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Stages of Motor Skill Learning

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Abstract

Successful learning of a motor skill requires repetitive training. Once the skill is mastered, it can be remembered for a long period of time. The durable memory makes motor skill learning an interesting paradigm for the study of learning and memory mechanisms. To gain better understanding, one scientific approach is to dissect the process into stages and to study these as well as their interactions. This article covers the growing evidence that motor skill learning advances through stages, in which different storage mechanisms predominate. The acquisition phase is characterized by fast (within session) and slow learning (between sessions). For a short period following the initial training sessions, the skill is labile to interference by other skills and by protein synthesis inhibition, indicating that consolidation processes occur during rest periods between training sessions. During training as well as rest periods, activation in different brain regions changes dynamically. Evidence for stages in motor skill learning is provided by experiments using behavioral, electrophysiological, functional imaging, and cellular/molecular methods.

Index Entries: Motor learning; plasticity; memory; electrophysiology; gene; functional imaging; protein synthesis.

Introduction

Motor learning is a model for procedural learning. It is often studied to elucidate mechanisms of cortical plasticity in general. In the literature, the term *motor learning* is used for a variety of learning paradigms involving movement (e.g., conditioning that requires the association of a stimulus with a motor reflex response *[1]*), learning the control of reflex gains *(2)*, learning to improve a reaction time *(3)*, learning a finger tapping sequence (serial reaction time task *[4]*), or adjusting movements to external perturbations *(5)*. Specifically, motor *skill* learning describes the acquisition of a complex movement sequence such as learning to weave or to ride a bicycle *(6)*. Learning these complex movements was also termed *segmental motor learning*, because the movements are often decomposed into segments or chunks *(7)*.

Motor skills are learned slowly over several training sessions. Once a skill is mastered, it is retained for long periods of time, with minimal

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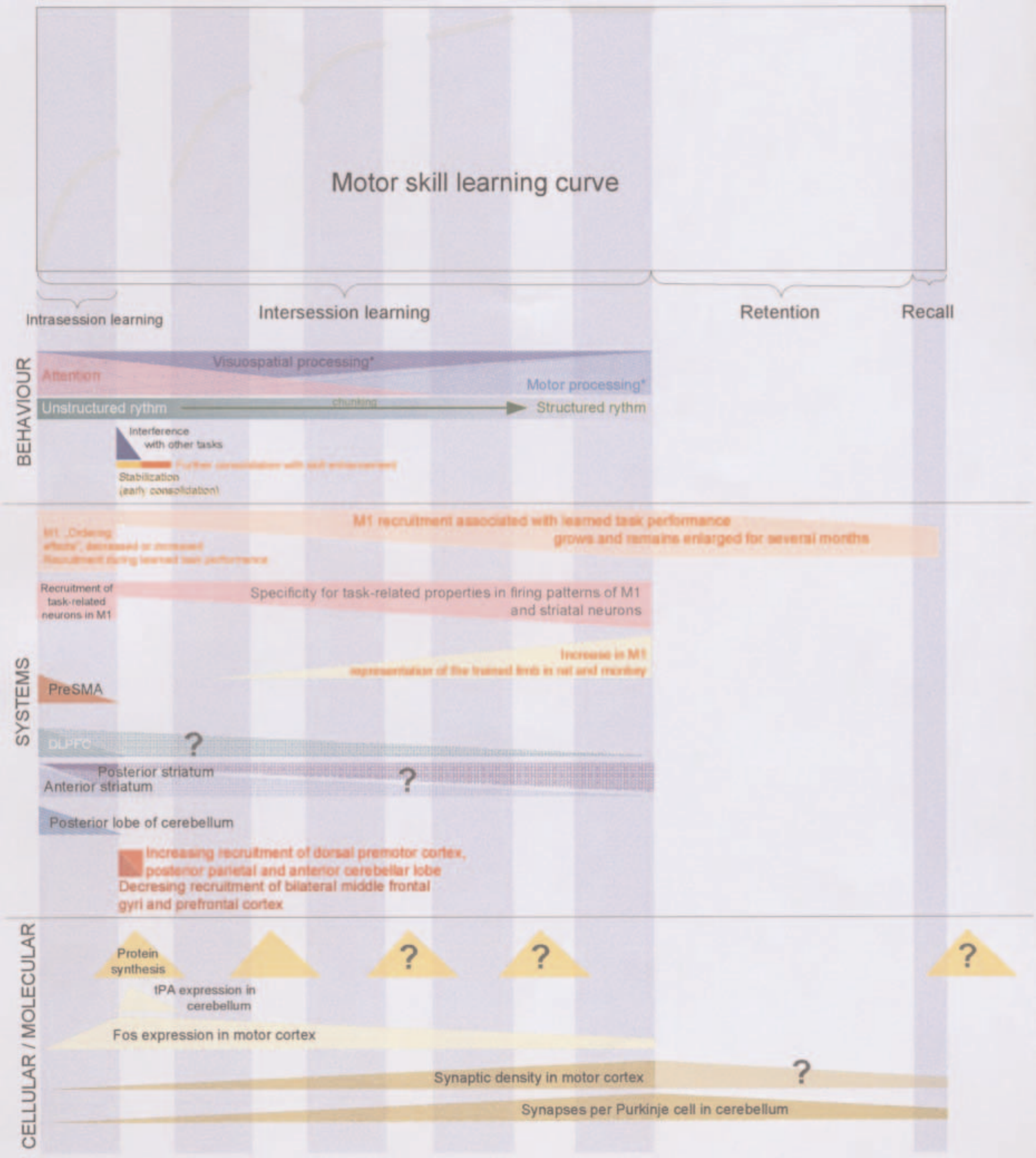

