

Perspectives and problems in motor learning

Daniel M. Wolpert, Zoubin Ghahramani and J. Randall Flanagan

Movement provides the only means we have to interact with both the world and other people. Such interactions can be hard-wired or learned through experience with the environment. Learning allows us to adapt to a changing physical environment as well as to novel conventions developed by society. Here we review motor learning from a computational perspective, exploring the need for motor learning, what is learned and how it is represented, and the mechanisms of learning. We relate these computational issues to empirical studies on motor learning in humans.

From the motor chauvinist's point of view the entire purpose of the human brain is to produce movement. Movement is the only way we have of interacting with the world. All communication, including speech, sign language, gestures and writing, is mediated via the motor system. All sensory and cognitive processes may be viewed as inputs that determine future motor outputs.

Why do we need motor learning?



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Learning involves changes in behaviour that arise from interaction with the environment and is distinct from maturation, which involves changes that occur independent of such interaction. The goal of learning

is, in general, to improve performance. Whereas some simple species show no motor learning, the need for motor learning arises in species in which the organism's environment, body or task change. Specifically, when such changes are unpredictable, they cannot be pre-specified in a control system, and therefore flexibility in the control process is required. Skills such as running on complex terrains or manipulating novel tools place a premium on motor learning. Similarly, as body size and proportions change with development, significant changes in the controller are required. Finally, learning is the only mechanism fast enough to allow us to master new tasks that are specified by social conventions, such as writing or dancing.

Although much of our motor repertoire is acquired during our lifetime, we do not start life with a motor tabula rasa¹. Many human traits that might be assumed to be learned, such as facial gestures, are seen in children born blind and deaf². Such an innate pattern of behaviour is driven by evolutionary pressures to hardwire motor skills into the brain before birth. The range of innate motor behaviours across species, such as the fixed action patterns of birds and bees in courtship and social interaction, is truly remarkable. Innate wiring can speed up motor skill acquisition by providing a good starting point for future motor learning. However, there is likely to be a trade-off between innate behaviour and the ability to learn novel skills. Innate behaviour requires pre-specifying neural connections and making them robust to possible perturbing factors, but might leave less flexibility for novel skills. Indeed, motor learning can require the breaking down of relatively rigid innately specified synergies manifest in reflexes and central pattern generators³.

To truly understand motor learning it must be considered as a process that takes place both during an individual's life and over generations. Motor learning is a consequence of the co-adaptation of the neural machinery and structural anatomy³. For example, the tremendous dexterous abilities of humans arise not only from specific neuronal developments such as the larger corticospinal tract but also from the anatomy of the hand, with its specially evolved thumb. Generally in motor learning we consider how the brain adapts to control the body. However, it is also possible to fix the controller (i.e. the brain) and adapt the system (the body), or to co-adapt the two, which in general will result in better performance than adapting only one.

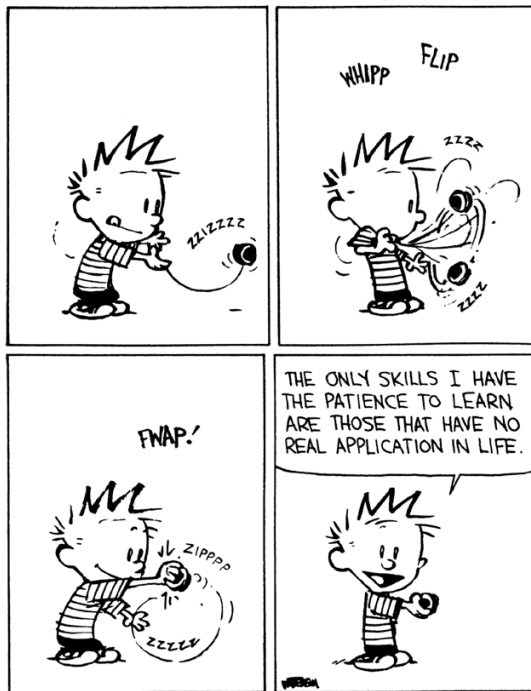
Daniel M. Wolpert*
Sobell Dept of
Neurophysiology,
Institute of Neurology,
Queen Square, London,
UK WC1N 3BG.
*e-mail:
wolpert@hera.ucl.ac.uk

Zoubin Ghahramani
Gatsby Computational
Neuroscience Unit,
University College
London, 17 Queen
Square, London,
UK WC1N 3AR.

