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Common mechanisms of human perceptual and motor learning

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Abstract

The adult mammalian brain has a remarkable capacity to learn in both the perceptual and motor domains through the formation and consolidation of memories. Such practice-enabled procedural learning results in perceptual and motor skill improvements. Here, we examine evidence supporting the notion that perceptual and motor learning in humans exhibit analogous properties, including similarities in temporal dynamics and the interactions between primary cortical and higher-order brain areas. These similarities may point to the existence of a common general mechanism for learning in humans.

Procedural learning refers to the ability to gradually improve the performance of a newly acquired skill, usually over multiple training sessions. It has been known for decades that procedural learning can occur in both the perceptual and motor domains^{1,2}, with the resulting improvement in the baseline performance of a particular skill lasting for lengthy periods of time. These different forms of procedural learning have been studied across a wide range of disciplines, and these investigations have improved our understanding of the processes involved.

Intriguingly, the characteristics of perceptual, notably visual, and motor memory formation show striking similarities across the various stages of learning. Fast learning develops during the first training session when individuals practise a new visual or motor task and leads to the initial encoding or acquisition of a memory. Learning in this first session usually involves rapid improvements in the performance of the task^{3–10}. Following termination of practice, a learnt memory can stabilize — a phenomenon referred to as consolidation — which allows the memory to become resistant to interference by competing stimuli or tasks and prevents its decay (that is, forgetting)^{11–16}. Such stabilization involves modifications in the intracellular signal transduction cascades at the synaptic level and neuronal protein

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synthesis, as well as reorganization of the neural networks that represent the memory¹⁷. In the context of procedural learning in the visual and motor domains, consolidation does not only refer to stabilization of the acquired memory but also to improvements in performance that occur after the end of practice (so-called offline gains), which become evident in subsequent test sessions. These offline gains occur in the absence of additional practice^{3,4,18–24} and are influenced by sleep stages^{4,21,25–30}. Indeed, previously consolidated memories may be reactivated during sleep or wakefulness, resulting in memory modification that may be mediated by a process of reconsolidation^{31–34}. Thus, modification of a previously consolidated memory may result in its degradation, maintenance or further strengthening^{12,20}. Long-term retention of a memory refers to the ability to maintain the acquired performance levels following a period of weeks to months without additional training^{3,18,35–37}.

The goal of this article is to explore the commonalities in the characteristics of visual and motor memory formation in humans that have been outlined above. We also discuss similarities between learning in the motor and visual domains in relation to the involvement of primary cortical areas and top-down attentional mechanisms, as well as the conditions under which learning generalizes (transfers) to the untrained eye or hand or to an untrained stimulus or movement. Most of the similarities that we discuss have emerged from the evaluation of texture discrimination and motor sequence learning tasks^{18,19} (BOX 1). When relevant, we mention procedural learning paradigms other than these tasks, although we do not elaborate on motor adaptation paradigms, in which individuals are subjected to externally induced perturbations and their return to pre-perturbation performance levels for a task is evaluated (for a review of these paradigms, see REF. 38).

Box 1

Texture discrimination and sequential finger-tapping tasks

In the texture discrimination task, individuals are presented briefly with a three-diagonal-line target array (which is embedded in a background of horizontal lines) on a monitor and are then asked whether the array has a vertical or horizontal orientation. In order to monitor that subjects are fixating their gaze at the centre of the visual field and minimizing their eye movements, subjects are also required to discriminate between the letters ‘T’ and ‘L’ at the centre of the display¹⁸. Following presentation of the array (the target stimulus), a brief patterned mask appears on the screen. The time interval between presentation of the target stimulus and presentation of the mask (stimulus-to-mask onset asynchrony (SOA)) is gradually decreased within the session, increasing the difficulty of the task. The performance outcome measure, the SOA discrimination threshold (which is measured in milliseconds), is the interval at which approximately 80% of the target stimulus responses are correct¹⁸.

