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The Neural Basis of Cognitive Efficiency in Motor Skill Performance from Early Learning to Automatic Stages

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Abstract

Skill acquisition represents a progression from high to low reliance on the conscious control of action. The ability to produce action without drawing upon limited attentional resources has traditionally been the defining characteristic of skill automaticity. As such, learning represents a progression from low to high efficiency in the cognitive processes needed to plan, execute and update skilled movement. In this chapter, we summarize neuroimaging findings that illustrate the evolution of such efficiency in terms of the neural adaptations that underlie skill learning automatization. As a backdrop to these findings, we first review the cognitive characteristics of skill automaticity as well as a contemporary theoretical framework for how we perform action based on sequencing movement elements. This provides a vantage point from which neural basis of skill automaticity can be considered in terms of associative and sensorimotor learning processes that provide for more efficient action in terms of cognitive requirements. We then contrast this with a summary of the contextual interference effect, which represents a cautionary account for the negative learning consequences associated with training protocols that appear to expedite skill automaticity.

11.1 Introduction

As we acquire a motor skill, two general characteristics typically emerge (Fitts, 1964; Fitts & Posner, 1967; Gentile, 1972, 1998). First, performance improves. Second, skill performance becomes automated (Fitts, 1964). Of these two characteristics, it is the latter that has particularly fascinated society. This is not surprising given that the time constraints under which we must perform many of our everyday behaviors demand we automate action (e.g., driving a car on a busy street). Moreover, it is the transition from the effortful to the effortless that is the quintessential subjective experience of transitioning from learning to automaticity. The experience of reduced effort coincides with increased mechanical (Bernstein, 1967) and metabolic (Almåsbaek et al., 2001) efficiencies. However, the concept of automaticity has been more aligned with gaining efficiency with respect to diminishing the cognitive demands required to perform skilled action. Automaticity implies the absence of conscious awareness and therefore the absence of attention, the fundamental process for cognition in the sense that cognition and associated terms such as cogitation, recognition relate to knowing, *cognoscere* in Latin (Chaney, 2013).

The neural underpinnings for the transition from costly, cognizant skill learning to efficient relatively attention-free behavior is the central theme of this chapter. To describe neural adaptation associated with establishing skill automaticity, we review findings from studies that have utilized fMRI or PET neuroimaging approaches to assess brain activity associated with early learning and automatic stages of skill learning. While automaticity might reflect learning associated changes in neurocognitive processes that contribute to skilled action, we then present the contextual interference effect (Shea & Morgan, 1979) as a case where neural patterns of automaticity can be established quite early in learning to provide temporary performance gains as opposed to long-term skill learning. First, though, we provide a brief historical context of automaticity followed by an overview of the cognitive characteristics of skill automaticity and a theoretical framework for the progression of skill performance strategies employed across the stages of skill learning.

11.1.1 Developing views on skill automaticity

One of the earliest considerations of autonomous processes in human function is attributed to Aristotle (Korsgaard, 2008; Bernacer & Murillo, 2014). According to Aristotle, repetition of a task gave rise to enhanced task performance owing to a developed disposition that rendered action less subservient to conscious control and thus, more spontaneous (Bernacer & Murillo, 2014). Thus, rather than Descartes' view of a fixed dichotomy between controlled and automatic behavior (Jonides et al., 1985), that automaticity relied on repetition was suggestive of progression across a continuum of controlled and automatic performance (Whitaker, 1983), which is in line with contemporary theories of motor skill learning (e.g., Fitts & Posner, 1967).

In the late 19th Century, two students working in the Harvard Psychological Laboratory under William James, Gertrude Stein and Leon Solomons, evaluated the automaticity of writing (Solomons & Stein, 1896; Stein, 1898). That well-practiced writing was performed "outside of awareness" (Solomons & Stein, 1896) was interpreted as being necessary to overcome resource capacity limits, particularly with respect to attention (James, 1890). As with many cognitive theories (e.g., Miller, 1956; Kahneman, 1973; Posner, 1979), the theme of limited capacity became the central *raison d'être* for automaticity. For example, LaBerge and Samuels (1974) stipulated that skilled performance exceeds limited attention resources and so at least a subset of cognitive and motor processes must be automated to allow for successful performance. Limited

capacity refers to information processing restrictions due to finite availability of cognitive resources being insufficient to meet the current demand from ongoing processes. Skilled behavior can potentially overwhelm these limits given the high information load associated with processes responsible for sensation, perception as well as skilled action preparation, execution, monitoring and updating. Reduced reliance on limited resources meant that automated skills could be performed in parallel with other tasks with little or no interference (Jastrow, 1891; Bahrack et al., 1954; Brown & Carr, 1989; Cohen et al., 1992). Diminished resource demands have been attributed to less reliance on sensory feedback processing (Keele, 1968) as automaticity allows movement to be performed under feedforward control as opposed to feedback control (Wolpert et al., 1998; Miall et al., 2001; Puttemans et al., 2005). Feedforward control, where production of skilled action does not rely on concurrent sensory input to guide the action, is possible when movement production is based on an internal model (Wolpert et al., 1998; Kawato, 1999), which has been described as involving a motor program (Schmidt, 1975, 2003) or motor chunk (Verwey, 1999).