J. Randall Flanagan
Dept of Psychology,
Queen's University,
Kingston, Ontario,
Canada K7L 3N6.

Adaptation of the body can occur both through evolutionary pressures over generations or within the individual's life, for example in use-dependent muscle hypertrophy.

What is learned in motor learning?



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From a computational viewpoint the brain is a processing system that converts inputs to outputs. The outputs are the motor commands acting on ensembles of muscles and the inputs are the aggregate of sensory feedback provided by our sense organs and derived internally from an efference copy of the descending motor command. Motor control can be thought of as the process of transforming sensory inputs into consequent motor outputs. The problem of motor learning is one of mastering and adapting such sensorimotor transformations.

The transformation between sensory and motor signals can be broken down into kinematic and dynamic transformations. Kinematic transformations convert between coordinate systems, such as between joint angles of the arm and the position of the hand. For example, to control a computer mouse, we must learn the kinematic transformation between the location of the mouse and the cursor on the screen. Dynamic transformations relate motor commands to the motion of the system. For example, we must also learn to relate the forces applied to the mouse to its resulting movement, a transformation that will depend on the inertia of the mouse and the friction between the mouse and pad.

Each transformation is bidirectional and to specify the direction under consideration a definition is adopted in which 'forward' indicates the causal

direction – for example, mapping motor commands onto their sensory consequences. 'Inverse' indicates the opposite direction, for example, transforming a desired sensory consequence into the motor commands that would achieve it. Although these transformations are governed by the physics of our bodies and environment, we distinguish the representation of such transformations within the central nervous system from the actual transformations by the phrase 'internal model'. Thus, the internal forward dynamic model is a model within the brain that can predict the sensory consequence of an action⁴.

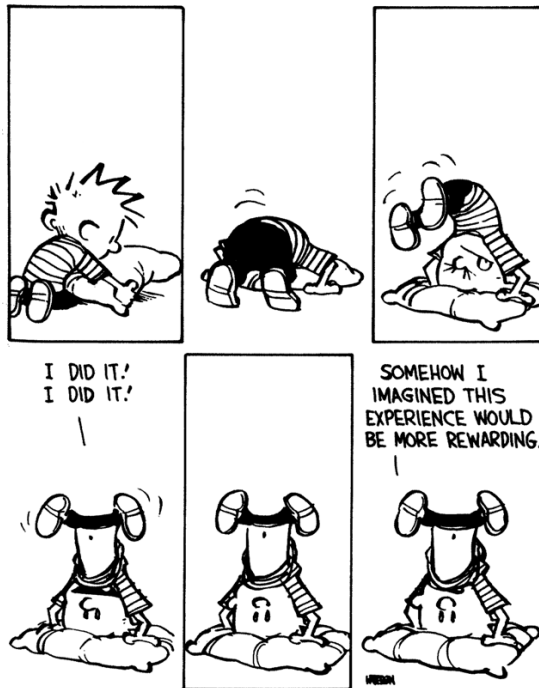
Skilled motor behaviour requires both inverse and forward internal models. Motor learning can be viewed as the acquisition of forward and inverse internal models appropriate for different tasks and environments. We need to acquire an inverse model in order to estimate accurately the motor commands required to achieve a desired sensory response. The feedforward control this allows is essential for most natural movements in which feedback is available too late to guide the movement. There have been many control systems proposed in the literature that use direct control, that is, control architectures that do not explicitly use internal models. However, any good controller can be thought of as implicitly implementing an inverse model of the system being controlled. A more contentious question is whether the central nervous system (CNS) needs forward models for control.

We believe that to learn the appropriate motor commands required for desired actions, the CNS must also use a forward model to predict the sensory consequences of these commands⁴⁻⁸. Such a prediction can be used in several ways. It can be used to cancel sensations arising from self-motion, which explains our inability to tickle ourselves⁹. Forward models can be used to estimate optimally the state of the body and the environment, and might even be used for mental practice.

