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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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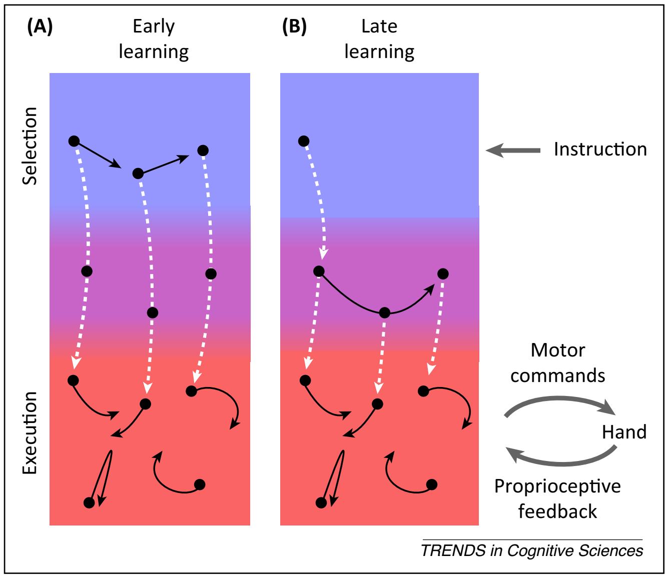

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Figure 1. Levels of skill learning. The execution level (red) encodes motor primitives, which produce stable spatio-temporal patterns of muscle activity. Each primitive is formed by a dynamical neural network with a stable state–space trajectory (indicated 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

Box 1. Intermediate-level learning

Automatization of an effortful selection process could take place in two ways. The repeated simultaneous or sequential selection of motor primitives could lead to the formation of a new execution-level representation that encodes the whole complex movement (sequence/synergy) (Figure IA). This predicts that pyramidal tract neurons in M1 are activated for a particular complex movement, but not for the constituent movement elements when executed in isolation. An execution-level representation requires a representation of all implementation details of each skilled movement.

Alternatively, the sequence or synergy could be represented at an intermediate level (Figure IB). Structurally, such representations would be formed through similar dynamical systems as in Figure IA – this would, however, not specify the implementation details of each movement, but instead call upon the simpler motor primitives at the execution level. This predicts that pyramidal tract neurons are activated similarly whether the movement element is executed in isolation or in the context of a complex movement. By contrast, in premotor areas neurons should be sensitive to the context of the action, for example, by firing only for particular sequential transitions between movement elements [58,69].

An execution-level representation predicts that learning a specific hand movement as part of one sequence should not generalize to another sequence. By contrast, an intermediate-level representation allows transfer because the two sequences would rely on the same execution-level representation. A professional pianist who can execute a specific chord transition within a new context would therefore rely on such intermediate representation. Similarly, transfer between hands must also rely on a representation that can activate appropriate movement primitives for either hand [70]. Thus, intermediate-level representations provide efficient and flexible encoding for complex movements.

By contrast, encoding at the execution level enables the system to optimize details of the movement elements that are specific to the context. Co-articulation - the change of kinematics or dynamics dependent on the preceding or following movement- is found in many contexts, including sequential arm movements [71]. Intermediate-level representations would not allow full co-articulation because the individual movement elements must remain operational in other contexts.

Evidence for an intermediate-level presentation is provided by increased skill encoding in premotor and supplementary motor areas [43], and by the relatively flexible generalization of learned movement skills [12]. Furthermore, an intermediate representation allows hierarchical chunking of action sequences and modular representations (see main text).

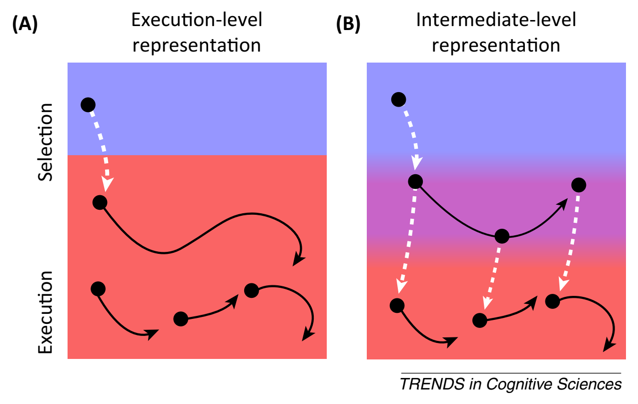

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Figure I. Differentiating execution- and intermediate-level skill representations.

production of the movement, and that the skill is now represented elsewhere [32].