11.1.2 Extended practice requirements for skill automaticity

There is no singular agreed upon definition of motor skill automaticity, which introduces difficulty in determining the point at which a skill is automated. Several approaches in this respect have been presented in the literature. One approach focuses on the level of practice associated with the skill. Specifically, automaticity is thought to arise from extended practice. However, extended practice itself is not defined in terms of actual practice volume. Moreover, extended practice requirements would be expected to depend on the skill as well as the individual learner. The popular 10,000 hours of deliberate practice quanta for skill expertise has been commingled with skill automaticity even though automaticity is but only one dimension of expertise (Singer, 2002). It is likely that the level of extended practice necessary for automaticity is well below 10,000 hours as skill automaticity has been demonstrated with far less practice (e.g., Karni et al., 1995). Quantification issues aside, the provision of extended practice does not necessarily guarantee that skill automaticity will be achieved (Lang & Bastian, 2002). For this reason, some propose that overtraining must be implemented to ensure that extended practice leads to automaticity (Puttemans et al., 2005; Moors & De Houwer, 2006). Overtraining involves the provision of additional practice beyond the point at which skill performance reaches asymptote.

11.1.3 Cognitive characteristics of skill automaticity

More formal, cognition-oriented criteria of skill automaticity have been drawn from Schneider and Shiffrin's (1977) description of an automatic mode of information processing (for example, see Ashby & Crossley, 2012). One criterion is that an automated skill can be performed simultaneously with another task without any loss of performance in either the skill or the paired task (Passingham, 1996; Wu et al., 2004; Lehericy et al., 2005; Poldrack et al., 2005; Wu & Hallett, 2005; Wu et al., 2008; for an example in sport, see Leavitt, 1979). An extension of this criterion involves assessing motor skill attention demands using dual-task methodology (Posner & Keele, 1969; McLeod, 1980; Abernethy, 1988; Wright & Kemp, 1992; Verwey et al., 2010). Here, the primary task, the presumed automated skill, is performed with a secondary probe reaction time (RT) task. Reduced attention demand from the primary task is inferred when there is little increase in probe RT under dual-task conditions in comparison to performing probe RT alone.

Skill automaticity might also be characterized by the degree of performance inflexibility that is observed following a period of training. Performance inflexibility refers to the extent in which performance of the skill deteriorates when the sensory or task environment is changed from the conditions that were present during learning. For example, Proteau et al. (1992) demonstrated that manual aiming performance was impaired by introducing visual feedback after a period of practice without visual feedback availability. Automated skills are thought to be inflexible to the extent that they will not be modifiable when new conditions are introduced during additional practice (Schneider & Chein, 2003). In Experiment 2 of Helie et al. (2010), extended practice involving about 11,000 trials was provided for a visual stimulus categorization task that involved key-press responses. When new stimulus-key response mappings were introduced following extended practice, performers demonstrated significant performance losses in terms of increased error and RT. These losses persisted even after the provision of 600 additional practice trials with the new stimulus-response mappings.

11.1.4 Cognitive framework for skill automatization

While performance criteria might be useful to test for skill automaticity, they provide little to the understanding of the underlying neurocognitive changes that contribute to observed characteristics of automaticity. Thus, there has been some effort devoted to developing cognitive frameworks of skill automatization based on research addressing how we sequence basic movement elements into skillful action. Specifically, findings from studies involving discrete key-press sequences have led to the notion that motor skill automaticity is associated with the development of sequence knowledge at different processing levels (Hikosaka et al., 1999; Abrahamse et al., 2013; Verwey et al., 2015). According to the cognitive framework for sequential motor behavior (C-SMB; Verwey et al., 2015, see Figure 11.1), a motor skill can be represented perceptually, symbolically and motorically and these representations are processed respectively by perceptual, central and motor processors. Moreover, the manner in which the skill is represented and consequently processed changes as the skill is acquired. The idea is that sequential motor skills are initially based on spatial and perhaps even verbal sequence forms of central-symbolic representations, which are relatively slow and cognitively demanding to apply. Extensive practice allows elements to be chunked into motor sequence representations. These allow for a skill to be performed with much less cognitive demand because these motor chunks are executed by a motor processor that loads cognitive processing resources only for selecting and initiating these motor routines. So, as sequential motor skills evolve with practice, the role of central-cognitive processing resources changes from selecting and initiating individual movements to selecting and initiating integrated movement patterns. This processing change would be responsible for the rapid movement execution along with reduced flexibility and limited interference with other tasks.