The inverse model takes as one of its inputs the desired state of the system. At present there is a debate as to whether the CNS specifies the desired trajectory independently of the controller. In other words, are planning (specification of the trajectory) and execution (control) sequential stages? Alternatively, one could consider the controller as a dynamical system that generates behaviour without the need for a detailed plan of the trajectory¹⁰.

In summary, the acquisition of forward and inverse models is requisite for learning motor tasks that involve sequences of actions to achieve high-level goals. There are two important problems in the sequencing of actions: selecting the appropriate sequence elements, and determining their timing. Sensory feedback from one action is used not only to evaluate that action but to trigger subsequent actions^{7,11}. How such complex tasks are learned is an important future area of research.

What is the computational basis of motor learning?



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There are three principal ways in which the learning system can interact with the environment; these three ways correspond to three computational paradigms for learning: (1) supervised; (2) reinforcement; and (3) unsupervised learning. We consider the motor learning system taking in sensory inputs and producing motor outputs. In supervised learning, the environment provides, for each input, an explicit desired output or target. The goal of the learning system is to learn the mapping from inputs to outputs specified by this teaching signal from the environment. The performance of the learning system can therefore be measured by the discrepancy between the system's output and the desired target – that is, the error. Mathematically, one can define learning rules, such as the delta rule and back-propagation¹², that minimize the error as a function of the parameters or 'synaptic weights' of the system. These rules specify how to change the synaptic weights so as to decrease the error on the output.

In supervised learning the target output can be provided by an external teacher, for example, during imitation learning. However, the target output can also be specified internally, based on sensory signals and higher-level goals. Such self-supervised learning is involved in the acquisition of a forward model that tries to predict the sensory consequence of an outgoing motor command. Here, the desired output of the model is readily available – it is the actual sensory consequence.

Additional transformations might have to be applied to the error signal before it can be used to train an internal model. For example, when we throw a dart the error we receive is in visual coordinates. This sensory error must be converted into motor command errors

suitable to update the inverse model. The two principal methods proposed in the motor control literature for solving this problem are 'distal supervised learning'¹³ and 'feedback error learning'¹⁴. Distal supervised learning uses a forward internal model of the system to convert sensory errors into required changes to the motor command; feedback error learning uses a simple feedback controller to achieve the same conversion of errors. Both these methods also address one of the important problems arising from the redundancy of the motor system – that the relationship between the inputs and outputs of an inverse model can be one-to-many¹³.

In reinforcement learning¹⁵, for each input to and output from the learning system, the environment provides feedback in the form of either reward or punishment. The overall performance measure that the system tries to maximize is the sum of total future rewards, which can be weighted to favour immediate gain over longer-term gain. This is distinct from supervised learning in that the environment need not provide a target behaviour at each point in time, but instead simply specifies whether the overall behaviour is good or bad. A second distinguishing property of reinforcement learning is that the rewards or punishments that the system receives can depend in non-trivial ways on the history of past motor commands of the learning system. Consider a thirsty person trying to take a drink from a water fountain. We can regard the amount of water per unit time ingested as a positive reinforcement signal and the amount of water splashed on the face as punishment. The person generates a long sequence of motor commands for posture maintenance, and movements of the mouth and lips. Clearly, the amount of water drunk and splashed depends on the whole sequence of actions. At the end of the task the person is faced with the 'temporal credit assignment' problem: which set of past actions should be attributed as good and which as bad? This is just the sort of problem reinforcement learning algorithms are good at solving¹⁵.

The concept of an overall punishment signal, or cost, from reinforcement learning has been very influential in motor control. Because of kinematic redundancy almost any task can, in principle, be achieved in infinitely many ways¹⁶. Given all the possibilities, it is surprising that almost every study of the way the motor system solves a given task shows highly stereotyped movement patterns, both between repetitions of a task and between individuals on the same task. Such stereotypy arises when we consider tasks within the optimal control framework¹⁷, in which a dynamic system (e.g. the arm) must be controlled so as to minimize a cost function (e.g. error reaching to a target). Mathematically, optimal control theory and reinforcement learning theory are equivalent. The difference is in emphasis: the former focuses usually on continuous state systems with known dynamics and known cost function, whereas the latter focuses on discrete state systems with unknown dynamics and cost functions that have to be learned through experience. An important idea in