Fig. 1. Schematic summary of evidence suggesting that motor skill learning progresses through separate stages in which different mechanisms of acquisition and storage predominate (*see* text). A sample motor learning curve is presented at the top.

decay. Conversely, declarative knowledge that enables the recognition or identification of a thing can be acquired in one exposure but is only retained for a brief period. The long memorization of motor skills is intriguing and suggests a very efficient storage mechanism.

Growing evidence suggests that motor skill learning progresses through stages. Identification of separable stages may be conceptually useful, allowing experimental designs with higher specificity for certain aspects of the process. The evidence for stages in motor skill learning across different experimental domains—behavior, electrophysiology/brain activation, cellular and molecular—is schematized in Fig. 1 and reviewed here.

Behavior

Time-Course of Motor Learning

Anyone who has studied a musical instrument knows that simple pieces can be learned quickly, often in one training session. However, more complex pieces require repeated training over several days. Which elements are simple and which elements are complex depend on the level of experience. Trying to force a complex piece by practicing all day ("massed training") is usually unsuccessful. Many behavioral studies have confirmed that training with breaks ("spaced training") is more efficient *(8,9)*.

A common feature of spaced training paradigms is that improvements in performance are already observed within single training sessions (Figs. 1 and 2). End-session performance often is not retained over the break and subjects begin the next session at a lower performance. For example, a player improves in playing a piano piece during 1 h of practice. The next day, the player will begin at a lower level of performance and will require some initial training to regain previous levels. If training then continues, the player will improve further. Based on these observations, within-session improvement was regarded as a "warm-up" phenomenon *(10)*. Many studies do not measure within-session improvement; rather, they use mean session performance when plotting learning curves over several training days (referred to as "intersession learning"). Naturally, mean session performance improves much slower compared with within-session performance. With gradual improvement of mean session performance, "warm-up" becomes less likely, reflecting a ceiling effect of performance. If within-session improvements are not accounted for, learning curves may be misinterpreted. For example, consider a case in which performance drops back to baseline in response to an intervention; mean session performance following the intervention may then be lower than mean performance in the first session but may be identical to performance at the very beginning of session one *(11)*.

Walker and co-workers *(12)* found that when subjects learned a finger-tapping sequence and slept between training sessions, additional performance gains occurred during the rest phase. This suggests that the motor system is capable of some form of "self-rehearsal" during sleep. Functional improvements without practice were also reported for mental rehearsal of the movement *(13,14)*.

Recent evidence suggests that within- and intersession improvements have discernable neural mechanisms (*see* Functional Brain Systems). Within-session and intersession learning has been documented in many different human and animal motor skill learning paradigms *(15–17)*. Figure 2 presents two examples.