It is also possible, however, that the region continues to preform the same function, but does so using less presynaptic activity – in other words it has increased its efficiency [33]. A dramatic example comes from a recent study showing decreased metabolic activity after extended sequence training in primates [34] – despite approximately matched activity of output neurons for trained and untrained movements. These findings may be interpretable with the emergence of a single dynamical system or motor primitive that is able to generate the desired behavior without further input from the selection level.

The overlap of neuronal recruitment and increased efficiency has made inferences from fMRI studies problematic. There is evidence for both increases and decreases in motor and premotor areas [35], which may also depend on the phase of learning (Box 2). Although a recent meta-analysis [36] suggests a consistent picture with activity increases in premotor cortex with learning, these results are biased by the fact that the authors only considered signal increases; when considering only negative changes in a complimentary analysis, they found evidence for decreases in similar areas. Thus, learning may lead to both signal increases and decreases – which in the worst case may average each other out, making learning-related changes invisible to classical fMRI analysis.

Neuronal correlates: stabilization and specialization

An important alternative idea in the search for neural correlates of skill learning is that training leads to the stabilization of the underlying neural network [37]. Reductions in neural variability during the production of the skill with learning have been observed in several different systems [22,38–40]. Concomitant with these neuronal changes, the skilled behavior itself also becomes more invariant [41–43]. As a result, it is often unclear whether the reduced neural variability causes the decrease in motor variability or whether it is the indirect consequence of reductions in variability in motor execution and subsequent sensory feedback. However, recent studies have attempted to control for this confound and still show clear decreases in neural variability for matched behavioral output [42].

The reduction of neural variability can be taken as a sign for the emergence of a new, specialized skill representation that can stably reproduce the same spatiotemporal output (Figure 1B). Could these changes be revealed in the human brain using fMRI? Even though different skilled movements will engage overlapping populations of neurons, functionally related neurons may cluster closely enough in space [44] to make these differences detectable using high-resolution imaging. Differences between activity patterns associated with different complex movements have recently been revealed using multi-voxel pattern analysis [45,46]. Furthermore, it has been shown that, with learning, the differences between these patterns increase relative to noise [43], supporting the notion that skill learning leads to increased neuronal specialization. Evidence for increased functional specialization also comes from fMRI studies using repetition suppression [31].

Box 2. Stages of learning

Skill learning is associated with complex, often non-monotonic, changes of neural activity across the time-course of learning [31]. Early phases of learning are often associated with increases in overall activity, followed by reductions in activity and neural variability in later phases [22]. This has led to the idea that skill learning develops in discrete stages with different learning rules and plasticity mechanisms [72,73]. While stages of learning may be a useful descriptive concept, it is very tempting to use it to explain non-linear changes across the time-course of learning, which is a form of circular reasoning (using a descriptor of Y to explain Y). The problem is that we currently do not have a clear behavioral criterion to distinguish different stages and to determine when one transitions into the next. While the rate of learning slows down as learning progresses, the same is true for simple exponential decay, which is governed by a single process. An absolute temporal criterion also cannot be found – a recent review allows the early stage of learning to last between 'minutes' to 'several months' – depending on the situation [72].

For the concept of learning stages to be fruitful, a description of the underlying processes is required. What signals the motor system to re-enter the stage of 'early' learning? What dictates the transition to 'late' stages of learning? Until independent criteria are established, the notion of learning stages remains descriptive without explanatory value. Indeed, it is more likely that the explanation for non-monotonic neuronal changes arise from the interplay of multiple plasticity processes that are always active no matter whether we are early or late in learning, similarly to current proposed models for adaptation [74].