motor learning has been to try to reverse-engineer the cost function the CNS uses¹⁸⁻²⁰, that is, to ascertain what is being optimized from observed movement patterns and perturbation studies. For example, it has been proposed that there is noise in the motor command and that the amount of noise is proportional to the magnitude of the motor command²¹. In the presence of such noise the same sequence of intended motor commands, if repeated many times, will lead to a probability distribution over movements. Aspects of this distribution, such as the spread of positions or velocities of the hand at the end of the movement, can be controlled by modifying the sequence of motor commands²². In a simple aiming movement, the cost is the final error, as measured by the variance of the final position around the target. Assuming the presence of signal-dependent noise, a model that minimizes this cost accurately predicts the trajectories of both saccadic eye movements and arm movements²².

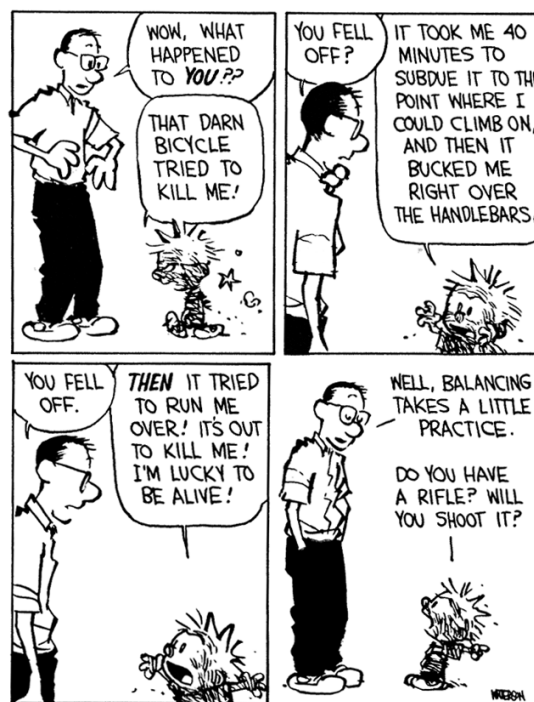
Finally, in unsupervised learning, the environment provides inputs but gives neither desired targets nor any measure of reward or punishment. One of the simplest forms of learning rule for unsupervised learning is the Hebbian learning rule. In this rule and later variants, the strength of a connection is increased when there is a coincidence of the firing of the pre-synaptic and post-synaptic neuron. It has been shown that Hebbian learning in simple linear networks²³ implements an unsupervised learning algorithm known as principal components analysis (PCA). This algorithm finds a lower dimensional representation of high dimensional inputs such that this representation preserves the most information available in the inputs, although it does this under the highly restrictive assumption that the inputs are Gaussian-distributed. Hebbian learning models based on PCA have been used to understand tuning properties of visual cortical neurons²⁴ and to implement simple unsupervised learning methods for finding motor primitives²⁵. The main problem with purely unsupervised learning is that there is no guarantee that the representations learned will be useful for decision making and control.

Although there are many ways of implementing these three computational paradigms for learning, a powerful unifying framework for understanding them is Bayesian learning. Supervised and unsupervised learning can be seen as using Bayes rule to combine the current model ('the prior') with new data ('the evidence') to generate an updated model ('the posterior'). Bayesian decision theory provides a framework for reinforcement learning, in which the model and the cost function are both learned from the environment.

There is evidence that different neural structures might be particularly adapted for different computational forms of learning²⁶. For example, the dopaminergic systems in the basal ganglia have been

tied to signals that one would expect in reinforcement learning, such as expected reward²⁷, and dysfunctions of these systems are related to movement disorders, addiction and other problems that could be related to reinforcement signals. Similarly, signals in the cerebellum have been linked to errors required for supervised learning²⁸. It has been shown that climbing fibres, which might act as a training signal to the cerebellum, code reaching errors at the end of a movement²⁹.

What makes motor control difficult?



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The algorithms discussed in the previous section can in theory be used to learn internal models required for skilled performance. However, there are several features of the human motor system that significantly complicate learning and control. First, there are considerable time delays in both the transduction and transport of sensory signals to the CNS. For example, visual input can take around 100 ms to be processed. When this sensory delay is combined with efferent delays associated with movement, the combined delay is appreciable. As a consequence, sensory information cannot be used to guide the initial part of a movement and skilled performance requires feedforward control supported by inverse models.

