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Motor skill learning between selection and execution

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Learning motor skills evolves from the effortful selection of single movement elements to their combined fast and accurate production. We review recent trends in the study of skill learning which suggest a hierarchical organization of the representations that underlie such expert performance, with premotor areas encoding short sequential movement elements (chunks) or particular component features (timing/spatial organization). This hierarchical representation allows the system to utilize elements of well-learned skills in a flexible manner. One neural correlate of skill development is the emergence of specialized neural circuits that can produce the required elements in a stable and invariant fashion. We discuss the challenges in detecting these changes with fMRI.

What is skill learning?

Motor skill learning generally refers to neuronal changes that allow an organism to accomplish a motor task better, faster, or more accurately than before. Beyond this accepted understanding of the common use of the word, there is little agreement in the literature about a more precise, scientific definition. Most researchers, however, agree on what skill learning is not. In other words, skill learning is currently mainly defined by its demarcation from other forms of learning.

First, skill learning is generally seen as separate from declarative knowledge [1] – in other words, it is not measured in terms that we can verbalize, but instead by what we can do (but see [2]), thereby falling under the broad umbrella of procedural knowledge. Furthermore, skill learning is usually distinguished from motor adaptation, which is defined as the recalibration of well-trained movements (such as locomotion, eye or reaching movements) to changes in environment [3]. This form of learning involves a parametric change driven by a sensory-prediction error on a trial-by-trial basis, and has been shown to depend on the integrity of the cerebellum [4–6].

Within these boundaries, the term skill learning refers to improvements in accuracy or speed in a wide variety of tasks, including the serial reaction time [7], fast sequential finger tapping [8], sequential force control [9], visual tracing [10], tracking [11], and synergy or hand configuration [12] tasks. In contrast to adaptation, skill learning typically involves the generation of a novel movement pattern, and is characterized by shifts in the speed–accuracy relationship [9,10,13].

An important characteristic of skill learning is that it involves various levels of the motor hierarchy (see Glossary). The main purpose of this paper is therefore to present a hierarchical framework of motor skill learning, within which we will review current behavioral and neural findings.

Selection versus execution

A first division in skill learning can be made between the levels of action selection and action execution [10]. The output of the execution level causes muscle activity – in other words, it includes motor cortical neurons that project to the spinal cord. Recent stimulation and recording studies in primary motor cortex (M1) suggest that small movement elements, so-called motor primitives, are encoded in the dynamics of sub-networks of neurons which produce replicable spatio-temporal patterns of coordinated muscle activity (Figure 1A) [14,15].

The selection level [16] then activates the appropriate motor primitives in a task-specific manner (white broken

Glossary

Chunking: segregation of long sequences of movements into subparts, and concatenation of motor responses into groups of responses, characterized by increased temporal intervals and probability of errors at chunk boundaries.

Discrete sequence production task (DSP): a task in which participants execute a known sequence as fast as possible, either from memory [8,43] or supported by sequential cues [51].

Motor hierarchy: the notion that movements are generated through the interaction of different representational levels, ranging from movement goals (selection level) down to the specification of the actual muscle commands (execution level).

Motor primitive: spatio-temporal pattern of muscle activity that occurs across a range of complex movements. Thought to be encoded in the spinal cord and/or primary motor cortex.

Repetition suppression: observation that the second presentation of a stimulus or second execution of a movement elicits less activity than the first presentation. By varying the dimensions on which two consecutive trials in an fMRI experiment differ, this technique is used to infer functional specialization.

Serial reaction time task (SRTT): task in which participants have to respond to visual stimuli using a finger press at a prescribed pace (often 1 Hz). Through repeated exposure to a constant sequence of stimuli, the motor system (often implicitly) learns to predict the next stimulus and/or response. Learning is evidenced by faster reaction times for stimuli within a fixed versus a random sequence.

Synergy: the term muscle synergy is sometimes used synonymously to motor primitive. In this review we use the term synergy to simply refer to a frequently occurring combination of muscle activities [68].

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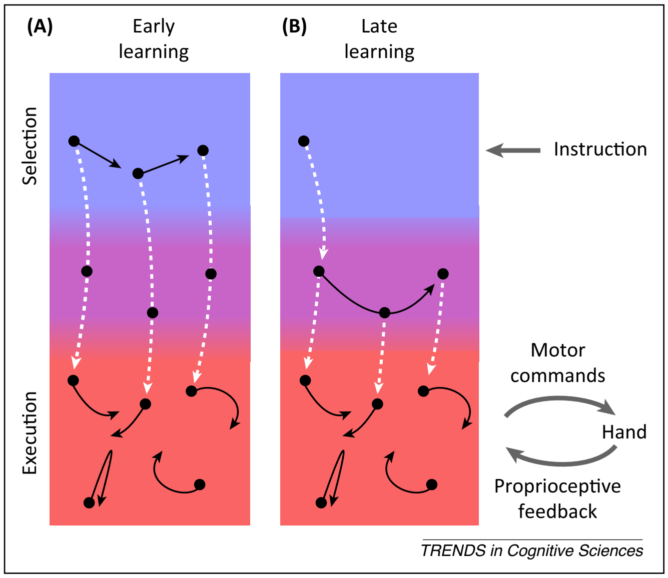

