

Motor Sequences

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Introduction

Motor learning refers to two different processes: adaptation and skill acquisition. Adaptation relates to our ability to compensate for environmental changes, including visual, kinematic, or dynamic changes in the characteristics and attributes of external stimuli and/or objects. On the other hand, the ability to learn a movement sequence and the incremental improvement in its performance refer to the sequence learning aspects of skill acquisition which are the main focus of our present discussion. The generation of sequential actions is central to most of human intelligent behaviors ranging from everyday skills such as tying one's shoe laces to using a computer or playing the piano. The acquisition, representation, and retention of motor sequences are believed to build on and benefit from the availability of basic, simple motion elements ('primitives'), which are then ordered and concatenated into particular sequences, thus giving rise to the diverse, complex, goal-directed motor repertoire of humans and other animals. Long-lasting changes in motor performance related to sequence learning are known to evolve following several distinct phases and usually require many practice sessions. Subsequent sections discuss several topics related to sequence learning, starting with the presentation of two different mechanisms of sequence learning (i.e., explicit vs. implicit). The article then describes up-to-date theories concerning the specificity of these different learning mechanisms and their time course and discusses the neural substrates and brain areas subserving sequence learning. Finally, it reviews some of the current literature, pertinent to sequence learning, concerning shifts in representation, consolidation, and the effect of sleep on the retention and off-line improvement in the performance of learned sequences.

Implicit versus Explicit Sequence Learning

When considering the learning of sequential tasks, one needs to distinguish between explicit and implicit learning. Explicit learning is frequently assumed to be similar to the processes operating during conscious problem solving and includes conscious attempts to construct a representation of the task, a directed search of memory for similar or analogous task-relevant

information, and conscious attempts to derive and test hypotheses related to the structure of the task. This type of learning has been distinguished from alternative models of learning, termed 'implicit' learning. The term 'implicit' learning denotes learning phenomena in which more- or less-complex structures are reflected in the overt behavior although the learners are unable to verbally describe these structures. Numerous studies have examined implicit learning of serial-order information using the serial reaction time (SRT) task established by Nissen and Bullemer. In this task, participants see a target stimulus, typically an asterisk, appearing at one of four locations on a computer display and are required to indicate its location by making a key press. Participants are initially trained on repeating a given sequence. However, learning is assessed by presenting participants with a block of experimental trials (e.g., a block of random trials) and then examining differences in reaction time (RT) existing between sequence and random blocks of trials. It was shown that the RTs in trials in which an overpracticed sequence was presented were significantly shorter than for random sequences, suggesting that participants have unconsciously learned the sequence and anticipated the next element (Figure 1).

There is a vast literature debating what is really learned in the implicit sequence paradigm in general and in the SRT task in particular. From a theoretical point of view, the description of a given sequence structure is not trivial because a given structure typically has several different structural components, such as frequency-based statistical structure (i.e., the redundancy of a specific element appearance in the pattern), relational structures (the occurrence of a specific element after or before a different element), and spatial structure (the position of the different elements in space, as in the case of fluent finger spelling). A literature review shows that all these components have an influence on the rate in which a sequence is learned.

Stages in Motor Learning: Transferability and Effector Specificity

A study conducted in monkeys, in which a sequence of 10 button presses is learned by trial and error, has shown that the time course of improvement of two performance measures, key press errors and RT, was different (Figure 2). The key press errors reached an asymptote within a shorter period of training compared with the RTs, which continued to decrease throughout a longer time. This finding suggested that the acquisition of sequence knowledge (as measured

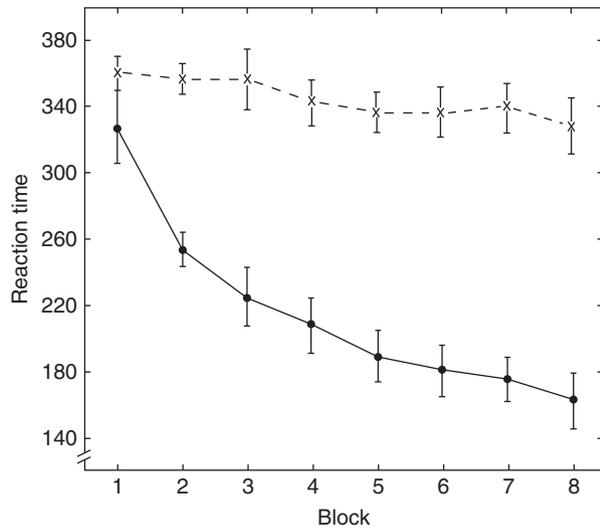


Figure 1 Implicit acquisition of a practiced sequence. Participants see an asterisk appearing at one of four locations on a computer display and are required to indicate its location by making a key press. After a training period on repeating a given sequence, the participants are presented with a block of random trials. The differences in reaction time (RT) existing between the trained sequences and the random blocks of trails are shown by depicting the mean of median reaction times in milliseconds in each block. Filled circles, repeating sequence; x's, random sequence. Bars represent standard errors. From Nissen MJ and Bullemer PT (1987) Attentional requirements for learning: Evidence from performance measures. *Cognitive Psychology* 19:1–32.

by key press errors) may take place quickly, but long-term motor sequence learning (as measured by RT) may take longer to become established. Thus, different aspects of the task are learned in different timescales. It was shown that the learned procedure is effector-dependent: when monkeys were asked to use the hand that has not been used for long-term practice of the given sequence, their performance became very poor. However, this was not true for a newly learned sequence. These results suggest that the memory for a visuomotor sequence, which is accessible for both the trained hand and the untrained hand in the early stage of learning, becomes largely inaccessible to the untrained hand in the late stage of training, that is, the performance gain is not transferred to the untrained hand. It was further demonstrated that the whole sequence, rather than the individual elements, is learned: When the order of the component elements of a well-learned sequence was reversed, the performance became very poor, as if the monkeys were performing completely new sequences. The results suggested that the monkeys acquired the memories for individual elements separately. This was not true in the early learning stages. Further studies in monkeys and in humans demonstrated that although effector-dependent and -independent learning occur simultaneously,