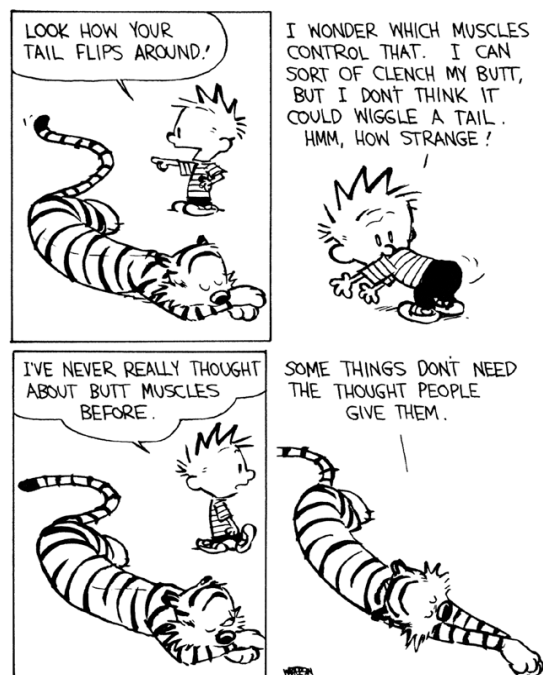
However, there is still a problem of temporally registering actual and desired behaviour. By temporally advancing sensory signals through prediction, forward models can be used to co-register actual and desired behaviour. In addition to delays, the sensory inputs and motor commands suffer from intrinsic neural noise, which limits the ability of the motor system to perform simultaneously rapid and

accurate movements^{21,22,30}. To counteract the effect of such noise the CNS can optimally estimate the current state by combining the actual sensory feedback with a forward model's predictions⁵.

The musculo-skeletal system is highly non-linear, in the sense that summing two sequences of motor commands does not result in the sum of the corresponding movements. Furthermore, the relationship between motor commands and movements (i.e. the dynamics) changes every time we interact with a novel object or environment; this property of being ever-changing is known as non-stationarity. One suggestion is that such complex non-linear and non-stationary behaviour can be achieved through learning multiple simple internal models³¹⁻³³.

Finally, the motor system receives thousands of sensory inputs and ultimately controls thousands of motor units, which gives it a very high-dimensional control problem to solve. For example, consider the 600 or so muscles in the human body as being, for extreme simplicity, either contracted or relaxed. This leads to 2^{600} possible motor activation patterns, more than the number of atoms in the known universe. Representing such high dimensional data is implausible. One solution to this is to generate lower dimensional representations of this high dimensional space¹⁰.

How is motor learning represented?



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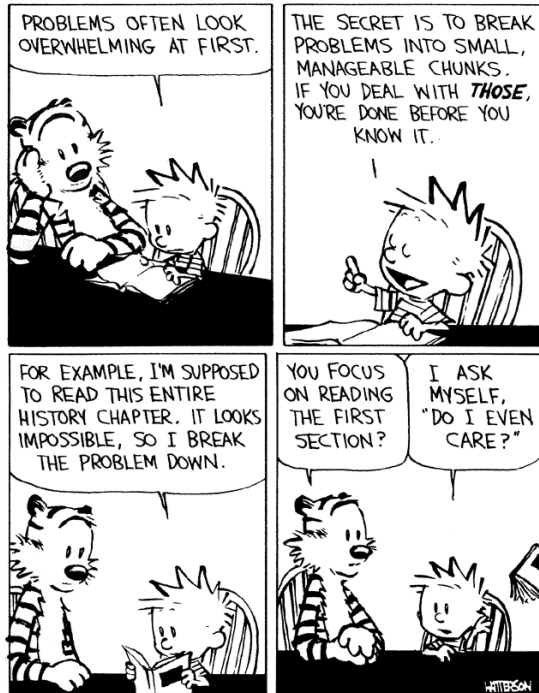
In principle, internal models can be represented in motor memory in many different ways. How they are represented in the CNS has important functional implications. The representation determines the coordinate systems of the neurons' code and what

changes to the mapping are easy to learn. We can distinguish between two extremes of representation. Lookup tables simply store the output for each possible setting of the input. Lookup tables are infinitely flexible, but suffer from their inability to generalize to novel inputs. They are also computationally costly as they grow in size exponentially with the dimension of the input. These problems with lookup tables can be partly alleviated by allowing some local generalization and by limiting the table to only relevant parts of the input space, that is, inputs that have been experienced. This approach has been successfully implemented for adaptive robot controllers and proposed as a model of human motor learning^{31,34}.