Another feature of the motor learning time-course is that different elements of a movement are learned at different rates. Flanagan and colleagues *(18)* asked subjects to move a handle on a straight line between two points. The movement was externally perturbed by a motor that pulled the handle off the movement trajectory. Deviations from the straight line and changes in grip force were measured. As subjects learned to compensate for the external perturbations, grip force was adjusted five to seven times faster than the movement trajectory. Grip force adjustments may be accomplished by an "internal model" of motor control (the encoding of the forces required by the task) that accounts for the object (handle to be moved) as well as the desired trajectory. The actual trajectory is irrelevant for grip force. The desired trajectory is communicated to the neural grip force

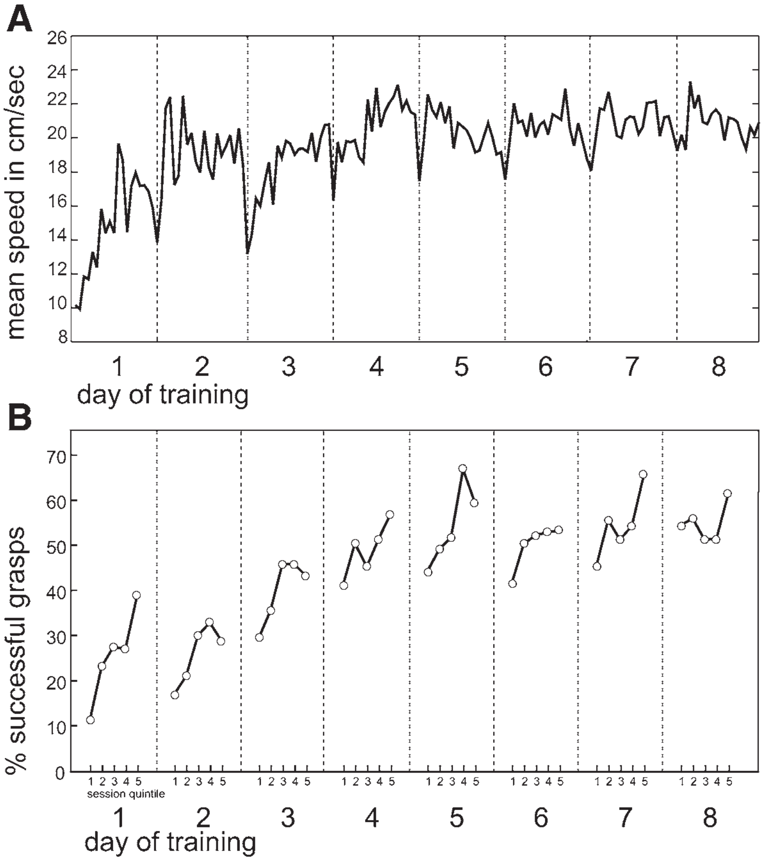

Fig. 2. Two exemplary learning curves for two motor skill learning paradigms in rat. Both learning curves demonstrate within-session learning as well as a gradual improvement of mean sessions performance (intersession learning). **(A)** Maximum running speed mastered on an accelerating rotarod (cylindrical rod with a 7-cm diameter accelerating at 1 cm/s^2) is plotted over time. Twenty running trials are performed per session. Sessions are separated by vertical dashed lines. **(B)** Success in reaching for a food pellet located outside of the cage (in percent of total number of reaching trials) is plotted over time. Each session consists of 100 reaching trials. Sessions are separated into quintiles of 20 trials to capture within-session performance gains.

controller by sending a copy of motor commands, which are intended for the arm to accomplish the desired trajectory. In the study by Flanagan and colleagues, improvement of the trajectory was observed only after several trials, which allowed for gathering of sufficient sensory (somatosensory and visual) feedback information to improve the motor commands determining the trajectory. This observation has led to the hypothesis that subjects can learn to predict the behavior before they master its motor control.