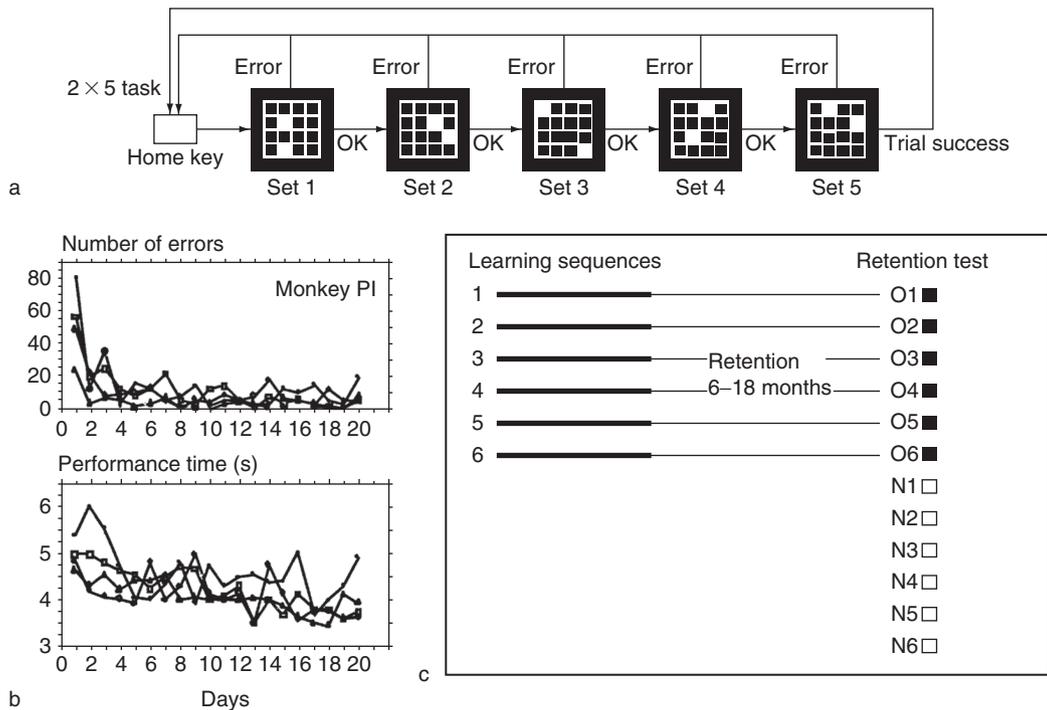


Figure 2 Long-term retention test of motor skill in monkeys. (a) A procedure of the 2×5 sequence task. A monkey has to press the two illuminated buttons in the correct order to proceed to the next set until completing five sets (called a 'hyperset'). Each hyperset is presented repeatedly in a block until the monkey performs the whole hyperset for a total of 20 trials. A different hyperset is then used for the next block. (b) The learning curves of monkey PI for four hypersets during the initial practice period of 20 days are shown as the number of errors before completing 20 trials successfully (top) and the mean performance time for the successful trials (bottom).

effector-dependent representation might take longer to establish than effector-independent representation does and that they are mediated by different neural substrates.

It is reasonable to assume that a gain in performance reflects a change in brain processing triggered by practice. Many skills, while acquired, are retained over long time intervals, suggesting that training can induce long-lasting neural changes. Previous results from neuroimaging studies in which performance is modified over time have shown that many different stages can occur. As an effect of repetition or practice, several studies report that activations in particular brain areas decreased. In other studies, specific brain areas showed increase in the magnitude or extent of activation. In some reports, a shift in activated areas was observed between unskilled and more skilled performance of a task. Thus, decreases, increases, and shifts in activations are reported as an effect of practice. The differences in activations might be related, in part, to the amount of practice or repetition a participant has had with a task. A study conducted by Karni et al. demonstrated that motor skill learning (sequential finger opposition task) requires time and has two distinct phases, analogous to those subserving perceptual skill learning. An initial, fast improvement phase ('fast learning'), when the extent of activation in primary motor cortex (M1) decreases (habituation-like response), is followed by slowly evolving, posttraining incremental performance gains ('slow learning'), when the activation in M1 increases compared with control conditions. **Figure 3** depicts the differential evoked responses in M1 in the trained versus the untrained (control) sequence. Overall, this study showed that limited training experience can be sufficient to trigger performance gains that require time to become evident. It was proposed that skilled motor performance is acquired in several stages: fast learning, an initial, within-session improvement phase, followed by a period of consolidation of several hours duration, and then slow learning, consisting of delayed, incremental gains in performance emerging after continued practice. This time course may reflect basic mechanisms of neuronal plasticity in the adult brain that subserve the acquisition and retention of many different skills. Later, using a simple single finger opposition task, Tracy et al. showed that even during a brief