At the other extreme are parametric representations, such as the kinematics equations one would find in a robotics textbook that relate joint angles and link lengths to the position of the hand. Such representations are not very flexible as they can only model mappings obtained by varying the small number of parameters. On the other hand, they generalize globally to changes in these parameters (e.g. changes in the link lengths). In between these two extremes are mappings that generalize within a limited region of the input space. For example, basis function representations represent the mapping by combining a number of local 'basis functions' of the input^{35,36}. A basis function is a unit with a local receptive field, for example, a unit whose activity decreases with distance from its preferred stimulus (the centre of the basis function).

One way in which the representation can be examined is to alter the input-output mapping over a limited region and examine the subsequent generalization to novel inputs^{33,37,38}. Any changes in the input-output mapping for inputs not experienced during the training are attributable to the nature of the representation. For example, when a single visual location was remapped to a novel hand location, the entire visuomotor map was found to rearrange, suggesting that there is a global representation of this mapping³⁹. Furthermore, the change in this mapping was most consistent with a representation based on spherical coordinates centred about the eye. Dynamic mappings have been examined by asking subjects to make point-to-point movements in a force field generated either by a robot attached to their hand⁴⁰ or by a rotating room⁴¹. Over time they adapt and are able to move naturally in the presence of the field. Using this paradigm it has been shown that: (1) learning of dynamics generalizes in joint-based coordinates⁴⁰; (2) learning depends on the states experienced but not on the order in which they are experienced⁴²; and (3) state-dependent fields are learned more efficiently than temporally changing fields⁴³. In addition, both forward and inverse models are simultaneously adapted during learning, with the forward model leading^{44,45}.

What are the building blocks of motor learning?



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Recently, focus has begun to shift away from examining learning of a single internal model to consider how we are able to learn a variety of tasks. Many situations that we encounter are derived from a combination of previously experienced situations, such as novel conjoints of manipulated objects and environments. Internal models can be regarded conceptually as motor primitives, which are the building blocks used to construct intricate motor behaviours with an enormous range. By modulating the contribution to the final motor command of the outputs of a set of internal models, an enormous repertoire of behaviour can be generated. One architecture that is capable of learning to act in multiple situations is the MOSAIC model^{32,46}. In this architecture a set of forward models (predictors) are used as a set of hypothesis testers to assess which predictor best models the current task. This information is then used to weight the outputs of a set of corresponding inverse models (controllers). This system can simultaneously learn multiple predictors and controllers as well as how to select the controller appropriate for a given task.

Recent studies have shown that after learning two different contexts the CNS can appropriately mix the outputs; this has been demonstrated within the visuomotor domain⁴⁷, and across the visuomotor and dynamic domains⁴⁸. Our understanding of the mechanisms of motor learning has gained from examining how learning one task can interfere with learning others. When trying to learn two different dynamics^{49,50} or visuomotor rearrangements⁵¹, interference occurs when they are presented in quick succession but not when they are separated by

several hours. This suggests that motor learning undergoes a period of consolidation during which time the motor memory is susceptible to being disrupted. However, if the context is different then opposite internal models can be simultaneously maintained in motor working memory and subsequently consolidated. For example, subjects can learn and consolidate two opposing force fields if the position of the forearm is different for the two fields (in this experiment, subjects held a handle, which was either vertical or horizontal)⁵⁰. This suggests that the internal model captures a mapping between motor commands and sensory consequences that is determined by the force field but does not represent the force field *per se*. Moreover, experiments have shown that subjects are able to learn visuomotor and dynamic transformations independently when presented in close temporal proximity and even when presented in parallel^{48,51}. Thus, sensorimotor modality might be an important factor influencing the organization of motor working memory.