 Insert Figure 11.1 About Here

11.1.5 Historical and contemporary views on neural changes associated with skill automaticity

The presence of permanent adaptations in cognitive processes that underlie enhanced performance are expected to be accompanied by structural and functional changes in the

neurobiological substrates of motor skill automaticity (Matsuzaka et al., 2007; Ashby et al., 2010). Work by the neurophysiologist and Nobel laureate, Sir Charles Scott Sherrington (1974), offered some of the earliest examination of the neural correlates of movement automaticity (Ashby et al., 2007). Sherrington's perspective was that skill automaticity represented "spontaneous" behavior underpinned by reflexive action, which arose from extensive practice (Burke, 2007). While skill automaticity is no longer viewed as being reflexive, Sherrington's idea that neural ensembles could be formed from experience (i.e., neuroplasticity) to enable movement production at any level of the central nervous system (e.g., Sherrington, 1910) gave rise to the concept of hierarchical movement control (Pew, 1966; Bernstein, 1967; Koechlin et al., 2003; Fuster, 2004). This in turn gave rise to the claim that novel motor skills require control at the resource demanding and least efficient executive cortical levels (e.g., prefrontal cortex), but as they are practiced, their control is transferred to more efficient cortical regions such as the premotor and primary motor cortices (e.g., Ashby et al., 2010), or subcortical regions such as the basal ganglia (e.g., Wu et al., 2004). Thus, the hallmark feature of skill automaticity, efficiency, is derived from practice dependent neuroplastic changes. These changes do not necessarily reflect diminished neural involvement in skilled action but rather the development of neural connections that facilitate performance speed and accuracy and in parallel, reduce the cognitive demands of performance.

11.2 Neural changes from early skill learning to automatization

The autonomous stage of motor skill performance (Fitts, 1964) is preceded by learning stages that involve cognitive demanding and effortful associative and motor adaptation processes (Fitts, 1964; Fitts & Posner, 1967; Gentile, 1972, 1998; Hikosaka et al., 2002). Early skill learning relies on activity in the primary motor cortex (M1), the basal ganglia and the cerebellum (Hikosaka et al., 2002; Penhune & Doyon, 2002; Shadmehr & Krakauer, 2008; Krakauer & Mazzoni, 2011; Shmuelof & Krakauer, 2011; Penhune & Steele, 2012; Hardwick et al., 2013 - see Figure 11.2). In addition, several frontal regions including the dorsolateral prefrontal (DLPFC), premotor (PMC) and supplementary motor area (including the supplementary motor area proper, SMA, and the pre supplementary motor area, preSMA) have been shown to contribute to early skill learning (Grafton et al., 1992; Jenkins et al., 1994; Jueptner et al., 1997b; Toni et al., 1998; Ghilardi et al., 2000; Grafton et al., 2002; Verwey et al., 2018). Frontal lobe cortical activity underlying skill learning follows an anterior to posterior direction according to an associative-motor hierarchy for movement preparation and control (Koechlin et al., 2003; Fuster, 2004). As an example, within the associative-motor hierarchy, associative processes might relate to the selection of desired responses according to task goals, stimulus conditions or preceding responses (Toner & Moran, 2015) whereas motor processes are involved in producing the action itself, which might include adapting muscle force specification to meet the skill goal (Taylor & Ivry, 2012). Early in learning, resource demanding executive prefrontal cortices are relied on to inform lower motor levels (i.e., premotor and primary motor cortices; Fuster, 2004). However, as learning progresses, cortical activity in the frontal lobe diminishes in an anterior to posterior direction (Wu et al., 2004; Lehericy et al., 2005; Poldrack et al., 2005; Puttemans et al., 2005; Wu et al., 2008), which corresponds to a transition from executive to motor levels of control and consequently, a reduction in the central resource demands. This process does not appear to be irreversible though as automated skills can be consciously attended to by once again invoking activity in the prefrontal cortex (Jueptner et al., 1997b; Kubler et al., 2006). Heightened cortical activity associated with early skill learning has also been reported in parietal

(specifically the somatosensory region, S1), temporal and occipital regions along with the anterior and posterior cortices and the precuneus (Jenkins et al., 1994; Toni et al., 1998; Schendan et al., 2003; Robertson, 2007; Shadmehr & Krakauer, 2008; Laird et al., 2011; Lohse et al., 2014).

 Insert Figure 11.2 About Here

11.2.1 Fast and slow skill learning stages

Progression of skill learning from early to later levels of experience is thought to follow fast and slow stages (Karni et al., 1998; Dayan & Cohen, 2011). Both fast and slow learning stages are experience dependent since the performance improvements only occur with actual task practice. An intermediate stage highlights offline forms of motor learning and includes motor memory consolidation processes (Robertson et al., 2004; Walker & Stickgold, 2004; Immink, 2016). The fast learning stage is characterized by large performance improvements during initial skill practice. Fast learning is thought to involve attention demanding, associative processes (Hikosaka et al., 1999; Hikosaka et al., 2002; Lohse et al., 2014; Verwey et al., 2015; Verwey et al., 2018). As skilled motor tasks are comprised of a series of independent movement elements, associative processes contribute to sequence learning where individual movement “building blocks” (Verwey & Dronkers, 2018) are associated to form movement representations based on “chunked” sequence elements (Grafton et al., 1995; Clegg et al., 1998; Verwey, 1999; Abrahamse et al., 2010; Verwey & Wright, 2014; Wright et al., 2016; Immink et al., 2017). Early in learning, particularly with discrete key-pressing sequences (Verwey, 1999; Abrahamse et al., 2013), performance of movement sequences is slow and demanding because initiation of each response element relies on stimulus information processing (Abrahamse et al., 2013; Verwey et al., 2015; Verwey et al., 2018; see Figure 11.3, panel B, reaction mode). To render sequential performance less stimulus dependent, sequence learning can then progress to increased involvement of premotor processes (Lohse et al., 2014) which utilize verbal or symbolic representations (Gentile, 1972, 1998; Verwey et al., 2015; Verwey et al., 2018) such as when a phone number is verbally recited to enter the requisite sequence on the phone key pad (Fendrich & Arengo, 2004; see Figure 11.3, panel B, central-symbolic mode). Forming associations between successive movement elements renders faster and less resource demanding sequential behavior as a sequence representation or “motor chunk” provides for more efficient motor preparatory processes (Abrahamse et al., 2010; Verwey et al., 2015; Verwey et al., 2018; see Figure 11.3, panel C, chunk mode). “Chunked” sequence representations are then further refined in the slow stage of learning, which emphasizes effector specific (Hikosaka et al., 2002) mechanisms that contribute to motor representation formation (Lohse et al., 2014; Verwey et al., 2015; Verwey et al., 2018), and overlapping activity of effectors executing successive movements (like the coarticulation found with skilled typists; Shaffer, 1975; Jordan, 1995; Engel et al., 1997). Motor representation driven performance is fast because it does not rely on attention demanding sensory feedback or premotor/associative processing. The tradeoff to speeded performance is the lack of flexibility inherent in feedforward modes of performance.