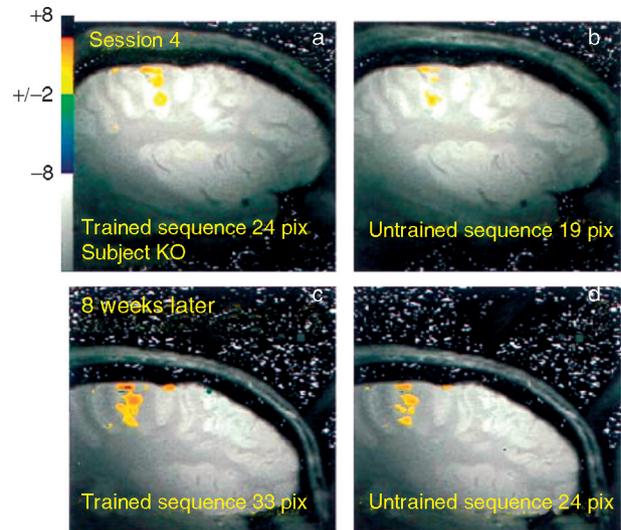


Figure 3 Differential evoked responses in human M1 to the trained vs. the untrained (control) sequence. (a, b) Training and performance during scanning done with the left (nondominant) hand. (c, d) Emergence of differential activation after 3 weeks of daily practice on the designated training sequence. Maintained differential activation 8 weeks later with no additional training in the interval. Z-score values are indicated by the pseudo-color scale. Reproduced from Karni A, Meyer G, Hipolito CR, et al. (1998) The acquisition of skilled motor performance: Fast and slow experience-driven changes in primary motor cortex. *Proceedings of the National Academy of Sciences of the United States of America* 95: 861–868. Copyright (1998) National Academy of Sciences, USA.

practice, there was a vast difference in activation in the corpus striatum, thalamus, and cingulate gyrus so that the neural circuit implementing this simple task varied over a brief window of practice.

A Schematic View of the Neural Representations of Motor Sequence Learning

Out of numerous views and results, sometimes controversial, that can be found in the literature on neural representation of learning motor sequences, this article discusses two major approaches, one claiming that there exist two parallel systems for neural coding of sequences and the other differentiating between the explicit and implicit learning processes. This approach bridges different observations and notions concerning sequence learning.

Two Parallel Systems of Coding

When people learn to perform a novel motor task, a corresponding memory trace is generated in the

(c) General schedule of the long-term retention test. After retention periods of 6–18 months, the monkey was instructed to perform the previously learned hypersets (O1–O6) and new hypersets (N1–N6) in a 1-day session. Reproduced from Hikosaka O, Rand MK, Nakamura K, et al. (2002) Long term retention of motor skill in macaque monkeys and humans. *Experimental Brain Research* 147: 494–504, with kind Permission of Springer Science and Business Media.

brain. This type of memory encodes procedural aspects of the task rather than facts and is termed 'procedural memory.' In the early stages of learning, a sequential motor procedure is composed of a series of sensorimotor processes, executed in a discrete manner (Figure 4(a)). However, the amount of computation needed to generate a novel sequential task is highly demanding. Such computations include the need to perform a series of coordinate transformations (e.g., from allocentric to egocentric or from eye-centered to hand-centered coordinate frames) and to deal with ordinal and temporal aspects of sequence generation, such as concatenating among sequential elements within the sequence. In order to address the question of how the system simplifies such complex computations and in order to relate to the finding that different learning stages are characterized by ability/inability to transfer the performance gain to the untrained hand, a hypothetical scheme for sequence learning has been suggested. This scheme, which attempted to suggest a plausible organization of motor sequence learning in the brain, proposed that a motor procedure is acquired and encoded independently by two cortical systems: one system encoding the sequence in spatial, extrinsic coordinates and the other one encoding the sequence in motor, intrinsic coordinates (Figures 4(b) and 4(c)). In the suggested scheme, each of these two parallel processes operates using a single type of coordinate system (either spatial or motor coordinates), hence providing a more parsimonious mode of representation. Based on a number of empirical studies conducted in monkeys and humans, the model proposes that (1) the procedural sequence is acquired in spatial, visual coordinates (green connections in Figure 4) before it is acquired in motor, intrinsic coordinates (blue connections in Figure 4); (2) the motor coordinate representation persists permanently, whereas the spatial representation is only temporary; and (3) the motor coordinate representation is effector specific and the spatial coordinate representation is not effector specific. The scheme may also be valid for the paradigms in which procedural memory is acquired implicitly, such as the SRT task.

As discussed earlier, the acquisition of a motor sequence in the brain is subserved by two distinct types of processes: implicit and explicit. An important question is whether the neural substrates of the two learning processes overlap and whether the acquisition of one learning type interacts or interferes with the other. Some studies reported that the neural substrates of implicit and explicit learning overlap at the levels of the prefrontal cortex and basal ganglia and that explicit learning of sequences, which exerts