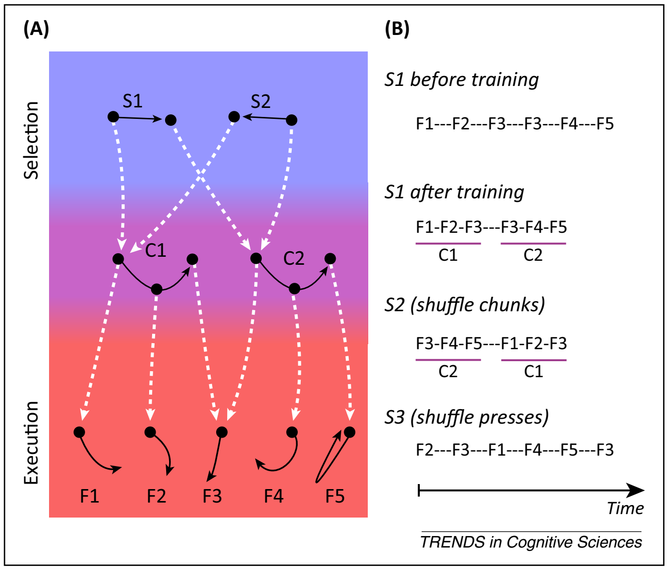

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Figure 2. Hierarchical representation enables movement chunking. **(A)** Sequence units at the selection level can trigger chunks (C1, C2) at the intermediate level (purple), which then in turn trigger individual movement elements (F1–F5). The chunk representations are efficiently shared across sequences S1 and S2. **(B)** Training on sequence S1 can lead to behavioral savings (faster and more accurate production) in novel sequences. Savings occur when the acquired chunks (C1 and C2) are preserved (S2), but not when they are broken up (S3).

These new representational analysis methods are therefore beginning to provide new insight into the neural organization of skill. Traditionally, signal decreases in premotor areas have been taken to indicate that these regions only play a role early in learning, and later make way to more execution-related representations [32,35]. It can be shown that some premotor regions actually exhibit a stronger representation of the learned skill despite equal or lower overall activity [43]. More importantly, it is now possible to more precisely pinpoint the actual structure of such representations (see below and [47]).

Chunking

Motor chunking is one of the key arguments for a hierarchical representation of motor skill. Proposed by Lashley in 1951 [48], the concept of motor chunking has come again to prominence over the last years. With learning, in addition to sequence completion becoming faster and more accurate, performance starts to show idiosyncratic temporal groupings or chunks [49]. Elementary movements that are bound into one chunk (Figure 2A) are retrieved faster and more accurately than when the selection level triggers them individually [50]. In addition to a more fluent sequence production, this hierarchical organization also has the advantage that acquired chunks can be used in the context of novel sequences [49]. For example, learning of one sequence (S1) that consists of two chunks (C1, C2) generalizes to the execution of another sequence (S2), which contains the same chunks in a different order (Figure 2B). Thus, a chunk- or intermediate-level representation of motor skills ensures both flexibility and efficiency in motor skill learning.

One challenge is to identify chunk boundaries from behavioral data. Traditionally, chunks were defined by especially long temporal gaps or error increases at the beginning of the chunk [49,51,52]. One group has suggested [53] that the correlational structures between neighboring inter-press-intervals (IPIs) may also be used as a criterion for chunk length. They hypothesized that IPIs are correlated more within than between chunks, because within each chunk the individual presses are controlled by a common process.

Whereas older approaches require averaging across trials, recent methods are able to detect chunks at a trial-by-trial level while still using the consistency of IPI profiles across a series of trials [54]. A Bayesian model has been been proposed [55] that combines response times and error rates, as well as their correlations across presses, to detect chunk boundaries with high sensitivity. The new approach enables automatic detection of dynamic changes in chunking structure over the course of learning, and provides evidence not only for the segregation of sequences into chunks but also for the increase of chunk length with learning (concatenation).

At a neural level, chunk formation is likely distributed across cortical premotor and striatal centers. A recent study in mice has shown firing patterns in both the direct and indirect pathways that suggest a role of the basal ganglia in chunk selection and execution [56]. Some striatal medium spiny neurons showed phasic activity increases at the beginning of a series of four lever presses, suggesting a role in the initiation of the chunk. Others exhibited tonic increases of decreases in the firing rate during chunk execution, possibly providing sustained disinhibition of the selected motor chunk. Importantly, the majority of cells were specific to the actions performed, but invariant to the speed of these actions. This suggests that the striatum is involved in controlling whole chunks of concatenated movements without representing the implementation details of the movement elements.