In the sequential finger-tapping motor learning task, individuals are asked to tap, usually with their left, non-dominant hand, a five-digit sequence as quickly and accurately as they can during a limited time period¹⁹. Trials are usually separated by short breaks. Performance outcome measures include the average number of correct sequences performed per trial and the number of errors. In implicit finger-tapping tasks (such as the

serial reaction time task), subjects may not be informed of the presence of a repeating sequence and are instructed to respond to visual cues on the screen by tapping the appropriate key on a response box²². Thus, performance improvements may evolve in the absence of declarative knowledge of the repeating sequence²².

Commonalities in learning stages

Fast learning

Acquisition of a simple motor or visual skill starts with within-session fast learning, which is commonly observed when an individual is initially exposed to a new task and involves a rapid improvement in task performance^{3–10} (FIG. 1). In the visual domain, individuals can improve their performance in the texture discrimination task from ~50% to 100% correct responses over a timescale of several minutes³. Over a similar time period, in the motor domain, individuals can show large improvements (of 40–60%) in the number of correct sequences executed in a sequential finger-tapping task⁴.

Various processes may influence fast learning in both modalities, including top-down mechanisms that engage attentional and executive resources^{1–3,9,10,18,39–43}. In the visual domain, the involvement of top-down processing in fast learning is supported by data showing that learning of a texture discrimination task in one eye rapidly reaches asymptotic performance and transfers from the trained to the untrained eye (but not to the untrained visual field or stimulus orientation)³. In motor sequence learning, studies in non-human primates and neuroimaging data in humans indicate that fast learning involves a frontoparietal-associative striatum–cerebellar circuit that also engages attentional and executive resources, such as the prefrontal cortex^{2,9,10,39,41,42,44,45}. Neuroimaging studies involving positron emission tomography (PET) and/or functional MRI (fMRI) have shown that reaction times and the accuracy of force production in fast sequence learning relate to activity in frontoparietal networks^{9,10,41}. Thus, interregional coupling associated with top-down processing may be important for early skill learning⁴¹.

Stabilization of memories

The classical notion of memory consolidation was proposed by Müller and Pilzecker in 1900 (REF. 46) and refers to the stabilization of memories over time, which reduces their susceptibility to interference. Indeed, studies have shown that when a second, competing memory is formed during a limited time window of several hours after encoding the first memory, it can interfere with consolidation of the original memory, disrupting learning^{20,47}. Such interference (FIG. 1) is evident in different motor learning paradigms^{14,15} and has been shown to occur in classic perceptual learning as well^{11,16,48}. For example, in the motor domain, performance of a novel sequence of finger movements following training in a different motor sequence interfered with learning of the original sequence²⁰. Similarly, in the visual domain, texture discrimination learning was disrupted when a novel orientation of the texture elements in the visual pattern was introduced after training with the original texture¹¹.

An additional shared property of learning in the visual and motor domains is the ability of memories that have already been consolidated to undergo further modification upon their retrieval through reconsolidation¹⁷. This process of modifying transiently reactivated memories can result in degradation, maintenance or further strengthening of the reactivated memory^{17,20,32–34}. Modification of perceptual memories was shown to occur in a face recognition task in which participants were required to identify whether the presented face was similar to the face that they had originally memorized. It was demonstrated that when observers were presented with a sequence of similar but not identical faces over many days, memories of the faces became merged, resulting in novel faces being identified as already familiar^{49,50}. In the motor domain, it was shown that following reactivation of an already consolidated motor sequence memory, training with a new motor sequence negatively affected memory modification and resulted in its degradation, demonstrating the lability of reactivated memories²⁰. The primary motor cortex (M1) has a crucial role in modification of previously consolidated motor sequence memories¹². Indeed, it was recently demonstrated that modification of a reactivated, previously consolidated motor sequence memory was blocked by a ‘virtual’ lesion in M1, which was induced by the application of inhibitory 1 Hz repetitive transcranial magnetic stimulation (rTMS)¹².