Neurophysiological evidence for the concept of fast and slow learning stages is based on activity within cortico-striatal-cerebellar systems (Doyon & Ungerleider, 2002; Hikosaka et al., 2002; Doyon et al., 2003; Dayan & Cohen, 2011). Specifically, associative learning processes,

relied upon within the fast stage (Hikosaka et al., 2002; Lohse et al., 2014; Verwey et al., 2018), have been correlated with increased activity in the DLPFC (Hikosaka et al., 2002), dorsal and ventral PMC (dPMC, vPMC, respectively; Hardwick et al., 2013), the SMA, S1, precuneus, striatum (caudate nucleus, anterior and posterior putamen) and cerebellum (Lehericy et al., 2005; Wu et al., 2008; Lohse et al., 2014). In contrast, the slow learning stage, which emphasizes sensorimotor adaptation (Hikosaka et al., 2002; Lohse et al., 2014; Verwey et al., 2018) appears to involve increased activity within M1, dPMC, superior temporal lobe and the posterior putamen (Hikosaka et al., 2002; Lehericy et al., 2005; Coynel et al., 2010; Hardwick et al., 2013; Lohse et al., 2014). Changes associated with practice reveal decreases in SMA, vPMC, precuneus and cerebellum activity coinciding with increases in activity in M1, posterior putamen and globus pallidus (Grafton et al., 1995; Hazeltine et al., 1997; Lehericy et al., 2005; Wu et al., 2008; Ashby et al., 2010; Lohse et al., 2014). Overall, findings from neuroimaging studies are consistent with a transition from associative, fast learning, to motor, slow learning, processes as practice progresses. Moreover, neuroimaging studies provide evidence for decreased reliance on higher level control of movement that is concomitant with an anterior to posterior shift in frontal lobe activity (Wu et al., 2008) along with increased cortico-striatal connectivity (Toni et al., 1998).

 Insert Figure 11.3 About Here

11.2.2 Differentiating learning related neural changes based on skill function and performance strategies

It should be noted that there is some disagreement exists in the literature with regard to changes in brain region activity associated with motor learning. For example, some have shown that with practice, M1 activity increases (Grafton et al., 1995; Hazeltine et al., 1997), while others have reported no change (Karni et al., 1995) or M1 activity decrease (Shadmehr & Holcomb, 1997). Lohse et al. (2014) found that left M1 activity increases initially but then decreases with extended practice. Similarly, some have reported learning associated increases in cerebellar activity (Jenkins et al., 1994; Doyon et al., 1996), which contrasts with others' report of decreased cerebellum activation (Friston et al., 1992; Grafton et al., 1994; Seitz et al., 1994; Jueptner et al., 1997a; Doyon et al., 2002; Lohse et al., 2014). These mixed findings have been explained in terms of the variety of motor tasks that have been investigated (Hardwick et al., 2013). For example, some studies have involved unimanual sequence learning tasks (e.g., Jenkins et al., 1994; Karni et al., 1995) while others have involved bimanual movements requiring inter-limb coordination (e.g., Puttemans et al., 2005). Some tasks involve high motor control demands due to having to learn new spatial and temporal movement dynamics requiring adaptations to muscle recruitment and joint coordination (e.g., Pearce et al., 2000; Bezzola et al., 2011; Di Paola et al., 2013). Other tasks have involved playing musical instruments with differing temporal rhythms (e.g., Buccino et al., 2004; Herdener et al., 2010) while some tasks have low motor control demands associated with pressing sequences of keys in response to visual stimuli (e.g., Doyon et al., 1996; Verwey, 1999; Seidler et al., 2002; Abrahamse et al., 2013).