These findings are paralleled by human neuroimaging experiments identifying that stronger concatenation of adjacent motor elements into a chunk correlates with increased blood oxygen level-dependent (BOLD) activity in the bilateral putamen [54]. Non-invasive stimulation in humans has also demonstrated that the pre-SMA [57] is crucial for chunk initiation – corresponding to electrophysiological findings suggesting that individual units in the pre-SMA are tuned to whole three-element series of movements [58]. These results indicate that the basal ganglia, SMA, and pre-SMA play an important role in a more abstract representation of movement chunks, consistent with the proposed roles of representations at the selection and intermediate levels.

Modularity of skill features

The dynamical systems view holds that the spatio-temporal evolution of an action is encoded in the intrinsic dynamics of a pattern generator at the execution level [15]. For simple movements, such as reaching, the required muscle commands seem to be inseparably represented from their timing [59]. Recent computational work further shows that this principle could scale up to more complex sequential movements such as writing a full word [60]. Thus, in this low-level view of motor skill encoding (see Figure IA in Box 1), complex movements are represented as an integrated whole.

By contrast, the motor system may acquire a more flexible representation of movement sequences that specifies their organization in space and time separately (Figure 3A). Both the spatial (black dots) and the temporal sequence (red dots) could be represented at the intermediate level and interact when triggering the corresponding execution-level representations of individual movements. Indeed, recent behavioral work advocates such an organization [47,61]. Participants were trained on specific spatio-temporal sequence of finger presses. Their performance was then assessed when the temporal feature (the rhythm), the spatial feature (the sequence of keys), or both were changed (Figure 3B). Consistent with an intermediate-level representation, they showed a behavioral advantage in both the spatial and temporal transfer conditions as compared to a novel spatio-temporal sequence (Figure 3C; see also [62]). Using multivariate analysis of fMRI data, a direct correlate of the independent representation of spatial and temporal features could be shown in overlapping regions in premotor cortex (Figure 3D) [47]. By contrast, M1 represented the two sequence features in non-separable fashion. This distribution of sequence encoding provides clear evidence for a hierarchical representation of skill.