Between-session learning

The ability not only to stabilize a memory but also to enhance it offline (in the absence of practice) is an important feature of perceptual and motor learning. These offline gains could be mediated by memory consolidation and reconsolidation³¹ (FIG. 1). In the framework of reconsolidation, it is possible that each additional training session for an already consolidated perceptual or motor task involves retrieval of the consolidated memory and integration of inputs available during the additional training sessions, resulting in improved performance¹².

Between-session learning has been frequently shown in texture discrimination and motor sequence learning tasks^{3,4}. Offline improvements in texture discrimination thresholds or in the speed and accuracy of the performed motor sequence can occur following a delay of hours without additional training^{3,4}. In both domains, these improvements, which were evident in the following training session, were of lower magnitude than the improvements that occurred during within-session fast learning. Of note, offline improvements may be influenced by practice schedule and between-session sleep^{1,21–23,51–54} and by the specific features and context of the trained stimulus or task^{3,18,19,51,55–57}. The neural substrates associated with offline between-session improvements in visual and motor tasks include the primary visual cortex (V1) and M1, respectively^{3,12,18,19,56,58–61}.

In the visual domain, offline between-session improvements in performance are often specific to features, such as retinal location and stimulus orientation, and to the trained eye^{3,18,56}. Such improvements are associated with plasticity in V1, in which neurons are differentially tuned to each of these features^{3,18}. Consistent with V1 involvement in learning, increases in blood-oxygen-level-dependent (BOLD) activity in specific subregions of V1 were observed following training in the texture discrimination task^{58,59}. In addition, the amplitude and latency of visually evoked potentials recorded over V1 using

electroencephalography (EEG) correlated with texture discrimination performance following training^{60,61}. In the motor domain, offline performance gains that are specific to the trained hand and the practiced sequence engage M1 (REFS 12,19,24,41), which is in line with animal studies demonstrating that protein synthesis in this brain region is required for successful motor learning⁶². The involvement of M1 in offline motor learning was supported by a study showing that the BOLD signal increased in this region following 4 weeks of training to perform a sequence of finger movements¹⁹. Indeed, this study showed that M1 had undergone experience-dependent reorganization and that this reorganization persisted for several months, along with the behavioural gains in task performance¹⁹. Between-session learning in a different motor sequence task (the serial reaction time task (SRTT)) was also shown to rely on M1 processing. In this study, inhibitory 1 Hz rTMS was applied to participants immediately after practising the task to create a virtual lesion in M1. This lesion blocked subsequent offline learning when test sessions were conducted within the same day²⁴.

In addition to its role in offline motor sequence learning, M1 contributes to the learning of non-sequential ballistic finger movements¹³ and to adaptation to novel movement dynamics⁶³. Moreover, facilitatory transcranial direct current stimulation (tDCS) of M1 simultaneously with motor practice consistently improved offline learning of a sequential visuomotor task⁶⁴.

Together, these studies suggest that offline learning in the visual or motor domain is associated with plasticity in the relevant primary cortical areas. As discussed in the following sections, such learning is also associated with interactions between these primary cortical areas and higherorder brain regions^{39,65–71}.

Generalization of learning

Various studies have shown that procedural learning that occurs over several training sessions is specific to the trained eye or hand and to the physical features of the task and does not generalize^{3,18,19,51,55–57}. Other studies, however, have shown that generalization of such learning is possible in both the visual and motor domains.

In the visual domain, generalization of learning can occur if a double-training paradigm is used^{72,73}. In these studies, individuals were first trained so that they were able to successfully discriminate different contrasts of a visual stimulus at a certain location in their visual field. These individuals then underwent training in a different task (orientation discrimination) at a different location in the visual field. Subsequently, individuals were tested on their ability to perform the first task at the second location. Strikingly, they were able to perform this task successfully, with a level of performance that matched the level of performance at the original visual field location, showing that transfer of learning had occurred.

These results challenged the notion of limited generalization in visual perceptual learning and suggested that higher non-retinotopic brain regions and possibly recurrent interactions between these higher-order brain areas and V1 contribute to location transfer^{72,73}. Interestingly, shorter texture discrimination training sessions result in more efficient

perceptual learning and a larger degree of generalization^{23,74,75}. The extent of learning generalization could depend on the efficiency of the networks that are engaged in the formation of early local sensory representations and the readout of these networks by higher-order brain areas⁷⁶.