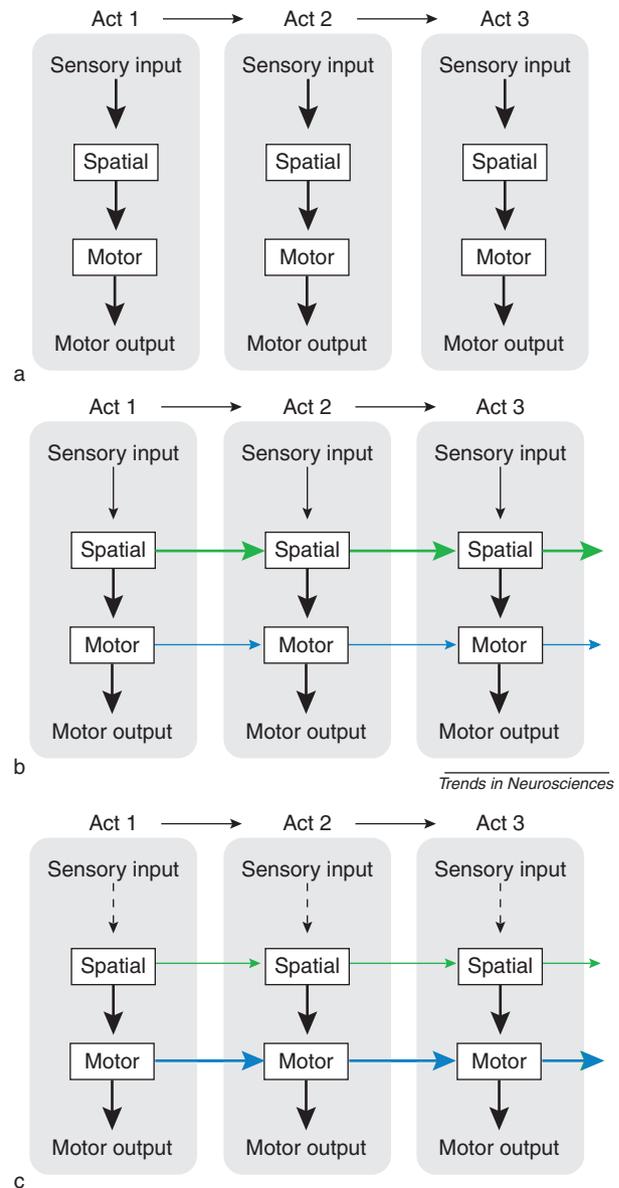


Figure 4 A hypothetical scheme for information processing during sequence learning. (a) The pre-learning stage, in which the participant performs three actions (Acts 1–3) step by step by relying on sensorimotor transformations for each action (vertical connection). (b), (c) By performing the actions in the same order, sequential processes are formed across the actions (horizontal connections). This occurs at each of the two stages of the sensorimotor transformation so that a given sequence is learned independently but from different perspectives: as a sequence in visual coordinates (spatial sequence, shown in green) and as a sequence in motor coordinates (motor sequence, shown in blue). The spatial sequence mechanism acquires the sequence quickly and flexibly by relying on attention and working memory (b), whereas the motor sequence mechanism acquires the sequence slowly and steadily through long-term practice (c). The thicker arrows indicate the dominant process occurring in the early (b) and late (c) stages and also the corresponding coordinates, that is, spatial in (b) and motor in (c). From Hikosaka O, Nakahara H, Rand M, et al. (1999) Parallel neural networks for learning sequential procedures. *Trends in Neurosciences* 22: 464–471.

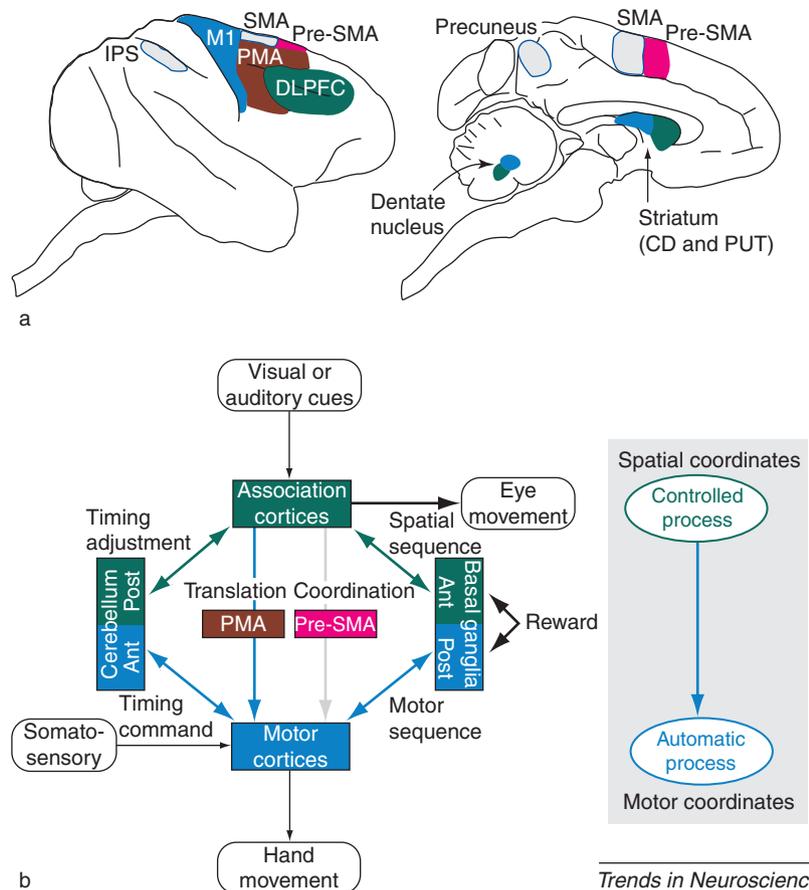


Figure 5 The association cortices (particularly prefrontal cortex) and the anterior part of the basal ganglia in monkeys constitute a loop circuit that operates as a spatial sequence mechanism (shown in green); the motor cortices (including primary motor cortex (M1) and supplementary motor area (SMA)) and the middle part of the basal ganglia constitute a loop circuit that operates in terms of motor coordinates (shown in blue). In addition, the anterior and posterior parts of the cerebellum contribute to the motor and spatial aspects of sequence generation by forming loop circuits with the motor and association cortices; their functions in the control of timing (indicated in the figure) are still speculative. The spatial and motor loops are capable of operating independently, acquiring and reproducing a given sequence in different coordinates. In addition, they have their own input and output: visual and auditory inputs and oculomotor outputs for the association cortices; somatosensory inputs and skeletomotor outputs for the motor cortices. The interaction between the two learning mechanisms is made possible in two ways: (1) by translation from spatial into motor coordinates by the premotor area and (2) by coordination or switching by the pre-SMA. From Hikosaka O, Nakahara H, Rand M, et al. (1999) Parallel neural networks for learning sequential procedures. *Trends in Neurosciences* 22: 464–471.

functional changes in the basal ganglia, directly inhibits implicit learning.

Figure 5 presents an anatomically supported model that describes the coordination between different brain areas mediating motor sequence learning, either in spatial or in motor coordinates, whereas Figure 6 depicts a scheme highlighting the hierarchy of the cortical structures based on their involvement in explicit/implicit representation. The organization of the cortical areas within the hierarchies depicted in both schemes is similar, and basically the two schemes supplement each other. Taken together, they suggest that the cortical structures that are strongly involved with explicit or implicit processes are mostly engaged with representing a new acquired sequence in spatial or motor coordinates, respectively. Hence, the

interference between implicit and explicit sequence learning may be related to the functional and anatomical overlap among the brain structures mediating the spatial and motor learning mechanisms.