Variations in reported neural activity might also be explained by the execution strategy that is employed to perform the motor skill. Specifically, using their multiple representation

point of view (i.e., perceptual, central and motor representations), Verwey et al. (2015) argued that sequence performance can involve different execution modes. These researchers explicitly distinguish between a reaction mode, a central-symbolic mode, and a chunking mode (Figure 11.3, panels B and C). In line with many real-world tasks, individuals performing sequential keying tasks in the laboratory usually begin by reacting to fixed series of key-specific stimuli in the so-called reaction mode. Quite rapidly, associations develop at various processing levels that prime the ensuing response with reduced reliance on key-specific stimuli. With practice, spatial or verbal representations develop at the central-symbolic processing level that require cognitive processes to extract motor information. Finally, the development of tight associations between motor representations leads to the development of motor chunks that in the chunking mode can be used to rapidly execute movement sequences with little need for central-cognitive processing. Importantly, after substantial practice, these execution modes can be strategically applied and may even be concurrently active. Consequently, skilled performers can switch between different processing strategies with little or no measurable performance changes.

To resolve disagreement in neural changes associated with skill acquisition, some have proposed differentiating motor skills based on their function. Some skills place an emphasis on learning sequences based on highly practiced movement elements (Robertson, 2007). An example of these types of skills involve sequences of key presses, which is common in lab-based paradigms for sequence learning such as the serial reaction time (SRT; Nissen & Bullemer, 1987; Abrahamse & Noordzij, 2011) and the discrete sequence production (DSP; Verwey, 1999; Abrahamse et al., 2013) tasks as well as skills involving typing. Sequencing key presses contrasts skills that emphasize development of complex movement patterns requiring sensorimotor adaptation or coordination of multiple limbs. This contrast is important as motor skills might rely on different brain networks. Specifically, during later stages of learning, discrete sequence tasks have been argued to utilize a cortico-striatal network while sensorimotor tasks rely on a cortico-cerebellar network (Doyon & Ungerleider, 2002; Doyon et al., 2003). A meta-analysis conducted by Hardwick et al. (2013) which contrasted learning sequential (SRT variants) and sensorimotor skills found that both skill types share reliance on the dPMC, contralateral M1 and the primary sensorimotor zone (O'Reilly et al., 2010) of the right cerebellum (lobule VI). Acquisition of keying sequence variants was associated with activation of the preSMA and SMA along with superior parietal lobule, right lateral cerebellum and left thalamus. This pattern of activity reflects the involvement of reaction mode processes in early learning of keying sequences where selection of sequence elements is driven by visual stimuli (Abrahamse et al., 2010; Verwey et al., 2015; Verwey et al., 2018). Instead, sensorimotor task learning elicited activation of only the SMA along with S1 and the right vermis and left and right lateral cerebellum. This pattern demonstrates the increased complexity of motor commands that must be developed in acquisition of sensorimotor tasks (Hardwick et al., 2013). Similar to Hardwick et al. (2013), Laird et al. (2011) distinguished different motor skills when describing neural networks associated with motor skill performance. Skills that predominantly involve fixed simple movement sequences (e.g., typing) involve premotor and supplementary motor cortices. However, Laird et al. (2011) describes two additional neural networks for more complex movement types based on the locus of upper-limb control. Skills that predominantly involve sensorimotor adaptation to hand or finger movements (e.g., grasping) utilize a network consisting of M1, S1, and the cerebellum, due to high degree of error correction needed in fine control of so-called haptic skills. Prehension skills are more complex than haptic skills as they include arm movement control as when objects must be reached for prior to grasping them.

Accordingly, these more complex skills supplement the M1-S1-cerebellar network with medial superior parietal activity.

11.2.3 Brain activity underlying automated skill performance

Neuroimaging studies describing brain changes associated with motor skill learning illustrate neural adaptations that preceded skill automatization. Early experience in performing novel skills, relies heavily on activity in the anterior frontal lobe regions, which are associated with conscious attentional processes, error correction mechanisms, and the subjective experience of effortful performance. These regions are also associated with explicit forms of motor learning that are more resource demanding than implicit forms that do not require conscious awareness (Grafton et al., 1995; Doyon et al., 1996). However, most of this work has concentrated on the early stages of learning (see Lohse et al., 2014) in contrast to the automatic stage. Thus, much of what is currently understood about functional brain changes underlying skill automaticity is based on studies addressing learning, not automated performance. Only a few neuroimaging studies have directly assessed the neural correlates of skill automaticity based on dual-task interference assessment (Pashler, 1994; Ashby & Crossley, 2012).

In all, six neuroimaging studies have applied dual-task interference assessment to determine skill automaticity (Wu et al., 2004; Lehericy et al., 2005; Poldrack et al., 2005; Puttemans et al., 2005; Wu & Hallett, 2005; Wu et al., 2008). Five of these have evaluated automaticity of sequenced finger movements (Wu et al., 2004; Lehericy et al., 2005; Poldrack et al., 2005; Wu & Hallett, 2005; Wu et al., 2008) while Puttemans et al. (2005) evaluated automaticity of a complex bimanual coordination task involving wrist flexion and extension. Comparison of changes in neural activity from early to automatic stages, revealed a pattern similar to that observed in early to late learning comparisons (Lohse et al., 2014). Namely, automaticity, as assessed by the dual-task interference criteria, was associated with decreased activity in the DLPFC and premotor cortices (preSMA, vPMC), cerebellum and precuneus (see Figure 11.4). Similar regional activity in late learning (Lohse et al., 2014) and skill automaticity (Wu et al., 2004; Lehericy et al., 2005; Poldrack et al., 2005; Puttemans et al., 2005; Wu & Hallett, 2005; Wu et al., 2008) might give the impression that there is relatively little change in neural activity between late learning and automatic stages. However, regional activation in later learning and automaticity might be due to entirely different functional roles (Little et al., 2004). As such, similar patterns of regional activation might conceal ongoing neural changes that take place between late learning and automaticity.