Hikosaka *(19)* suggested a model of staged motor learning, in which two types of information are being processed: a “spatial processing stream” that encodes the visuospatial coordinates of the novel movement and a “motor processing stream” that encodes the motor program that enacts the muscles. Experimental evidence stems from the observation that lead to this hypothesis were that early in training, when information about the movement was still spatially encoded and motor programs had not yet been formed, monkeys were able to transfer motor tasks learned with one limb to the opposite limb. Once the movement has been trained for longer periods, transfer between limbs is no longer possible. The processing streams are likely implemented by different functional brain systems (*see* Functional Brain Systems). Typically spatial encoding precedes motor encoding, but the opposite may also be true, as in the "serial reaction time paradigm". In this paradigm, subjects press one of four buttons with fingers two through five. Pressing the correct button leads to a reward signal on the computer screen. The computer knows the sequence of correct buttons (which is typically 10–12 items long and then repeats itself). Initially, the subject is not aware that a repeated sequence is presented. Eventually, the subject realizes this, but movement latencies decrease long before. Because latencies are a measure of motor performance, this observation indicates that motor (implicit) knowledge develops before explicit knowledge of the sequence *(20)*.

For complex movements, it may be essential that both motor and spatial encoding streams operate in parallel. Because spatial encoding depends on visual input, one part of the neural circuitry for spatial encoding may be the "mirror neuron system." These are neurons that fire in response to visual presentation of a movement; they have been identified in primates *(21)*. It is unclear whether this concept is applicable to rats or mice, in which mirror neurons have not yet been identified. Also, it is unknown whether lower species spend time watching each other, with the exception of when they are being threatened or sexually attracted.

Besides visuospatial and motor encoding, Sakai *(22)* emphasized the central role of temporal rhythms (timing patterns) for motor skill learning. Novel movements may be learned by splitting them into chunks (segments *[7]*) that are performed with certain rhythms. Gradually, chunks are combined to form the entire movement sequence. Chunking is a common training technique employed by piano players.

Interference

Interference denotes the observation that training of a new task leads to forgetting of a previously learned task. It is assumed that interfering tasks compete for the same information-processing resources in the brain. Interference phenomena provide insight into the time-course of motor learning.

Learning to track a moving object with the finger while vision is inverted by prism glasses is affected differently by preceding tasks that require different processing resources *(23)*. Attention-dependent tasks interfere with the early phase of learning, whereas visuospatial-transformation-dependent tasks interfere with a later phase. These findings indicate that learning the finger-tracking task initially depends on attention. Only later does the ability to perform visuospatial transformations become important.

Interference experiments have also been used to explore the time-course of consolidation of a motor memory. Consolidation of a task can be disrupted if a secondary task is learned immediately after the first task *(5)*. If training of the secondary task begins 4 to 5 h later, there is no interference; during these 4 to 5 h, interference is gradually reduced *(24)*. Walker and co-workers *(14)* provided evidence for further dissection of the consolidation process. A first phase of consolidation (between 10 min and 6 h following the end of training) renders the memory resistant to interference. Further consolidation occurs during subsequent sleep and leads to performance gains.

Functional Brain Systems

Motor skill learning accesses brain circuits that are different from those that control already acquired movements. Activation of these circuits changes during the course of motor skill learning. From the behavioral evidence presented earlier, one may hypothesize that association areas are preferentially activated in the early stages, when visuospatial to motor associations need to be formed. Later, cerebello- and striato-motor-cortex loops may improve movement efficiency *(25)*.

Using functional imaging techniques, several studies have characterized brain activation patterns during motor skill learning. Most of these studies have employed tasks that were learned over one session (1 d). Few studies have compared within-session and intersession activation changes using the same task *(26,27)*.

Dynamic recruitment of primary motor cortex (M1) has been identified during within-session and intersession learning. Within one training session, habituation effects (i.e., the reduction of M1 recruitment typically observed when movements are repeated) diminish. Hence, the area of cortex that is recruited for trained finger-tapping sequences maintains its size, as opposed to a random sequence for which habituation occurs. Over the course of several training sessions, the area of motor cortex recruited during execution of the sequence grows and remains enlarged for several months *(11,27)*. Intersession effects are not merely related to greater performance (e.g., faster movement) but seem to reflect the encoding of the motor program *(26)*. In another study, M1 activation was reported to increase during single-session learning of a serial reaction time task *(28)*. The opposite was reported for visuomotor learning *(26)*. The mechanism by which M1 is recruited during motor learning may also depend on prior experience: training of a finger-tapping task leads to greater M1 recruitment in piano players than in inexperienced controls *(29)*.