The Role of Different Brain Areas in Sequence Acquisition, Representation, and Implementation

The prefrontal cortex is located at the top of both schemes describing learning of motor sequences (Figures 5 and 6). Compelling evidence exists in favor of the prefrontal cortex involvement in the process of explicit sequence learning and the acquisition and representation of the spatial aspects of a newly acquired sequence. Furthermore, it is considered to be related to several functions relevant to sequence learning, such as working memory, rehearsal,

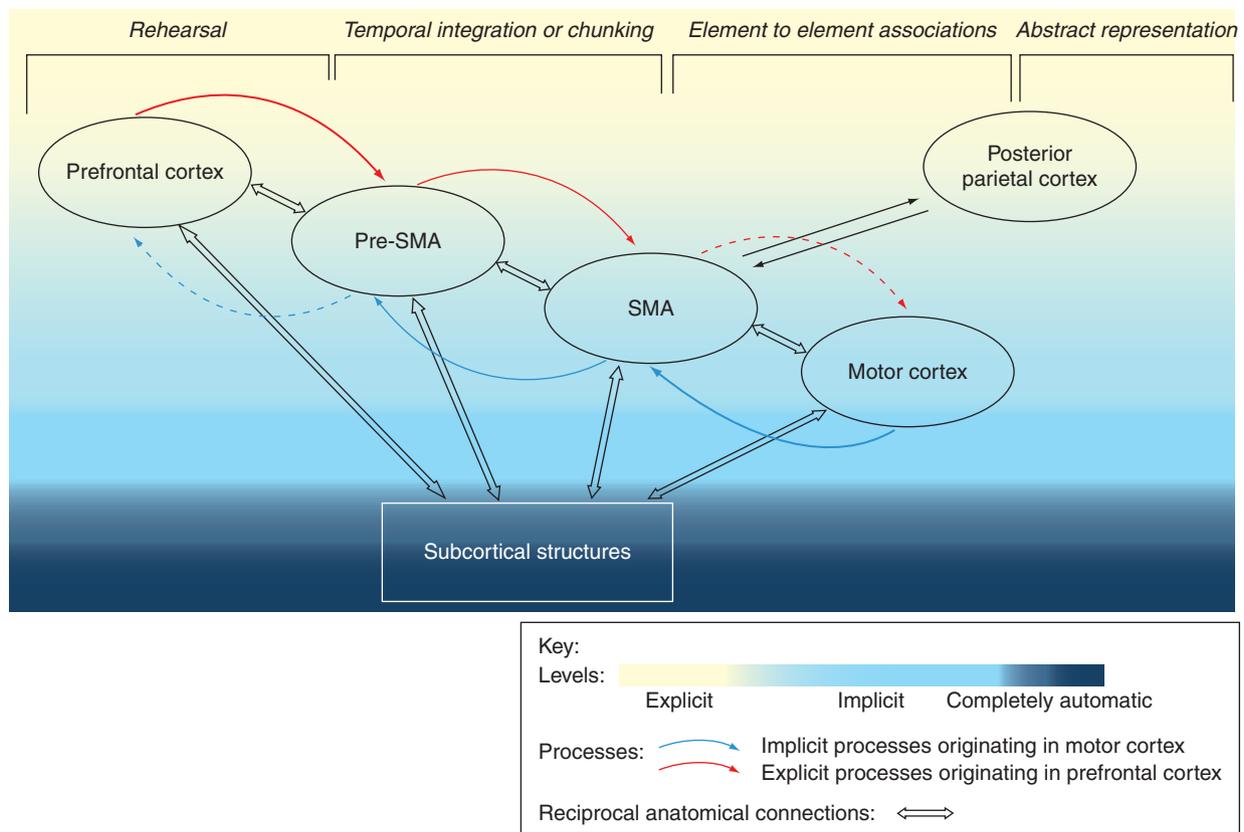


Figure 6 A set of cortical structures subserve the control of motor sequences. Depending on the instructional set, a participant's intentions, and the development of awareness, implicit or explicit processes predominate or interact during sequence learning, triggering specific mechanisms and leading to the formation of different types of representations of the learned sequence. For instance, when the intention to learn the sequence is explicit, either as a consequence of awareness or as an instructional set, explicit processes will originate in prefrontal cortex and will propagate to premotor areas. In this case learning will be based on mechanisms such as rehearsal and chunking. When learning is implicit, as a result of simply performing sequential movements without intention to learn or awareness of the sequence, implicit processes originate in motor cortex and propagate to the premotor areas. In such instances learning might be based on element-to-element associations or temporal coding. Of course, in most cases, these two types of processes will interact with each other and will change in importance depending on the stage of the learning process. From Ashe J, Lungu O, Basford A, and Lu X (2006) Cortical control of motor sequences. *Current Opinion in Neurobiology* 16: 213–221.

and executive control. Lately, it has been shown that the prefrontal cortex is strongly activated during explicit learning in the SRT task, a standard visuomotor RT paradigm, and that single dorsolateral prefrontal neurons encode the temporal order of a sequence of actions.

Based on the hierarchy depicted in **Figure 6**, the medial premotor cortex is situated a step below the prefrontal cortex. A large body of work, including lesion studies, suggests that the medial premotor cortex has an important role in the temporal organization of sequences, including the chunking together over time of multiple, separately performed movements.

While the functional properties of the supplementary motor area (SMA) and pre-SMA overlap, it is still generally accepted that the repetition of earlier acquired sequences is more strongly manifested in the activity of SMA neurons and that there is a greater tendency of the activity of pre-SMA neurons to reflect

representation of new sequences. Pre-SMA and premotor areas (including SMA) may be involved in coordinating between the spatial and motor sequence mechanisms (**Figure 5**). A specific feature of the pre-SMA with respect to learning is that its neurons tend to become active during acquisition of novel explicit sequences, and their inactivation causes deficits in learning of novel sequences.