 Insert Figure 11.4 About Here

Neuroimaging studies of automatic motor skill performance reported reduction in anterior cingulate cortex (ACC) activity from early to automatic skill performance stages. The ACC functions along with the DLPFC to control attention (Kondo et al., 2004) and is involved in error monitoring and correction during performance (Carter et al., 1998). To allow the acquisition of new movement patterns, the ACC is also thought to be involved in suppression of previously established movement patterns (Swinnen, 2002).

In contrast to previous reports of the importance of M1 activity for performing well-learned motor skills (Grafton et al., 1995; Hazeltine et al., 1997), Puttemans et al. (2005)

reported decreased M1 activity at the autonomous stage. This finding was consistent with decreased M1 activity in the late skill learning stage reported in a meta-analysis of neural changes across skill learning stages reported by Lohse et al. (2014). As discussed previously, differences in neural activity between studies might relate to different skill performance strategies (Verwey et al., 2015) or might relate to task specific motor control demands (Laird et al., 2011; Hardwick et al., 2013). Differences in performance strategies and motor control demands might engage functionally different cortico-striatal neural circuits (Doyon et al., 2002; Doyon et al., 2003) resulting in disparate changes in regional activity. For example, Lehericy et al. (2005) reported reduced activity in the cortico-striatal circuit but only in relation to premotor cortices and the dorsal putamen. In contrast, activity in the posterior putamen increased (Lehericy et al., 2005). The dorsal and posterior putamen have been differentiated based on their involvement in associative and sensorimotor forms of learning (Jueptner et al., 1997a; Lehericy et al., 2005; Florio et al., 2018). Connectivity between associative and premotor cortices (vPMC) and the dorsal striatum is thought to underlie associative learning while connectivity between premotor (dPMC), motor and sensory cortices and the posterior putamen regulates sensorimotor learning as well as production of well-learned skills (Lehericy et al., 2005; Yin & Knowlton, 2006; Wu et al., 2015; see Figure 11.5, panels A and B). There is some debate on how associative and sensorimotor learning processes occur. In contrast to a serial shift from associative to sensorimotor processes (Hikosaka et al., 1999; Floyer-Lea & Matthews, 2005; Poldrack et al., 2005; Yin et al., 2009; Lohse et al., 2014; Figure 11.5, panel C), others have argued that associative and sensorimotor processes run in parallel during motor skill learning (Thorn et al., 2010; Thorn & Graybiel, 2014; Kupferschmidt et al., 2017; Figure 11.5, panel D).

 Insert Figure 11.5 About Here

11.3 Expediting automaticity at the cost of learning: A cautionary tale from the contextual interference effect

A natural extension of the discussion so far is that automaticity results from exposure to considerable amounts of training and coincides with the development of expertise. As noted earlier this is typically manifest as significant improvements in performance, while also exhibiting an absence of secondary task interference and the development of a motor representation, motor chunks, that exhibit some rigidity in the manner in which they are used (see Sakai et al., 2004). One might assume then that training environments that quickly move individuals to display characteristics of automatic skilled performance would be desirable. Indeed, considerable experimental effort has been exerted to identify features of the training environment that might be modified in order to move the performer to a more automated behavior. One feature in particular that has attracted attention over the past 30 years, studied under the rubric of the contextual interference (CI) effect, focuses on how training schedules for a set of related motor skills influences skill learning outcomes. (Shea & Morgan, 1979; Magill & Hall, 1990; Brady, 1998; Brady, 2004).

During experiments addressing the impact of CI for learning, greater CI is often engineered by arranging training such that the learner executes a set of skills in an interleaved format. Interleaved training, as it is called, creates relatively high interference throughout training because of the rapid changes in task demands across training trials. Conversely,

repetitive training creates less interference because it entails executing the same skill repeatedly prior to the introduction of other skills that will be practiced later in training (see Figure 11.6, panel A). Repetitive training provides for very rapid gains in performance (see Figure 11.6, panel B). This initial practice benefit of repetitive training is very robust has been observed in a wide variety of laboratory tasks (Shea & Morgan, 1979; Wright et al., 2005; Pauwels et al., 2014) as well as applied situations (Goode & Magill, 1986; Smith & Davies, 1995; Ollis et al., 2005). In addition, the advantage of repetitive training for facilitating quick performance gains has been demonstrated for different subject populations (Del Rey, 1982; Porretta & O'Brien, 1991), as well as in the clinical domain (Adams & Page, 2000; Knock et al., 2000; Wambaugh et al., 2014).

