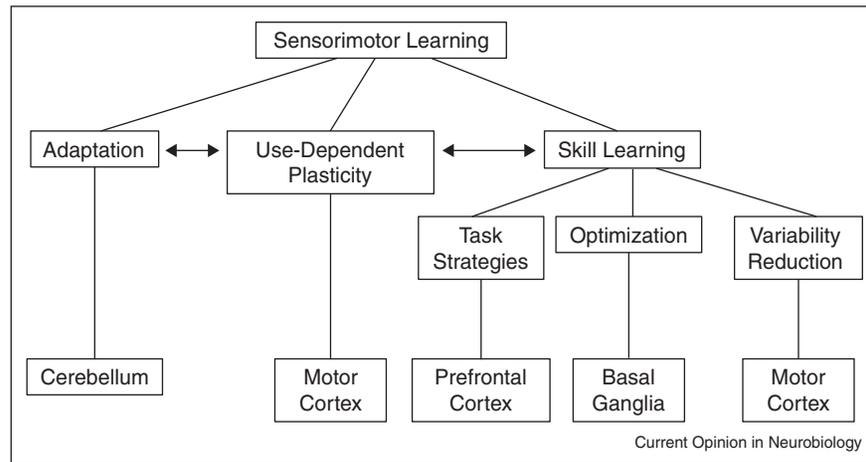
Serial Reaction Time Task (SRTT) [42]. This task has been used to argue that sequence order can be learned implicitly because onset times (reaction time (RT) plus movement time (MT)) are gradually reduced when subjects make sequential movements without explicit awareness that a sequence is present. In a recent innovative study, Moissello *et al.* took a critical look at the SRTT using a reaching task that allowed them to break the onset time measure into RT and MT [43<sup>\*</sup>]. Their main surprising finding was that there was no evidence for implicit learning of sequence order once one took account of explicit awareness of sequence fragments and the non-specific effect of practice on MT. This is a somewhat heretical result but adds to already existing skepticism as to whether purely implicit learning of sequence order is at all possible [44].

Can explicit awareness of sequence order and declarative memory enhance execution of sequence elements, that is, is there a way in which knowing what you have to do at the global task level improves the precision of component movements that are already practiced to a high level? Two recent studies suggest that the answer to this question is yes. Ghilardi *et al.* [45] showed that spatial accuracy was higher to an explicitly known well-practiced target in an array of 8 targets when the order of the other 7 targets was also known, compared to when the order of these remaining targets still had to be learned. Crump and Logan [46<sup>\*</sup>] found that already-skilled typists, using a familiar keyboard, showed a difference on a sequence execution measure (interkey stroke interval) if they were given a word that they had recently seen before versus a new word. These results are interesting because they go against the idea that as tasks become well practiced and automatic, they break free of explicit control. The possibility that explicit cognitive processes can always enhance overlearned skills suggests an interesting difference between skill learning and adaptation and raises the question as to whether HM could have learned to type if he had never done so before.

### Conclusions

Motor learning is a general term that covers multiple model-free and model-based learning processes that are likely to be differentially weighted across tasks and implemented by multiple functional and anatomical brain modules (Figure 1). Specifically, motor learning, at the very least, is made up of adaptation, use-dependent plasticity, operant reinforcement, and explicit cognitive processes. In this framework, it can be conjectured that adaptation and skill learning tasks lie along a spectrum with model-based processes prominent in the former and model-free processes prominent in the latter. Further elucidation of how these multiple processes interact in more complex sensorimotor learning tasks is an exciting direction for future research.

Figure 1



A proposed taxonomy for sensorimotor learning processes linked to specific brain structures. Note that the roles of the prefrontal cortex and the basal ganglia are not discussed in the present review.

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## 8 Sensory and Motor Systems

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