M1 is strongly related to the execution of movements, so establishing its role in the acquisition of a novel movement sequence is difficult. However, experiments designed to differentiate between the two contexts (instantaneous encoding of movements and encoding of motor sequences), such as generating different sequences composed of the same elements but in different temporal order, implied that the neural activity in M1 and dorsal premotor cortex also encodes sequential attributes of motor tasks and that its role in sequence production is independent of its

role in basic control of movements. Moreover, M1 is engaged at the early stage of motor consolidation. Thus, in contrast to the commonly held view of the motor cortex solely as being important for motor execution, it may also be fully equipped for the planning and production of sequential behavior.

The function of the cerebellum in sequence learning is controversial. The cerebellum is suggested to be involved in the coordination of the movements of different body parts and in the acquisition of timing or rhythm. Coherent changes of activity in the cerebellum and M1 were found during learning of timed motor sequences. In particular, during the initial stages of learning (when performance is poor), the activity in the cerebellum was greater than the cerebellar activity at the advanced learning stage. In M1, conversely, greater activity corresponded to better performance at the advanced learning stage.

Neuropsychological research suggests that implicit sequence learning in the SRT task is spared in patients with organic amnesia, so implicit SRT learning does not appear to depend on the medial temporal and diencephalic brain regions that are critical for explicit memory. Conversely, patients with Huntington's or Parkinson's disease have consistently shown SRT impairments, so the basal ganglia seem to be critically involved in SRT learning. Recent studies indicate that the anterior striatum affects learning of new sequences whereas the posterior striatum is engaged in recalling a well-learned sequence. It is important to note that the hypothetical parallel learning mechanisms (motor vs. spatial) provide advantages in parsimony, robustness, and adaptability of the system. The basal ganglia may have a key role in motivating procedural learning. Reinforcement (via dopaminergic neurons) might take place separately for the spatial (via the anterior striatum) and motor (via the middle striatum) sequence mechanism (Figure 5).

Movement Planning and Anticipation: Submovements and Coarticulation

The stereotyped kinematic patterns of planar reaching movements are not the expression of a prewired or an inborn motor pattern but the result of learning during ontogenesis. When infants start to reach, their reaching is characterized by multiple accelerations and decelerations of the hand, whereas experienced infants reach with much straighter hand paths and with a single bell-shaped hand velocity profile. It has been shown that it is possible to decompose a large proportion of infant reaches into an underlying

sequence of submovements that resemble simple adult reaching movements. Based on several studies with adult participants, it has been suggested that the CNS uses elementary simple movements, primitives, which are smoothly combined in order to compose more complicated trajectories.

Other evidence for the existence of primitive submovements has come from work on hemiplegic stroke patients, which shows that their first movements are clearly segmented and exhibit a remarkably invariant speed profile. The idea that curved and obstacle avoidance movements result from the superposition of more elementary movements was modeled by Burdet, who suggested a mathematical model for the learning of accurate human arm movements. Its main features are that the overall movement results from the superposition of smooth smaller submovements (primitives). A similar notion was also elaborated by Henis and Flash, who formulated the 'superposition' model for target switching experiments. It was found that arm trajectory modification in a double target displacement paradigm might involve the vectorial summation of two independent plans, each coding for a smooth point-to-point trajectory. The first plan is the initial unmodified plan for moving between the initial hand position and the first target location. The second plan is a time-shifted trajectory plan that starts and ends at rest and has the same amplitude and kinematic form as a simple point-to-point movement between the first and second target locations.

After extensively practicing a particular sequence, most of the participants undergo implicit or explicit anticipation, which results in a coarticulation – the emergence of both spatial and temporal overlap among adjacent articulatory units. It is well known that as humans learn to speak, the speech becomes smoother and more fluent. Coarticulation in speech production is a phenomenon in which the articulatory movements for a given speech sound vary systematically with the surrounding sounds and their associated movements. Coarticulation was also studied in hand motor sequence generation. It was shown that pianists could anticipate a couple of notes before they are being played, which resulted in hand and finger kinematic divergence; that is, the spatial configuration of the fingers was different according to the context in which a specific note was played. Such a divergence implies an anticipatory modification of sequential movements of the hand, akin to the phenomenon of coarticulation in speech. Moreover, a study of fluent finger spelling has shown that rather than simply an interaction whereby a preceding movement affects the consecutive one; the anticipated movement in a sequence can systematically affect the one preceding it (Figure 7).