 Insert Figure 11.6 About Here

11.3.1 Early performance automatization under repetitive training

Importantly, for the purpose of the present discussion, individuals that are trained in a repetitive rather than interleaved training environment not only reveal superior skilled performance much earlier in training but display characteristics of automated performance. For example, Li and Wright (2000) used a dual-task paradigm to pair a secondary choice reaction time (CRT) task that involved tone discrimination with the acquisition of a set of motor sequence skills acquired in either an interleaved or repetitive training format. During both training formats, the secondary CRT task was periodically presented shortly after the participant was informed about the particular motor sequence to be performed on the next trial presumably while the performer engaged in task preparation. Li and Wright hypothesized that the observed efficacy of repetitive training for skill acquisition would coincide with reduced attention demands reflected in lower dual-task cost relative to the alternative, interleaved training. The results supported this hypothesis indicating roughly 20% lower attention demand in conjunction with significantly greater performance improvement during repetitive as opposed to interleaved training. This finding was consistent with earlier reports for the need of much shorter inter-trial intervals during repetitive as opposed to interleaved training (see, Immink & Wright, 1998). Taken together, the implication of these data is that repetitive schedule can be used as an efficient format for training because performance improves at a relatively fast rate and at low cognitive cost.

It was proposed earlier that part of the reduction in attentional load during the learning of perceptual-motor skills was the development of units of action, referred to as motor chunks (Verwey, 1999; Verwey et al., 2015). This has been reported to involve the compilation of individual movement elements being compiled into motor sequence representation that allow a skill to be executed with little cognitive demand (Klapp, 1995; Sakai et al., 2004; Verwey et al., 2015). This is a central feature of the C-SMB (Verwey et al., 2015) described earlier in which the motor chunks developed from extended practice are executed by a motor rather than central (cognitive) processor. Thus, as sequential motor skills evolve with practice, the role of central-cognitive processing resources changes from selecting and initiating individual movements to selecting and initiating integrated movement patterns. This processing change would be responsible, at least in part, for the evolution of reduced attention demands reflected in limited interference with other tasks (Verwey et al., 2015). It is not surprising then that it has been

reported that individuals exposed to repetitive training exhibit characteristics of motor chunk development during the earliest phase of training. Wright et al. (2004) had individuals practice both simple and complex motor sequences in either a repetitive or interleaved training format across 4-days of practice. As expected, reaction time (RT) was initially longer when initiating the more complex sequences (Henry & Rogers, 1960; Klapp, 1995; Verwey, 1999). Participants assigned to interleaved training took a considerable portion of the four days of training to eventually initiate the more complex sequences with RT performance similar to that observed for the simpler sequence, indicative of motor chunk development. In contrast, for the individuals that experienced repetitive training, the RT did not differ as a function of sequence complexity from a very early stage in training, suggesting that integration of the individual movement elements in the more complex sequence had occurred affording faster initiation of the skill. Thus, a repetitive training format appears to be an effective training protocol since it is associated with characteristics previously ascribed to automated skill production while also associated with the rapid attainment of successful performance.

11.3.2 Performance automatization versus learning

Given this brief overview of the merits of repetitive training, one would be forgiven for assuming that this training approach should result in successful skill acquisition and as such should demand widespread acceptance and use. However, when addressing learning, a critical goal is the establishment of a “relatively permanent changes in the capability for skilled behaviour”, which is commonly assessed through the use of long-term performance evaluation (Schmidt & Lee, 2005, p. 302). This focus on long-term retention was more initially addressed as the performance-learning distinction (Salmoni et al., 1984) but has been formally revisited many times since (Schmidt & Bjork, 1992; Katak & Winstein, 2012). This distinction highlights the difference between transient influences on current behavior and those that reflect “relatively permanent” learning effects. Immediate performance during the early phase of skill acquisition is very likely influenced by any number of transient features such as the availability of rich sources of feedback, motivation, and/or attention (Katak & Winstein, 2012). To infer learning, it is argued that performance is assessed after sufficient time delays to allow temporary influences to dissipate. This is often accomplished in the motor neuroscience literature by the inclusion of retention tests after varying temporal delays (e.g., 24-hr, 7-days, or even months) after training has concluded.

The performance-learning distinction turns out to be critical when evaluating the CI effect. As detailed earlier, repetitive training results in very rapid, and in some cases large gains in performance beyond that observed from engaging in interleaved training. This benefit appears in part to be fostered by the development of motor chunks (Wright et al., 2004), which in turn, leads to reduced cognitive effort reflected in lower dual-task costs (Li & Wright, 2000). However, when delayed tests are administered, individuals exposed to repetitive training exhibit significant forgetting from the end of practice accompanied by the return of significant conscious effort. This is not the case for learners that encounter interleaved training. Sizeable demands are placed on attention throughout a significant portion of interleaved training (Li & Wright, 2000) which results in the development of resilient motor chunks that continue to be used up to 72-hrs after training supporting performance levels that are consistent with those observed at the end of training or in some cases slightly enhanced (Kim et al., 2018). Herein lies the cautionary note. While repetitive training affords rapid improvements in performance in addition to revealing characteristics of automaticity (i.e., reduced conscious contribution, rapid adoption of motor

representations), one would surely be less convinced of the effectiveness of this training format for facilitating learning in terms of long-term performance (see Figure 11.6, panel B).