Recent evidence indicates that the cerebellum plays a central role in the long-term storage of internal models^{29,52–55}. In addition it has been suggested that the spinal cord stores a small set of motor primitives or basis functions⁵⁶. The idea is to simplify control by combining a small number of primitives, for example, patterns of muscle activations (synergies), in certain pre-specified proportions rather than individually controlling each muscle^{57,58}.

How does motor learning relate to perception and cognition?



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Questions for future research

- What are the common elements of motor learning and other forms of learning? Are the differences between motor and other forms of learning (e.g. perceptual) at a cellular level or a systems level?
- How are internal models of external objects, such as tools, integrated with the internal models of our own body, such as the arm?
- What are the characteristics of motor tasks that lead to competition in motor working memory and are there multiple motor working memory systems?
- Are the internal models that are used in action also used in perception and cognition?
- Can certain pathologies, such as Parkinson's disease, apraxia or motor tics, arise from learning mechanisms that have gone awry?
- Can principles of motor learning be applied to the creation of more adaptive robots and neural prostheses?



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As stated at the beginning of this article, direct information transmission between people, such as speech, arm gestures or facial expressions, is mediated through the motor system, which provides a common code for communication. An important idea in psychology is that perception of the action of others,

including speech, involves the action system⁵⁹. Others' actions are decoded by activating one's own action system at a subthreshold level and there appear to be special neural mechanisms for decoding such information. Recently, these ideas have gained empirical support in neuroscience with the finding of 'mirror neurones', which respond both to self-generated actions and the actions of others^{60,61}. Human neuroimaging and magnetic stimulation studies have shown that the areas associated with action are also active during imitation and observation⁶²⁻⁶⁴. Moreover, premotor systems are activated when subjects view manipulable tools or even action verbs^{65,66}.

It could be that the same computational processes underlie action, the perception of action, and social cognition. Indeed we can draw analogies among them. In motor control, a forward dynamic model can be used to predict the sensory consequences of our actions and an inverse model can be used to determine motor commands given desired actions. In perception of action we could use an inverse model to compute the motor commands that we would have to use to generate the same action. Alternatively, forward models could be used to make multiple predictions, and based on the correspondence between these predictions and the observed behaviour we could infer which of our controllers would be used to generate the observed action. Finally, in social interaction, a forward social model could be used to predict the reactions of others to our actions. An inverse social model allows us to come up with appropriate actions to gain desired social outcomes. Although the behaviour of others in response to our actions is more noisy and non-linear than the response of our arm to a motor command, computationally they are not fundamentally different.

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Thinking about the unknown

Paul L. Harris

A long tradition of research suggests that children and adults with no formal education are prone to reason only on the basis of their first-hand experience, and do not encode and reason from novel generalizations supplied by other people. However, recent research reveals that when given simple prompts, even pre-school children can reason from adults' unfamiliar claims. A radical implication of these findings is that young children arrive at school with a pre-existing capacity for thinking and reasoning about the unknown. The assumption that early learning should be rooted in children's own empirical experience could be mistaken.

Paul L. Harris
Harvard University, 506
Larsen Hall, Graduate
School of Education,
Appian Way, Cambridge,
MA 02138, USA.
e-mail: paul_harris@
gse.harvard.edu

In the early 1930s, the Russian psychologist Alexander Luria embarked on a research expedition to Uzbekistan in Central Asia. Years later, Luria became internationally known for his pioneering work in neuropsychology but at this early stage in his career, he was interested in what he and his close colleague L.S. Vygotsky thought of as the 'historical nature' of psychological processes – the extent to which reasoning, memory and categorization are shaped by the social and economic practices of a given

era^{1,2}. Faced with the upheavals throughout the Soviet Union under Stalin, Luria and Vygotsky realized that a vast social experiment was taking place that would allow them to test their ideas. Peasants who had never been to school and had always worked in a traditional, non-technological economy involving animal husbandry, gardening and cotton crops were being given one or two years of basic education, taught to read and write, and inducted into collective farming. More generally, a cultural transformation that might ordinarily take several generations was being compressed into a few short years. In Uzbekistan, Luria and his colleagues gave a number of cognitive tests to two groups of peasants on either side of this historical chasm: 'traditional' peasants who had never been to school and continued to work within the pre-Revolutionary, peasant economy, and 'educated' peasants who had received a basic education, learned to read and write, and were working within a collective.