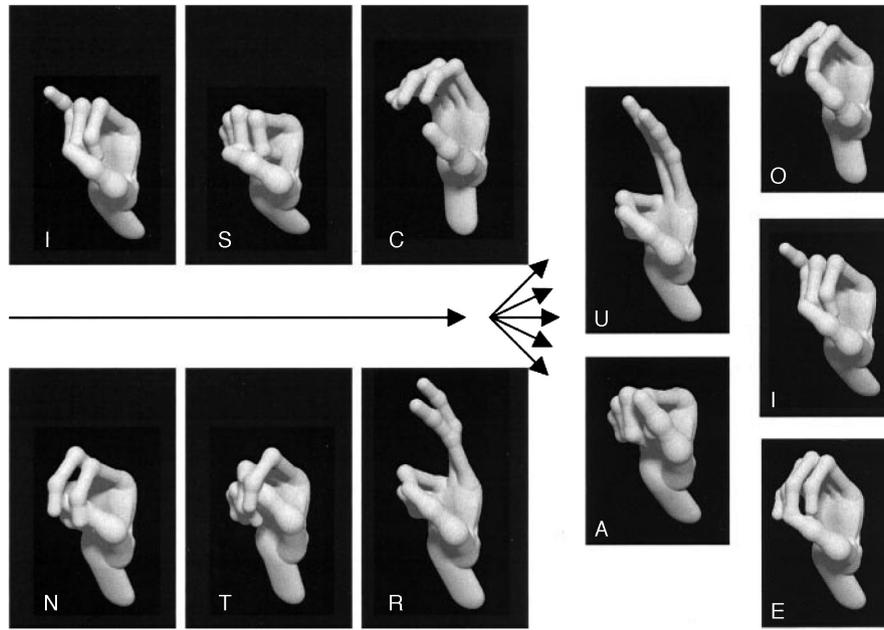


Figure 7 Cartoon images of hand shapes representing letters of interest in the American Sign Language manuscript alphabet, rendered with POV-Ray software. The layout illustrates the experimental design for a study of coarticulation: two fixed-letter strings (I-S-C and N-T-R) were followed by one of the five vowels (A, E, I, O, or U). Reproduced from Jerde TE, Soechting JF, and Flanders M (2003) Coarticulation in fluent finger spelling. *Journal of Neuroscience* 23(6): 2383–2393, with permission from Society for Neuroscience.

A recent study conducted by Sosnik et al. has shown that extensive training on writing like sequence movements, whereby participants have to connect four target points “as rapidly and as accurately as possible,” results in the coarticulation of consecutive segments of a given sequence of planar movements generated between a series of target points and that the outcome of prolonged training can be a novel, curved trajectory, which although corresponding to a longer path, affords smooth and rapid performance with no loss in accuracy (Figure 8). With accumulated experience, a qualitative change occurs in motor planning: from the generation of a sequence of individually planned component movements to the generation of globally planned, maximally smooth movement units, providing a highly effective solution to the challenge imposed by the double requirement to move “as rapidly and as accurately as possible.” These findings suggested that a profound hierarchical change can occur in motor planning: from syntax-dependent performance to unitary (modular), globally planned movement (coarticulation).

Consolidation and Sleep in Sequence Learning

So far in this discussion, only a distinction between an early versus a late stage of sequence learning has been made. However, as was recently summarized in

a review by Doyon et al., sequence learning actually occurs over several stages. The first stage is an early and fast one in which considerable improvements in performance occur very rapidly within a single training session. This stage is followed by a slow stage, during which further gains in performance are achieved over several practice sessions. Third, there is a consolidation stage, in which off-line, spontaneous increases in performance are achieved provided that another task is administered only beyond a critical period of 4–6 h; otherwise interference caused by the administration of the new sequence learning task can occur. The fourth automatic stage is one during which the skilled behavior requires minimal cognitive resources and is resistant to interference and to the effects of the passage of time. Finally, there is a fifth retention period in which the motor skill can be performed after long delays without further practice of the learned task.

An important mechanism for the retention of learned sequences in memory is consolidation. The term consolidation, which was coined more than a century ago, describes the reduction of the fragility of declarative memory – memory for facts and events after it has been acquired and encoded. Through consolidation, an initially fragile memory is transformed into a more robust and stable one. Consolidation has been exhaustively investigated with respect to declarative memory, but more recently it has been

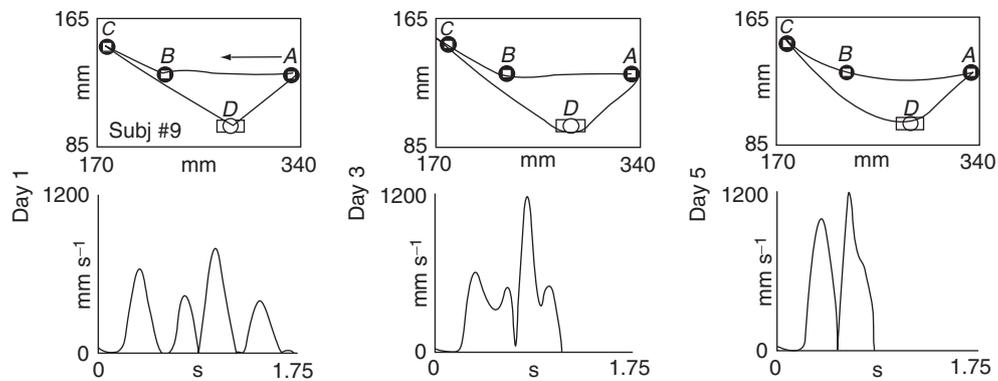


Figure 8 The evolution of coarticulated trajectories throughout training. Participants have to connect four target points “as rapidly and as accurately as possible,” resulting in the coarticulation of consecutive segments of a given sequence of planar movements generated between the series of points. There was a relatively high spatial alignment (obtuse angle) between the lines connecting target pairs *AB* and *BC* or *CD* and *DA*. For each training day, upper and lower plots denote trajectories and velocity profiles, respectively. Note the novel, curved trajectory that results. Reproduced from Sosnik R, Hanptmann B, Karni A, and Flash T (2004) When practice leads to co-articulation: The evolution of geometrically defined movement primitives. *Experimental Brain Research* 156(4): 422–438, with kind permission of Springer Science and Business Media.

extended to other memory systems, including procedural memory. Beyond the reduction in the fragility of the memory trace that occurs following the acquisition of a new skill, consolidation refers also to another phenomenon, namely, the off-line improvement in performance that can occur either between practice sessions or after the practice period has ended. There is evidence for both types of consolidation processes. This evidence will be discussed especially in the context of sequence learning.

Off-line improvements in the performance of a skill occur over time without practice and often depend on sleep. Overnight improvements are seen in the performance of short finger sequences. Only a negligible amount of improvement in performance is seen when the interval between sessions is spent awake. Learning another sequence before sleep can block this overnight improvement, showing that this learning requires an active and sequence-dependent mechanism. Moreover, the improvement depends on the time spent in a particular component of sleep or in the combination of several sleep components. Depriving the participant of the critical sleep component or of any sleep at all greatly reduces off-line improvements. Fatigue or circadian factors cannot account for this phenomenon. Instead, off-line improvements in sequence performance seem to reflect marked changes in the brain areas subserving the mechanisms involved in memory storage, retrieval, and sequence generation. There is evidence to suggest that overnight skill improvements are supported by replay of the previously learned task and involve both enhancement of neuroplastic mechanisms and reorganization of the learned information.