Costa and co-workers *(30)* investigated within-session and intersession learning using an acrobatic locomotor task in mice. The authors simultaneously recorded from M1 and the dorsal striatum. During the first training session, they observed fast recruitment of task-related neurons. Over subsequent sessions, refinement in these neurons occured such that striatal neurons became more velocity-specific and M1 neurons gained task specificity.

Re-organization of the somatotopical map in M1 during several days of motor training has been reported for monkeys *(31)* and rats *(32)*. The representations of body parts involved in the trained movement enlarge. In activity-control animals using the same body part with comparable intensity, the representations become slightly smaller *(31,33)*, contributing to significant between-group effects. In rats, these between-group effects are significant only after 10 training sessions but not after 3 or 7 *(34)*, indicating that modifications to somatotopy evolve slowly.

Various other brain regions are differentially activated during motor learning and are summarized in Table 1. Most studies—with the exception of two *(26,27)*—employ single-day learning paradigms. Activation in the rostral portion of the supplementary motor area (preSMA) was reported to decrease during learning of a visuomotor sequence task *(35)*. Monkeys showed less activity in preSMA neurons when performing overlearned sequence movements compared to novel sequence movements *(36)*. Neurons with these characteristics were rarely found in the caudal portion of SMA (SMA proper). The preSMA may be involved in the separation of a sequence into chunks (*see* Time-Course of Motor Learning): preSMA neurons fire at the beginning of a chunk *(36,37)*. Inactivation of preSMA by repetitive transcranial magnetic stimulation impairs chunking *(38)*.

Several studies have demonstrated a decrease in the activation of the dorsolateral prefrontal cortex (Brodmann area [BA] 44–46; refs. *26,28,37,39–42)*. This area (especially BA 44) is also active during observation of movements *(43)*. BA 44 is a possible homolog of the monkey area F5, where mirror neurons (*see* Time-Course of Motor Learning) can be found *(21)*. This area may be important for the observation of movements, a function likely to be relevant for early stages of motor skill learning.

The anterior striatum, which may contribute by attaching a motivational value to a skill *(44)*, is preferentially activated early in finger sequence learning *(40,42,45)*. Direct recording in monkeys supports this finding and also suggests that the posterior striatum is more strongly involved in later stages *(46)*.

Several studies have demonstrated higher involvement of the posterior lobe of the cerebellum during the early stages of motor skill learning *(26,39,41,47,48)*. According to Sakai *(22)*, these findings may reflect the evolution of a rhythm for the movement sequence (*see* Time-Course for Motor Learning). The posterior lobe of the cerebellum and prefrontal cortices are used for rhythm formation, a process requiring associative ("cognitive") circuits and attention. Later, when the rhythm has formed, motor circuits consisting of anterior cerebellum and premotor area become active.

Whereas the earlier cited studies focused on changes in activation during the training process, Shadmehr and Holcomb *(49)* studied the evolution of cortical activation during the posttraining consolidation phase. They showed that with passage of time after the end of training, the recall of learned movements is associated with greater activation of contralateral dorsal premotor, posterior parietal cortex, and the anterior cerebellar lobe. At the same time activation of bilateral middle frontal gyri and prefrontal cortex diminishes. The authors hypothesize that these changes in task-related activation patterns reflect the ongoing re-organization that leads to a stabilization of the motor memory.

Conflicting results from imaging studies (Table 1) may be explained by differences in subject samples (e.g., in degree of motor experience) and motor learning paradigms. A general problem is that changes in brain activation related to higher performance (e.g., faster movement; it is known that movement rate influences the activation pattern; ref. *50*) are difficult to separate from learning-related changes. Few studies have attempted to improve this separation by inclusion of conditions controlling for performance *(26,51)*. Further studies with larger samples sizes and different methodological approaches (e.g., functional imaging plus repetitive TMS to interfere with cortical function) are required to elucidate the dynamic involvement of brain regions in the learning process.