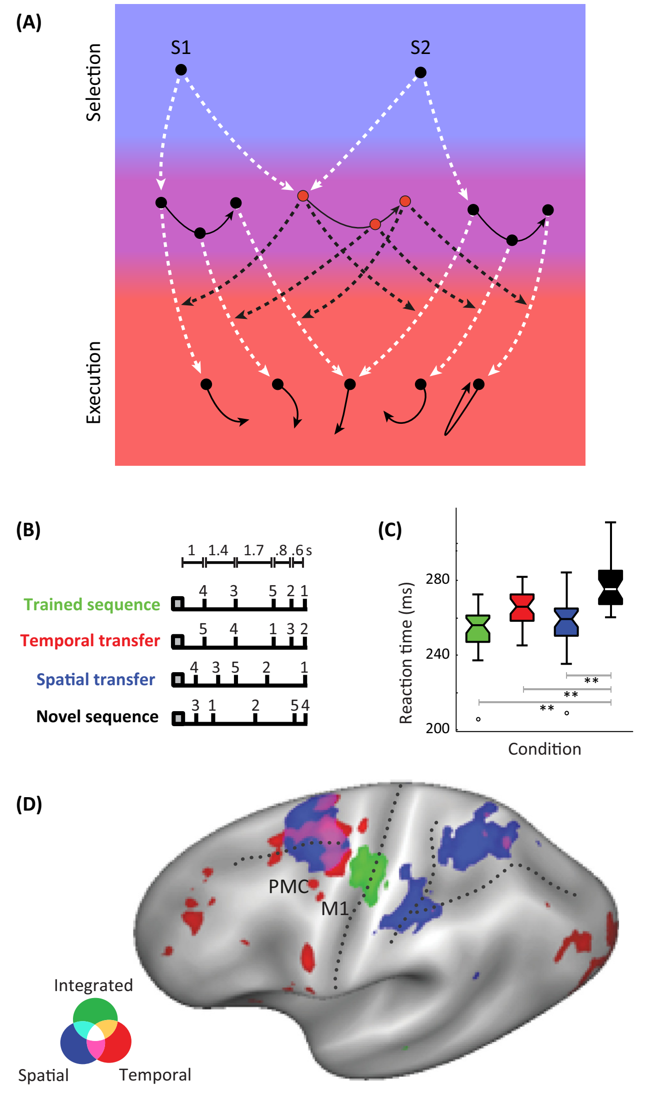

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Figure 3. Modular representation of sequence features. **(A)** Separate representation of temporal (red dots, a longer and a shorter interval) and spatial (black dots) sequence features [75]. The temporal representation modulates the signal originating from two different spatial representations (black broken arrows) [61]. This allows two different sequences S1 and S2 to utilize the same learned temporal structure. **(B)** Participants were trained on a specific spatio-temporal sequence (green) and then tested on a novel sequence (black) or on sequences that retaining either the temporal (red) or spatial (blue) structure. **(C)** Reaction-time results indicate independent transfer of spatial and temporal features to test conditions. Stars indicate significant differences. Circle indicate outliers in the data. **(D)** Separate but partially overlapping spatial (blue) and temporal (red) representations of finger sequences can be revealed bilaterally in premotor cortex (PMC) using multi-voxel pattern analysis. The two features are integrated in contralateral primary motor cortex (M1) only (green). Panels (B–D) are adapted, with permission, from [47].

A similar dissociation in the representation of sequences has been found in song birds [63]. Using aversive auditory conditioning, the authors were able to teach animals to selectively change temporal and spectral features of their song. The basal ganglia analog was required for the modification of the spectral properties (pitch), but not for changes in the temporal structure. By contrast, the activity in HVC (an analog to the premotor cortex) reflected the temporal but not spectral features of the song. Moreover, recent studies involving timed tapping sequences in monkeys suggest that individual units in medial premotor areas can encode not only the intervals between movements but also their unique position in the sequence of movements [64,65], suggesting a dedicated representation for the temporal features of movement sequences. A modular representation of temporal and spatial features at an intermediate level allows the learner to flexibly perform a trained sequence of movements in space with a new rhythm, for example when dancing to a new song.

Box 3. Outstanding questions

- **Neural specialization:** human imaging work has suggested that, when people learn multiple skilled movements, each movement becomes associated with a unique activity pattern [43]. There are currently very few animal models for this process. Such experiments would have the potential to illuminate how different movements are encoded in overlapping population of neurons, and shed light on the neural basis of interference.
- **Long-term learning**: does skill learning always progress from more abstract to more execution-oriented representations [19]? Or is skilled performance characterized by a strengthening of the hierarchical and modular structure of skill representations? How do neocortex, basal ganglia, and cerebellum interact to give rise to consolidated motor memories?
- **Chunking of action sequences:** what determines the formation of chunks versus the integrated representation of whole action sequences? Which neuronal mechanisms underlie the control of chunks?
- **Modularity of skilled movement representations:** is the separation into movement features a universal property of motor skill representation? How do different movement effectors (fingers vs vocal apparatus) or different kinematics (continuous vs discrete movements) influence how skilled movement sequences are stored?
- **Feedforward versus feedback control**: although the literature on skill learning emphasizes tasks that rely mostly on feedforward control, many skills in real life, such as skiing, playing tennis, or juggling, heavily depend on feedback. How does the brain learn to react more efficiently to incoming sensory information?

Concluding remarks

The next important challenge is to understand the neuronal underpinnings of hierarchical skill encoding (outstanding questions are listed in Box 3). Note that our current model is mainly representational and that we have resisted the temptation to provide a direct mapping between the different levels and specific neural regions because this relationship is likely to be complex. For example, different subregions of both cerebellum and basal ganglia form partially parallel loops with multiple cortical regions [66] and may therefore play a role in each of the levels. Consistent with this idea, it has been suggested that basal ganglia circuits play a role both in the selection of action, as well as in the binding of action elements into larger chunks [67].

Hierarchical encoding of motor skills endows the system with the ability to efficiently generate new combinations of motor primitives without the necessity of forming execution-related representations *de novo*. The behavioral advantage of this architecture may explain why evolution has not simply expanded the primary motor cortex with direct access to the spinal cord, but instead has resulted in the emergence of several premotor areas with predominantly indirect cortico-spinal projections via M1.