Several studies have shown that motor sequence learning can undergo intermanual transfer, which is a form of generalization, and that this process relies on activity in non-primary frontal regions^{39,66,67} as well as in M1 (REF. 66). Such intermanual transfer has also been shown to occur in between-session offline learning^{77–79}. Thus, in both motor and visual domains, it is possible that generalization of learning involves plastic interactions between the relevant primary cortical region and higher-order brain areas⁷⁴.

The specific conditions under which motor and perceptual learning generalize are incompletely understood and require additional investigation. Understanding these conditions may have clinical implications for the rehabilitation of neurological disorders that are characterized by deficits in motor or perceptual functions. For example, following stroke, functional recovery of a weak hand might be facilitated by training the non-paralysed hand⁸⁰.

The role of sleep

Sleep has an important role in perceptual and motor learning, as it promotes consolidation (FIG. 1). It has been reported that sleep can promote performance improvements and protect against interference^{1,11,26}. One example of such protection against interference is that sleep is thought to prevent deterioration in performance that can develop during waking hours^{23,75,81–83} (see REF. 54 for a review). Both consequences of sleep depend on training intensity^{23,84}. The role of sleep in protection against interference has been shown in texture discrimination tasks but remains to be investigated in motor sequence tasks.

Sleep-dependent consolidation promotes offline perceptual learning. Indeed, a sleep study showed that overnight improvements in texture discrimination following training are strongly dependent on rapid eye movement (REM) sleep²⁵. REM sleep may contribute to offline improvements through modulation of cholinergic neurotransmission⁸⁵, possibly promoting long-term potentiation (LTP)- and long-term depression (LTD)-related mechanisms^{84,86–88}. Such mechanisms may also be active during other sleep stages^{82,89}, as some studies have shown that the extent of texture discrimination learning is proportional to the duration of slow wave sleep (SWS) in the first quarter of the night and the duration of REM sleep in the last quarter of the night^{21,27}. Additionally, it has been shown that these sleep effects are present even after a 60–90-minute nap as long as it contains both SWS and REM sleep²⁸.

In motor sequence learning, individuals can be explicitly informed before commencing the task that they will be presented with a repeating sequence. For example, in a sequential finger-tapping task¹⁹, individuals are asked to tap a keyboard sequence that is displayed on a monitor as quickly and accurately as possible⁴. Offline motor sequence learning (explicit offline learning) that occurs in this paradigm relies on between-session sleep^{4,26,29,30}, which

suggests that higher-order brain areas associated with declarative knowledge (such as the hippocampus) are involved in consolidation of the trained memory^{65,68}.

In contrast to participants in this sequential finger-tapping task, individuals in the SRTT are not typically informed of the presence of a repeating sequence. Instead, they are instructed to respond to visual cues on a screen by tapping the appropriate key on a response box²². Offline learning that occurs in this paradigm (which is referred to as implicit offline learning) does not benefit from sleep⁹⁰ but depends on the passage of time²². However, when the same SRTT is manipulated so that individuals gain explicit knowledge of the performed sequence, offline learning becomes sleep-dependent²². Interestingly, implicit and explicit learning in the SRTT engage different neural substrates^{9,91}. For example, in a motor sequence learning study, the reaction time during implicit learning was associated with increased activity in the primary sensorimotor cortex, whereas during explicit learning, the reaction time correlated with activity in a frontoparietal network^{9,91}. Such dissociation between the effects of sleep on explicit and implicit knowledge of the learned skill remains to be explored in the perceptual domain⁹².