In conclusion, there is sufficient evidence that, depending on the stage of learning, motor control is handled by different brain regions and/or by certain brain regions differently. Some of these changes may be related to improvement in performance and not to learning *per se*, whereas others may reflect encoding or consolidation. Activation patterns, their function, and their time-courses need to be further characterized.

Cellular and Molecular Evidence

Changes in neuronal structure and function have been reported during motor skill learning and have provided evidence that learning advances through separate stages.

Protein Synthesis

Protein synthesis inhibition (PSI) interferes with learning and memory in various nonmotor paradigms, mainly by impairing the consolidation of acquired knowledge. This observation led to the hypothesis that consolidation requires modifications in neuronal circuitry—that is, plastic change in neuronal structure. *De novo* expressed proteins may be used to build novel structure.

Protein synthesis is also necessary for successful motor learning. When given systemically, the protein synthesis inhibitor cycloheximide impairs learning of an acrobatic locomotor skill in rat *(17)*. Learning between, but not within, sessions is disturbed. This suggests that protein synthesis is necessary for slow learning processes that require consolidation to maintain the skill over intersession periods of rest. To further characterize protein synthesis during motor learning, a protein synthesis inhibitor (anisomycin) was injected into motor cortex, parietal cortex, and cerebellum immediately following the end of the training session. Only injections into motor cortex impaired intersession learning *(52)*, suggesting that protein synthesis in motor cortex after training is required for successful motor learning. The effect of PSI was specific for the learning process—that is, overtrained animals did not show a decline in performance after systemic or intracortical injections.

Table 1
Overview of Function Imaging Studies of Motor Learning

Reference	Task	Imaging	Design		Frontal
39	Finger-tapping sequence	PET	New vs overlearned	Higher in new	9, 10, 32, 46, 47, 6 (premotor)
				Higher in overlearned	SMA proper
58	Writing task	PET	New vs overlearned	Higher in new	
				Higher in overlearned	4, 6, SMA
27	Finger-tapping sequence	fMRI	Intrasession		"Ordering effects" in 4 (M1), *see* text
			Intersession (d)		increase in 4 (M1)
48	Visuomotor task (over 4 blocks)	PET	Nonlinear	Decrease	6, 8, 9, 47
				Increase	4, 6, 24 (anterior cingulate)
51	Tracing task	PET	New vs overlearned	Higher in new	6 (premotor)
				Higher in overlearned	6 (SMA)
28	SRTT	PET	Correlation with reaction time	Positive	6, 46
				Negative	9
42	Finger-tapping sequence	fMRI	Nonlinear (over 45 blocks)	Decrease	4, 6 (lateral), 6 (medial), 46
				Increase	
				Increase–decrease	6 (SMA)
37	Visuomotor sequence task	fMRI	Three stages based on performance criteria	Decrease	DLPFC (8, 9, 46), pre-SMA, 24 (anterior cingulate)
				Increase	
				Increase–decrease	
45	Simple finger-thumb opposition	fMRI	Early vs late	Higher in early	8
				Higher in late	9
41	SRTT	PET	Linear (over 14 blocks)	Decrease	44
				Increase	SMA proper, 4, 6, 8, 10, 11, 44, 46
47	SRTT	fMRI	Three stages based on timing	Decrease	
				Increase	6 (SMA), 45
				Decrease–increase	24 (anterior cingulate), 6 (premotor)
40	Finger-tapping sequence	fMRI	Early vs late	Higher in early	4, 6, 10, 46
				Higher in late	4, 9, 43
26	Visuomotor adaptation	fMRI	Intrasession	Decreasing	4, 24 (anterior cingulate), 46
				Increasing	
			Intersession (d)	Decreasing	
				Increasing	4 (contra-anterior)

SMA, supplementary motor area; IPS, intraparietal sulcus; HC, hippocampus; PET, positron emission tomography; FRMI, functional magnetic resonance imaging; SRIT, serial reaction time task.

Brain region numbers represent Brodmann areas.

[a] Initial decrease followed by plateau.