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References

1 Schacter, D.L. and Tulving, E., eds (1994) *Memory Systems 1994*, MIT Press
2 Stanley, J. and Krakauer, J.W. (2013) Motor skill depends on knowledge of facts. *Front. Hum. Neurosci.* 7, 503
3 Wolpert, D.M. *et al.* (2011) Principles of sensorimotor learning. *Nat. Rev. Neurosci.* 12, 739–751
4 Diedrichsen, J. *et al.* (2005) Cerebellar involvement in anticipating the consequences of self-produced actions during bimanual movements. *J. Neurophysiol.* 93, 801–812
5 Tseng, Y.W. *et al.* (2007) Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J. Neurophysiol.* 98, 54–62
6 Smith, M.A. and Shadmehr, R. (2005) Intact ability to learn internal models of arm dynamics in Huntington's disease but not cerebellar degeneration. *J. Neurophysiol.* 93, 2809–2821
7 Willingham, D.B. (1998) A neuropsychological theory of motor skill learning. *Psychol. Rev.* 105, 558–584
8 Karni, A. *et al.* (1995) Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature* 377, 155–158
9 Reis, J. *et al.* (2009) Noninvasive cortical stimulation enhances motor skill acquisition over multiple days through an effect on consolidation. *Proc. Natl. Acad. Sci. U.S.A.* 106, 1590–1595
10 Shmuelof, L. *et al.* (2012) How is a motor skill learned? Change and invariance at the levels of task success and trajectory control. *J. Neurophysiol.* 108, 578–594
11 Imamizu, H. *et al.* (2000) Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature* 403, 192–195
12 Waters-Metenier, S. *et al.* (2014) Bihemispheric transcranial direct current stimulation enhances effector-independent representations of motor synergy and sequence learning. *J. Neurosci.* 34, 1037–1050
13 Telgen, S. *et al.* (2014) Mirror reversal and visual rotation are learned and consolidated via separate mechanisms: recalibrating or learning de novo? *J. Neurosci.* 34, 13768–13779
14 Overduin, S.A. *et al.* (2012) Microstimulation activates a handful of muscle synergies. *Neuron* 76, 1071–1077
15 Churchland, M.M. *et al.* (2012) Neural population dynamics during reaching. *Nature* 487, 51–56
16 Cisek, P. (2012) Making decisions through a distributed consensus. *Curr. Opin. Neurobiol.* 22, 927–936
17 Hick, W.E. (1952) On the rate of gain of information. *Q. J. Exp. Psychol. (Colchester)* 4, 11–26
18 Rosenbaum, D.A. *et al.* (1988) In defense of the advance specification hypothesis for motor control. *Psychol. Res.* 50
19 Hikosaka, O. *et al.* (2002) Central mechanisms of motor skill learning. *Curr. Opin. Neurobiol.* 12, 217–222
20 Gobet, F. *et al.* (2001) Chunking mechanisms in human learning. *Trends Cogn. Sci.* 5, 236–243
21 Miller, G.A. (1956) The magical number seven plus or minus two: some limits on our capacity for processing information. *Psychol. Rev.* 63, 81–97
22 Costa, R.M. *et al.* (2004) Differential corticostriatal plasticity during fast and slow motor skill learning in mice. *Curr. Biol.* 14, 1124–1134
23 Nudo, R.J. *et al.* (1996) Use-dependent alterations of movement representations in primary motor cortex of adult squirrel monkeys. *J. Neurosci.* 16, 785–807
24 Shmuelof, L. *et al.* (2014) The neural correlates of learned motor acuity. *J. Neurophysiol.* 112, 971–980
25 Penhune, V.B. and Doyon, J. (2002) Dynamic cortical and subcortical networks in learning and delayed recall of timed motor sequences. *J. Neurosci.* 22, 1397–1406
26 Floyer-Lea, A. and Matthews, P.M. (2005) Distinguishable brain activation networks for short- and long-term motor skill learning. *J. Neurophysiol.* 94, 512–518
27 Jenkins, I.H. *et al.* (1994) Motor sequence learning: a study with positron emission tomography. *J. Neurosci.* 14, 3775–3790
28 Toni, I. *et al.* (1998) The time course of changes during motor sequence learning: a whole-brain fMRI study. *Neuroimage* 8, 50–61
29 Ungerleider, L.G. *et al.* (2002) Imaging brain plasticity during motor skill learning. *Neurobiol. Learn. Mem.* 78, 553–564
30 Ma, L. *et al.* (2010) Changes in regional activity are accompanied with changes in inter-regional connectivity during 4 weeks motor learning. *Brain Res.* 1318, 64–76
31 Wymbs, N.F. and Grafton, S.T. (2014) The human motor system supports sequence-specific representations over multiple training-dependent timescales. *Cereb. Cortex* Published online June 26, 2014. http://dx.doi.org/10.1093/cercor/bhu144
32 Doyon, J. *et al.* (2003) Distinct contribution of the cortico-striatal and cortico-cerebellar systems to motor skill learning. *Neuropsychologia* 41, 252–262