As mentioned above, another facet of sleep's influence on learning is its ability to allow recovery from the deterioration in performance that develops during waking hours^{23,82,83}. Intensive perceptual training in texture discrimination can lead to a deterioration in performance occurring between sessions that are separated by a few hours^{81,93} and within a single training session^{23,94}. This phenomenon is not due to local fatigue of the eye, as performance deterioration in the trained eye can be transferred to the untrained eye^{93,94}. It was suggested that such deterioration in performance occurs when neural networks in early cortical visual areas become gradually saturated or undergo adaptation with repeated testing. The involvement of early visual areas in performance deterioration is supported by the finding that changes to the retinal area or stimulus orientation that are used in the task, which are both represented by early visual areas, prevent further deterioration in performance^{93,94}. SWS during naps⁸¹ and overnight sleep^{74,75} prevented deterioration in the texture discrimination task. It has been proposed that SWS reduces perceptual deterioration through the downscaling of synaptic strength (which increases and saturates over wakefulness) to a level that is sustainable in terms of energy and tissue volume demands (this proposal is known as the synaptic homeostasis hypothesis^{74,75,54,95,96}). Recently, it has been reported that performance of motor sequences also deteriorates across waking hours and recovers after sleep⁸³. Similar deterioration has also been reported using a tracking isometric pinch force task³⁵, in which participants were trained to hold a force transducer between the right thumb and index finger in order to maintain a red cursor within a moving blue target on a computer screen. Participants exhibited reduced performance after 6 hours of training.

SWS may also enable efficient systems level consolidation by reactivating neuronal circuits implicated in the initial memory encoding, possibly promoting reorganization of the memory trace, which leads to more persistent memory representations^{17,54,97-99}. As discussed above, generalization of learning may be achieved through interactions between M1 or V1 and higher-order brain regions^{68-71,86}. In the visual domain, coordinated interactions between V1 and the hippocampus during sleep¹⁰⁰ may explain sleep-dependent generalization of

learning⁷⁴. Interestingly, it has also been shown that functional interactions involving the hippocampus and striatum determine overnight consolidation of procedural motor memories^{65,68}. Overall, sleep has an important role in both perceptual and motor learning not only by stabilizing the acquired memory and producing offline gains in performance but also by enabling a spatially distributed representation of the encoded information across the brain⁵⁴.

Importantly, the role of sleep stages in motor and perceptual learning may vary according to the study design and task. Although it is unreasonable to assume a complete dissociation between the roles of different sleep stages in learning, available data suggest that SWS may be more important in preventing perceptual memory deterioration, whereas REM sleep may have a more prominent role in enhancing offline improvements in perceptual skills. In the motor domain, SWS may have a role in strengthening visuomotor rotation learning^{95,101}, whereas REM sleep and additional stages of non-REM sleep may be essential for motor sequence learning^{4,22,29,88,102}.

Engaging higher-order brain areas

We have discussed the involvement of V1 and M1 regions in perceptual and motor learning, respectively^{3,12,13,19,58–61}, and their contribution to learning specific physical properties or features of a task^{1,18,19,56,103–107}. Nevertheless, as mentioned above, recent evidence has documented generalization of learning in both domains. In the visual system, perceptual learning may transfer to untrained locations and orientations^{72–74}, suggesting a rule-based learning model in which higher-order processing brain areas learn the rules of reweighting V1 inputs through training¹⁰⁸. In the motor domain, intermanual transfer of motor sequence learning involves frontal regions, such as the supplementary motor area (SMA) and premotor cortex, as well as M1 (REFS 39,66,67,77). Thus, interactions between primary cortical areas and higher-order brain regions may contribute to the generalization of learning in both perceptual and motor domains^{66,67,72,73,77}.

Such interactions may conceivably contribute to the beneficial effects of reinforcement or reward on procedural learning^{35,92}. In the visual domain, individuals that had been deprived of food and water showed improved learning on a grating orientation discrimination task when training was paired with rewarding drops of water⁹². In the motor domain, individuals who were trained to pinch a force transducer in order to track a moving cursor when a monetary reward was given based on achieved performance showed improved consolidation and long-term retention of performance gains measured 30 days after training³⁵. The mechanisms underlying this effect may include the engagement of higher-order frontal areas that are involved in decision-making in combination with M1 (REF. 109). It remains to be determined whether the effects of reward on consolidation, which are measured the day after the initial training day, and on long-term retention are driven by common mechanisms.