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Figure 1. Levels of skill learning. The execution level (red) encodes motor primitives, which produce stable spatio-temporal patterns of muscle activity. Each primitive is formed by a dynamical neural network with a stable state–space trajectory (indicated by the curved black lines). It is also sensitive to proprioceptive feedback from the controlled limb. **(A)** Early in learning, the appropriate primitives are activated (white broken lines) from the selection level (blue), and this involves explicit processing of task instruction. **(B)** Skill learning may involve the formation of association between the selected elements at an intermediate level (purple), which enables easier recall and production of complex sequences or movement combinations.

lines). Motor selection must be sensitive to the expected rewards, the motor cost, and task instructions. Selection is a time-consuming process because it needs to consider multiple alternatives and then settle on the most appropriate set of motor primitives – and, as for all choice-reaction time tasks, the time necessary will depend on the number [17] and dissimilarity [18] of the response alternatives.

When learning takes place in a serial reaction time task (SRTT), initial decreases in reaction times are likely due to the fact that the selection level becomes more adept in predicting the next stimulus, rather than by improvement of the execution of the button press itself. Other motor tasks, such as visuomotor tracking or tracing of an arc [10], appear to involve learning at the execution level – the person knows exactly which movement to select, but improves the speed and accuracy with which this movement can be executed. Many skill-learning tasks, however, involve learning both at the selection and the execution level, with learning possibly progressing from an abstract to a more motor-oriented representation [19]. For example, in the discrete sequence production task (DSP), learning starts as in the SRTT at the selection level as the participant remembers the sequence. Because there is no imposed temporal gap between responses, the learner will then form an execution-oriented sequence representation that allows production of the elements in rapid succession (Figure 1B).

The formation of skill representations reduces the load at the selection level: the next action does not have to wait for the time-consuming processes of memory recall or stimulus-response mapping [20,21]. Instead, the selection level only needs to trigger the corresponding network, which binds the execution elements into one dynamical control network.

This process predicts that the learner should be able to produce movements using less motor planning or preparation time. Indeed, shifts in time–accuracy trade-offs should be considered as one of the hallmarks of skill learning [9,10]. A recent study [13] demonstrates such shifts also occur when learning to reach during mirror-reversed feedback. By contrast, a very similar task – adaptation to a visual rotation – does not show a time–accuracy trade-off. These results indicate that visual rotations are learned through recalibration of already automatized processes (adaptation) while mirror-reversal is initially achieved through a time-consuming selection processes, followed by subsequent automatization (skill learning).

Although skill improvements can be achieved through the formation of a new motor primitive at the execution level, many studies provide evidence that such representations are formed in a hierarchical fashion, with encoding also occurring at an intermediate level between selection and execution (purple, Figure 1B). Such hierarchical representations would allow generalization and the flexible generation of novel behaviors (Box 1).

Automatization of selection processes may not be limited to sequential tasks, and may also extend to the simultaneous activation of specific groups of muscles – the learning of new synergies. For example, in a recently developed finger configuration task [12], participants had to press down with a selected set of fingers onto a keyboard, while stabilizing the force produced by the non-selected set. Initially, participants were unable to produce some of these configurations directly, because the required muscle synergy was very unnatural. Instead participants sequentially adjusted each finger, slowly approximating the correct configuration. After multiple days of training they generated the same hand configuration directly in one coordinated movement. Thus, through learning participants moved from sequential selection to the development of a new synergy.

Most movement tasks involve both sequence and synergy learning. For example, a tennis serve involves the sequence of throwing the ball, taking a back swing, and accelerating the arm forward. Each of these phases involves the coordination of multiple body parts. A skill representation would bind these disparate elements together into a single skilful sequence of multi-joint movements.

Neuronal correlates: recruitment versus efficiency

What are the neural correlates of skill learning? Investigation of this question is complicated by the fact that plasticity may involve multiple overlapping processes. Learning leads to neuronal recruitment – in other words, neurons not previously activated by the task become engaged [22,23]. This process may explain why the activity observed in fMRI studies often increases with learning [8,24–26].

Equally commonly, however, studies find that activity decreases with learning, especially after prolonged training [27–31]. Often these signal decreases are interpreted as a sign the region has stopped to play a role in the