33 Poldrack, R.A. (2014) Is 'efficiency' a useful concept in cognitive neuroscience? *Dev. Cogn. Neurosci.* Published online June 13, 2014. http://dx.doi.org/10.1016/j.dcn.2014.06.001
34 Picard, N. *et al.* (2013) Extended practice of a motor skill is associated with reduced metabolic activity in M1. *Nat. Neurosci.* 16, 1340–1347
35 Steele, C.J. and Penhune, V.B. (2010) Specific increases within global decreases: a functional magnetic resonance imaging investigation of five days of motor sequence learning. *J. Neurosci.* 30, 8332–8341
36 Hardwick, R.M. *et al.* (2013) A quantitative meta-analysis and review of motor learning in the human brain. *Neuroimage* 67, 283–297
37 Costa, R.M. (2011) A selectionist account of de novo action learning. *Curr. Opin. Neurobiol.* 21, 579–586
38 Hahnloser, R.H. *et al.* (2002) An ultra-sparse code underlies the generation of neural sequences in a songbird. *Nature* 419, 65–70
39 Komiyama, T. *et al.* (2010) Learning-related fine-scale specificity imaged in motor cortex circuits of behaving mice. *Nature* 464, 1182–1186
40 Ganguly, K. and Carmena, J.M. (2009) Emergence of a stable cortical map for neuroprosthetic control. *PLoS Biol.* 7, e1000153
41 Tchernichovski, O. *et al.* (2001) Dynamics of the vocal imitation process: how a zebra finch learns its song. *Science* 291, 2564–2569
42 Peters, J. *et al.* (2014) Emergence of reproducible spatiotemporal acitivity patterns during motor learning. *Nature*
43 Wiestler, T. and Diedrichsen, J. (2013) Skill learning strengthens cortical representations of motor sequences. *Elife* 2, e00801
44 Dombeck, D.A. *et al.* (2009) Functional clustering of neurons in motor cortex determined by cellular resolution imaging in awake behaving mice. *J. Neurosci.* 29, 13751–13760
45 Diedrichsen, J. *et al.* (2013) Two distinct ipsilateral cortical representations for individuated finger movements. *Cereb. Cortex* 23, 1362–1377
46 Gallivan, J.P. *et al.* (2013) Where one hand meets the other: limb-specific and action-dependent movement plans decoded from preparatory signals in single human frontoparietal brain areas. *J. Neurosci.* 33, 1991–2008
47 Kornysheva, K. and Diedrichsen, J. (2014) Human premotor areas parse sequences into their spatial and temporal features. *Elife* 3, e03043
48 Lashley, K.S. (1951) The problem of serial order in behavior. In *Cerebral Mechanisms in Behavior: The Hixon Symposium* (Jeffress, L.A., ed.), pp. 112–146, Wiley
49 Sakai, K. *et al.* (2003) Chunking during human visuomotor sequence learning. *Exp. Brain Res.* 152, 229–242
50 Rosenbaum, D.A. *et al.* (1983) Hierarchical control of rapid movement sequences. *J. Exp. Psychol. Hum. Percept. Perform.* 9, 86–102
51 Abrahamse, E.L. *et al.* (2013) Control of automated behavior: insights from the discrete sequence production task. *Front. Hum. Neurosci.* 7, 82
52 Lungu, O. *et al.* (2014) Striatal and hippocampal involvement in motor sequence chunking depends on the learning strategy. *PLoS ONE* 9, e103885
53 Verstynen, T. *et al.* (2012) Dynamic sensorimotor planning during long-term sequence learning: the role of variability, response chunking and planning errors. *PLoS ONE* 7, e47336