Higher-order brain areas are engaged during motor learning as well as during perceptual learning of tasks that require processing of early visual representations^{69–71}. Perceptual learning models proposed that changes in synaptic weighting influence the interaction between low- and high-level visual representations^{73,108,110}. These models may explain

results showing that perceptual learning is more pronounced for stimuli that are presented at locations in the visual field to which a subject's attention is directed^{111,112}, suggesting that attention mediated by higher-level visual areas determines which representations in lower visual areas undergo plasticity, thereby gating learning¹¹³. Thus, attention may guide plasticity in lower visual areas, which in turn enables learning.

The visual system has the ability to perceive and recognize whole objects composed of basic individual visual elements by using visual cues (which are known as Gestalt grouping mechanisms). For example, it has been shown that detection of a visual target is facilitated by attention to nearby visual stimuli oriented similarly¹¹⁴. Therefore, the discussed interactions between early brain processing areas (such as V1) and higher-order brain regions may contribute to perceptual learning by engaging attentional mechanisms that enhance the perception of whole objects using Gestalt grouping cues¹¹⁵. In motor learning, interactions between early and higher-order brain areas may support learning of complex sequences from discrete chunks (groups) of single movements¹¹⁶. Thus, although the related primary cortical regions have an important role in consolidation of perceptual and motor learning, interactions between primary and higher-order brain regions may contribute to other aspects of learning, such as the ability to generalize the learnt information to different or more complex stimuli or movement sequences (FIG. 2). More evidence in both domains is required to test this hypothesis.

Conclusions and future directions

As discussed here, motor and perceptual procedural learning show various similarities. Thus, understanding the mechanisms underlying procedural learning in the motor domain may help to gain insight into the mechanisms that underlie procedural learning in the perceptual domain, and vice versa. Of note, it would be interesting to study the extent to which perceptual learning induces anatomical changes in the brain, which have been reported to occur in the microstructure of white matter during motor and spatial learning^{117–119}. In addition, it would be interesting to see whether our current knowledge of perceptual learning could provide guidance as to the amount of training that is needed to optimize lasting retention of newly acquired motor skills^{74,75} and to examine how motor learning in one task can generalize to untrained tasks^{72,73,110}. Developing a better understanding of learning generalization could be of great relevance to clinical neurorehabilitation.

The similarities between visual and motor learning also suggest that procedural learning in humans follows a general mechanism. Thus, it would be of interest to examine whether some of the between-domain similarities reviewed here are relevant to other sensory domains. For example, to what extent are the primary olfactory, tactile and auditory cortical regions involved in learning in their respective domains^{120–123}? Commonalities in learning across various sensory systems might have functional advantages, allowing, for example, cross-modal plasticity, in which plasticity in one modality could influence performance in a different modality^{124–128}. Such plasticity could conceivably be facilitated by top-down attentional feedback control of interactions between higher-order brain areas and primary sensory cortices¹²⁹.

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FURTHER INFORMATION

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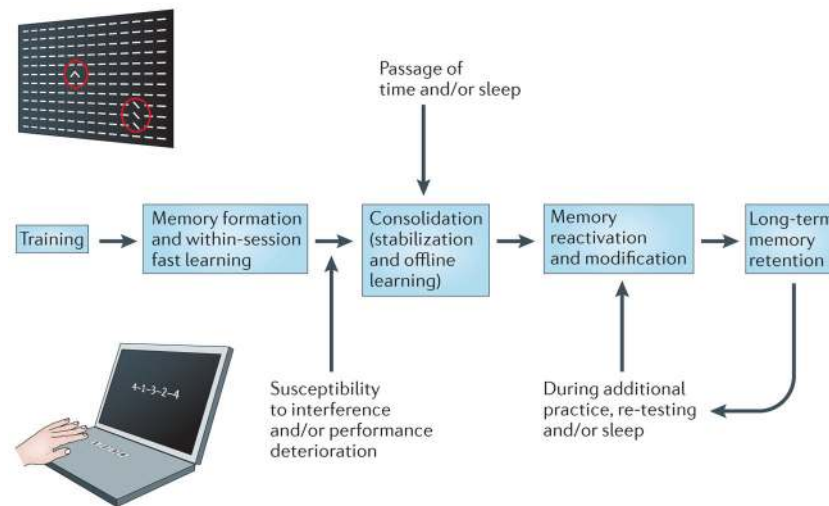