Overnight reorganization of information and of the memory trace might lead to changes in the representations of motor sequences that previously have been attributed only to practice. Moreover, the dependence of off-line improvement on sleep holds for the learning of sequential tasks (e.g., sequential finger movements) only when the skill is acquired intently and involves explicit learning. In the case of implicit learning, off-line learning is not sleep dependent but develops equally well during the day and overnight. It takes then 4–6 h for such off-line improvements to appear.

Historically, consolidation was described as the reduction in the fragility of memory for a new task. The capability to perform a new acquired skill is interfered with when the participant practices another new skill immediately after the first one. The amount of interference depends on the time that passes between the learning of the two skills. In particular, in the case of dynamic adaptation, learning a second task disrupts the memory trace for the first task, a phenomenon called retroactive interference. As the time between the two learning sessions increases, the memory trace of the first skill becomes more stable, and the interference of learning a second skill becomes weaker. There is some evidence to suggest that retention in memory of learned sequences might also be susceptible to disruption. Doyon et al. have suggested an integrated view of the plasticity that motor memory traces can undergo across learning stages. In the first learning stage, both motor adaptation and sequence learning recruit the corticostriatal and corticocerebellar systems, depending on the cognitive processes required for the task.

When the skill has been learned well, the neural representation of this motor behavior is thought to be distributed in a network of structures involving only one of these circuits. The corticostriatal and cortico-cerebellar systems are crucial for consolidation and for maintaining in long-term memory a new motor sequence or a new motor adaptation skill, respectively. Thus in the case of sequence learning, Doyon and Ungerleider have shown that the cerebellum is no longer essential, and long-lasting retention of the skill involves representational changes only in the striatum and in the associated cortical areas.

See also: Finger Movements: Control; Kinematics and Dynamics; Motor Skill Learning; Motor Timing; Posterior Parietal Cortex and Arm Movement; Posterior Parietal Cortex and Tool Usage and Hand Shape; Premotor Cortex in Primates: Dorsal and Ventral; Premotor Areas: Medial.

Further Reading

- Ashe J, Lungu O, Basford A, and Lu X (2006) Cortical control of motor sequences. *Current Opinion in Neurobiology* 16: 213–221.
- Burdet E and Milner TE (1998) Quantization of human motions and learning of accurate movements. *Biological Cybernetics* 76: 307–318.
- Carpenter AF, Georgopoulos AP, and Pellizzer G (1999) Motor cortical encoding of serial order in a context-recall task. *Science* 283: 1752–1757.
- Doyon J and Benali H (2005) Reorganization and plasticity in the adult brain during learning of motor skills. *Current Opinion in Neurobiology* 15: 161–167.
- Henis EA and Flash T (1995) Mechanisms underlying the generation of averaged modified trajectories. *Biological Cybernetics* 72(5): 407–419.
- Hikosaka O, Nakahara H, Rand M, et al. (1999) Parallel neural networks for learning sequential procedures. *Trends in Neurosciences* 22: 464–471.
- Hikosaka O, Rand MK, and Nakamura K (2002) Long term retention of motor skill in macaque monkeys and humans. *Experimental Brain Research* 147: 494–504.
- Jerde TE, Soechting JF, and Flanders M (2003) Coarticulation in fluent finger spelling. *Journal of Neuroscience* 23(6): 2383–2393.
- Karni A, Meyer G, Rey-Hipolito C, et al. (1998) The acquisition of skilled motor performance: Fast and slow experience-driven changes in primary motor cortex. *Proceedings of the National Academy of Sciences of the United States of America* 95: 861–868.
- Korman M, Raz N, Flash T, and Karni A (2003) Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. *Proceedings of the National Academy of Sciences of the United States of America* 100: 12492–12497.
- Lu X and Ashe J (2005) Anticipatory activity in primary motor cortex codes memorized movement sequences. *Neuron* 45: 967–973.
- Matsuzaka Y, Picard N, and Strick PL (2007) Skill Representation in the primary motor cortex after long-term practice. *Journal of Neurophysiology* 97: 1819–1832.
- Morasso P and Mussa-Ivaldi FA (1982) Trajectory formation and handwriting: A computational model. *Biological Cybernetics* 45(2): 131–142.
- Nissen MJ and Bullemer PT (1987) Attentional requirements for learning: Evidence from performance measures. *Cognitive Psychology* 19: 1–32.
- Penhune VB and Doyon J (2005) Cerebellum and M1 interaction during early learning of timed motor sequences. *NeuroImage* 26: 801–812.
- Roberston EM, Pascual-Leone A, and Miall RC (2004) Current concepts in procedural consolidation. *Nature Reviews Neuroscience* 5(7): 576–582.
- Seidler RD, Purushotham A, Kim SG, et al. (2002) Cerebellum activation associated with performance change but not motor learning. *Science* 296: 2043–2046.
- Sosnik R, Hanptmann B, Karni A, and Flash T (2004) When practice leads to co-articulation; The evolution of geometrically defined movement primitives. *Experimental Brain Research* 156(4): 422–438.
- Tanji J (2001) Sequential organization of multiple movements: Involvement of cortical motor areas. *Annual Review of Neuroscience* 24: 631–651.
- Tracy JI, Faro SS, Mohammed F, Pinus A, Christensen H, and Burkland DA (2001) Comparison of “early” and “late” stage brain activation during brief practice of a simple motor task. *Brain Research. Cognitive Brain Research* 10: 303–316.
- Walker MP (2005) A refined model of sleep and the time course of memory formation. *Behavioral and Brain Sciences* 28(1): 51–86.