Brain region						
Parietal	Temporal	Occipital	Basal ganglia	Thalamus	Cerebellum	Other
7 (precuneus) 40				Thalamus	Vermis, posterior lobe	
40	20, 21, 28, 38	17, 18				post. insula, HC
3		19			Anterior lobe, (vermis)	
39, 40					Posterior lobe	
				Putamen		insula
7 (precuneus), 40					tonsil	
7 (precuneus), 40				Thalamus		
39	22, 41, 42					
1, 7 (precuneus)			(Caudate, putamen)[a]		Vermis, contra-anterior Lobe	
40 (IPS)					Ipsi-anterior lobe	
40 (IPS)						
7 (precuneus)						
7 (precuneus, contra-anterior)	39		Putamen	Bilateral thalamus	Anterior lobe	
7 (ipsi-anterior), 31 (cingulate)	21	19		Contralateral thalamus	Posterior lobe dentate	
40	20, 21	18			Posterior lobe	HC
7, 31, 23 (postcingulate) 40	21, 27		Putamen	Thalamus		
					Posterior lobe	
7 (precuneus), 40			Putamen			
					Dentate nucleus	
7 (precuneus), 40			Caudate		Anterior lobe (bilateral)	
3	30, 36, 37	19				
5, 7, 23 (postcingulate)			Putamen		Thalamus (ipsi-anterior)	Posterior lobe Dentate
1, 2, 3 (contra-anterior)			Putamen (ipsi-anterior)			

Kleim and co-workers *(33)* suggested that protein synthesis is necessary for stabilizing M1 somatotopy. The forelimb representation in rat shrinks upon intracortical injection of a protein synthesis inhibitor. If administered to animals before training, learning is reduced. This finding is in agreement with our findings of learning impairment when PSI is induced during training *(52)*. Additionally, the former study showed that performance is lost in animals that receive anisomycin following a recall session of the trained movement. At first, this observation seems contradictory to our finding of stable performance in animals receiving PSI during the plateau phase of the learning curve *(52)*. Our animals were continuously trained, whereas the animals in the study of Kleim et al. rested for a week before they were retrained, then received anisomycin (same dose and injection technique as in our study), and were trained again. Assuming that a breakdown of M1 representations in response to PSI is responsible for the loss of skill in Kleim's experiment, either the breakdown or the loss of skill must have been prevented by training the animals continuously in our experiment. Alternatively, the memory in Kleim's experiment may have been turned labile by the recall (before PSI) and may then be rendered sensitive to PSI again, a phenomenon termed "reconsolidation" in other learning and memory paradigms *(53)*. Reconsolidation also occurs in human motor learning *(12)* and likely represents and intermediate stage of memory consolidation *(54)*. Reconsolidation may have been prevented by continuous training in our experiment.

Structure and Gene Expression

Limited data are available regarding gene and protein expression after motor learning. One gene coding for tissue plasminogen activator (a serine protease cleaving extracellular matrix proteins) is differentially expressed in cerebellum after a motor training session in rat *(55)*. It is increased 1 h after training ends, peaks at 4 h, and is still slightly elevated after 24 h. This protein may have a permissive role for tissue remodeling and structural plasticity.

Expression of the immediate early gene *c-fos* coding for the transcription factor Fos peaks early in learning and remains elevated in the plateau phase of the learning curve relative to control animals *(56)*.

An approximately linear increase in synaptic density was demonstrated in motor cortex during training of a skilled reaching task *(34)*. In an acrobatic locomotor task, an increase in synapses per Purkinje cell was observed in the cerebellum *(57)*.

Conclusion

Behavioral, functional imaging, electrophysiological, and cellular/molecular studies provide evidence that motor skill learning is a staged process. Different mechanisms appear to be active at different times. During training, there is sequential demand for different circuitry. Consolidation (i.e., stabilization of novel motor memory) occurs both during and after training. Task complexity may be an important determinant of how "staged" or segregated the process is. Complex motor tasks require several training sessions interspersed with periods of rest and sleep. For these tasks, acquisition and consolidation processes are interlocked, forming a complex sequence of events. To better understand this process, future studies need to detail the time-courses of brain re-organization during motor skill learning.

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