Figure 1. Perceptual and motor learning

The texture discrimination and sequential finger-tapping tasks (BOX 1) are commonly used to study visual and motor procedural learning, respectively. Both tasks are characterized by within-session fast learning, which involves rapid improvements in performance^{3–10}. Depending on the training conditions, the memory can be susceptible to interference for a limited time window of several hours following its acquisition^{11,20,47}, and deterioration in performance can develop across wakefulness^{23,81–83,93,94}. The memory also undergoes the competing process of consolidation after acquisition, which involves stabilization of the memory (enabling its resistance to interference by competing stimuli or tasks^{11,13–16,24}) and offline gains in performance^{3,4,18,19,20–24}. Slow wave sleep and rapid eye movement sleep involve memory reactivation, downscaling of synaptic strength and long-term synaptic plasticity-related processes. These processes support recovery from performance deterioration and offline learning^{4,21,25,75} by stabilizing and further enhancing the memory through consolidation. Reactivation of the memory during sleep or wakefulness (for example during re-testing on the task) can lead to memory modification, which involves the integration of new information^{12,98}.

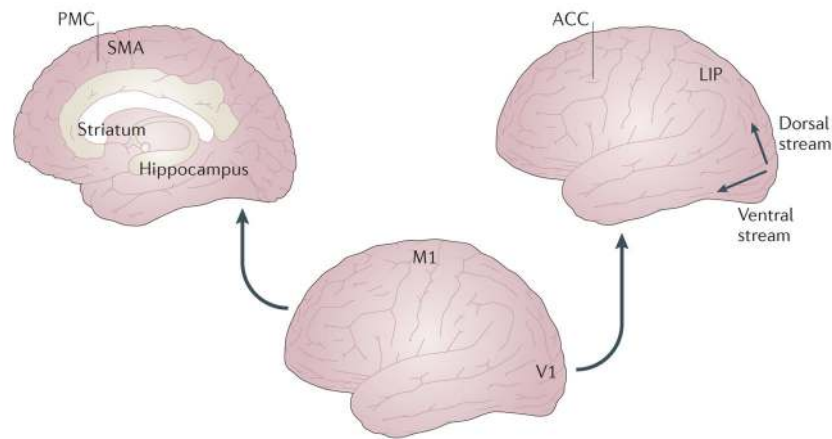


Figure 2. Interplay between primary cortical processing and higher-order brain areas

The primary visual cortex (V1) and primary motor cortex (M1) have important roles in perceptual and motor learning, respectively, by contributing to the retention of specific physical properties or features of a task. Learning-induced modulation of tuning curves determines the preferred orientation for responding to lines and bars in V1 cells¹⁰³ and the preferred direction for reaching movements in M1 cells¹⁰⁶. However, higher-order brain areas involved in decision-making and reinforcement are also engaged in between-session performance improvements, enabling rule-based learning and generalization. In the motor domain, frontal regions such as the supplementary motor area (SMA) and premotor cortex (PMC), as well as M1, are involved in intermanual transfer of motor sequence learning^{39,66,67,77}. The striatum and hippocampus, which are involved in offline motor learning, show sleep-dependent increased activity, as measured by functional MRI^{65,68}. This engagement of higher-order brain areas, which is well documented in motor learning, has also been shown in learning perceptual tasks that require processing in early visual areas^{69–71}. Thus, perceptual learning engages not only areas within the ventral stream (for example, V4) and dorsal stream (for example, the medial temporal area) but also areas involved in decision-making, such as the lateral intraparietal area (LIP) and the anterior cingulate cortex (ACC).