54 Wymbs, N.F. *et al.* (2012) Differential recruitment of the sensorimotor putamen and frontoparietal cortex during motor chunking in humans. *Neuron* 74, 936–946
55 Acuna, D.E. *et al.* (2014) Multi-faceted aspects of chunking enable robust algorithms. *J. Neurophysiol.* 112, 1849–1856
56 Jin, X. *et al.* (2014) Basal ganglia subcircuits distinctively encode the parsing and concatenation of action sequences. *Nat. Neurosci.* 17, 423–430
57 Kennerley, S.W. *et al.* (2004) Organization of action sequences and the role of the pre-SMA. *J. Neurophysiol.* 91, 978–993
58 Shima, K. and Tanji, J. (1998) Both supplementary and presupplementary motor areas are crucial for the temporal organization of multiple movements. *J. Neurophysiol.* 80, 3247–3260
59 Conditt, M.A. and Mussa-Ivaldi, F.A. (1999) Central representation of time during motor learning. *Proc. Natl. Acad. Sci. U.S.A.* 96, 11625–11630
60 Laje, R. and Buonomano, D.V. (2013) Robust timing and motor patterns by taming chaos in recurrent neural networks. *Nat. Neurosci.* 16, 925–933
61 Kornysheva, K. *et al.* (2013) Interaction of temporal and ordinal representations in movement sequences. *J. Neurophysiol.* 109, 1416–1424
62 Ullen, F. and Bengtsson, S. (2003) Independent processing of the temporal and ordinal structure of movement sequences. *J. Neurophysiol.* 90, 3725–3735
63 Ali, F. *et al.* (2013) The basal ganglia is necessary for learning spectral, but not temporal, features of birdsong. *Neuron* 80, 494–506
64 Crowe, D.A. *et al.* (2014) Dynamic representation of the temporal and sequential structure of rhythmic movements in the primate medial premotor cortex. *J. Neurosci.* 34, 11972–11983
65 Merchant, H. *et al.* (2013) Interval tuning in the primate medial premotor cortex as a general timing mechanism. *J. Neurosci.* 33, 9082–9096
66 Middleton, F.A. and Strick, P.L. (2000) Basal ganglia and cerebellar loops: motor and cognitive circuits. *Brain Res. Brain Res. Rev.* 31, 236–250
67 Hikosaka, O. (1994) Role of basal ganglia in control of innate movements, learned behavior and cognition – a hypothesis. In *The Basal Ganglia IV: New Ideas and Data on Structure and Function* (Percheron, G. *et al.*, eds), pp. 589–596, Springer
68 Diedrichsen, J. *et al.* (2010) The coordination of movement: optimal feedback control and beyond. *Trends Cogn. Sci.* 14, 31–39
69 Tanji, J. and Shima, K. (1994) Role for supplementary motor area cells in planning several movements ahead. *Nature* 371, 413–416
70 Wiestler, T. *et al.* (2014) Effector-independent motor sequence representations exist in extrinsic and intrinsic reference frames. *J. Neurosci.* 34, 5054–5064
71 Ben-Shaul, Y. *et al.* (2004) Neuronal activity in motor cortical areas reflects the sequential context of movement. *J. Neurophysiol.* 91, 1748–1762
72 Dayan, E. and Cohen, L.G. (2011) Neuroplasticity subserving motor skill learning. *Neuron* 72, 443–454
73 Karni, A. *et al.* (1998) The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. *Proc. Natl. Acad. Sci. U.S.A.* 95, 861–868
74 Smith, M.A. *et al.* (2006) Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biol.* 4, e179
75 Sakai, K. *et al.* (2004) Emergence of rhythm during motor learning. *Trends Cogn. Sci.* 8, 547–553