11.3.3 Neural correlates of the CI effect

An examination of the neural adaptations that occur across both interleaved and repetitive forms of practice are informative and may provide some guidance in thinking about automaticity in the context of skill acquisition and long-term retention. Initial neurophysiologic evidence revealed that interleaved training participants maintained a constant level of activation within some motor planning regions while increasing the activity in other regions that have been reported to be central to improvement in motor sequence performance across practice. Such changes have been described in detail in earlier sections (see Floyer-Lea & Matthews, 2005; Doyon et al., 2009; Dayan & Cohen, 2011; Penhune & Steele, 2012; Hardwick et al., 2013). Specifically, dPMC, vPMC, preSMA and the SMA premotor areas exhibited a blood-oxygenated level dependent (BOLD) signal that was at least 50% greater later in practice than earlier, implying significant action preparation continued late into interleaved training (see Figure 11.6, panel C). The lateral premotor areas (dPMC, vPMC) have been recognized for the development of associations between arbitrary sensory stimuli and actions or the acquisition of novel stimulus-response rules which would certainly be an early challenge when learning a new set of motor sequences. The medial premotor areas, including preSMA and SMA, have been associated with selecting, retrieving, and organizing subsets or whole movement sequences at different points of skill acquisition (Gerloff et al., 1997; Verwey et al., 2002; Nachev et al., 2008). Heightened recruitment of the medial premotor areas is consistent with the claim that interleaved as opposed to repetitive training encourages the development and use of motor chunks (Immink & Wright, 2001; Wright et al., 2004; Abrahamse et al., 2013; Verwey et al., 2015). Moreover, interleaved training results in a bilateral increase in activation in angular gyrus, superior parietal lobe, inferior temporal lobe, and precuneus with extended practice (Wymbs & Grafton, 2009; see Figure 11.6, panel C). These neural areas have been associated with the construction of novel visual-spatial mappings that would presumably be important for the acquisition of motor sequences (Hikosaka et al., 1999; Hikosaka et al., 2002).

In the case of repetitive training, Wymbs and Grafton (2009) reported more limited activation as fewer regions were recruited for a shorter proportion of the total training duration. The behavioral findings from Immink and Wright (1998) suggest that this limited activation reflects disengagement from response preparation early in repetitive training. Consequently, there is inadequate development of motor response information storage and retrieval processes needed to support long-term performance. Neurophysiological and behavioral findings provide an account for the reduced attentional costs observed early in repetitive training by Li and Wright (2000). While reduced attentional costs could be interpreted as reflecting a form of skill automaticity, it is clear that this form of automaticity has come at a significant cost to learning. The premature automaticity afforded by repetitive practice will eventually require greater investment of resources needed to perform in the long-term. For example, during delayed retention test, Lin et al. (2011) reported more extensive recruitment of prefrontal, premotor, and parietal regions by individuals trained in the repetitive format than those trained under the interleaved format. Thus, in contrast to repetitive practice, interleaved practice appears to have exhibited greater automaticity during delayed test performance and this advantage may be associated with the diverse set of other neural adaptations that are instigated by training under

high contextual interference. For example, Lin et al. (2011) revealed heightened M1 excitability long after interleaved training was complete (i.e., for up to 72-hr) which has been argued to be a relatively permanent neuroplastic change that enhances memory retrieval possibly via an impact of post-practice consolidation (see Breton & Robertson, 2014; Tunovic et al., 2014). A persistent change in M1 excitability resulting from interleaved training appears to occur concomitant with changes in resting state connectivity between the premotor cortex and other critical neural regions involved in consolidation of motor memories such as dorsolateral prefrontal cortex, inferior parietal lobule, hippocampus, putamen, and cerebellum.

11.4 Summary

The aim of this chapter was to describe the neural changes that afford the progression of skill performance from an early learning stage associated with slow, inefficient performance to the automatic stage, which is characterized by speeded performance and the absence of central resource demands. Based on the neuroimaging findings reviewed here, one consistent change in neural activation associated with achieving skill automaticity occurs in an anterior to posterior direction within the frontal lobe. Specifically, while early performance relies on activity in anterior frontal regions such as the DLPFC along with premotor cortices (vPMC, preSMA, SMA) and M1, skill automaticity only elicits sustained activation in most posterior region of the frontal lobe, the M1 (Wu et al., 2004; Lehericy et al., 2005; Poldrack et al., 2005; Puttemans et al., 2005; Wu & Hallett, 2005; Wu et al., 2008). The anterior-posterior frontal lobe axis has been described as representing an associative-motor hierarchy for movement preparation and control (Koechlin et al., 2003; Fuster, 2004). Thus, the anterior to posterior reduction in neural activity associated with automaticity can be interpreted as reflecting reduced dependence on associative processes. Within the motor levels of the hierarchy, reduced PMC and SMA activity also indicates changes in how automated skills are prepared.

The neural changes underlying skill automaticity can be further understood through the C-SMB cognitive framework (Verwey et al., 2015). Early learning activation of anterior frontal regions suggests initial reliance associative processes that utilize central-symbolic representations to prepare the response. Reliance on the central processor to prepare the response is slow and imparts high demands on limited central resources. Finally, exposure to extensive practice is central to most accounts of the attainment of automaticity. In the present chapter we highlighted the importance of designing practice that is geared toward recruiting the network of neural regions associated with early skill learning to ensure that the acquired sequential motor behavior can then be executed relatively attention-free for an extended period of time.

FIGURE 11.1

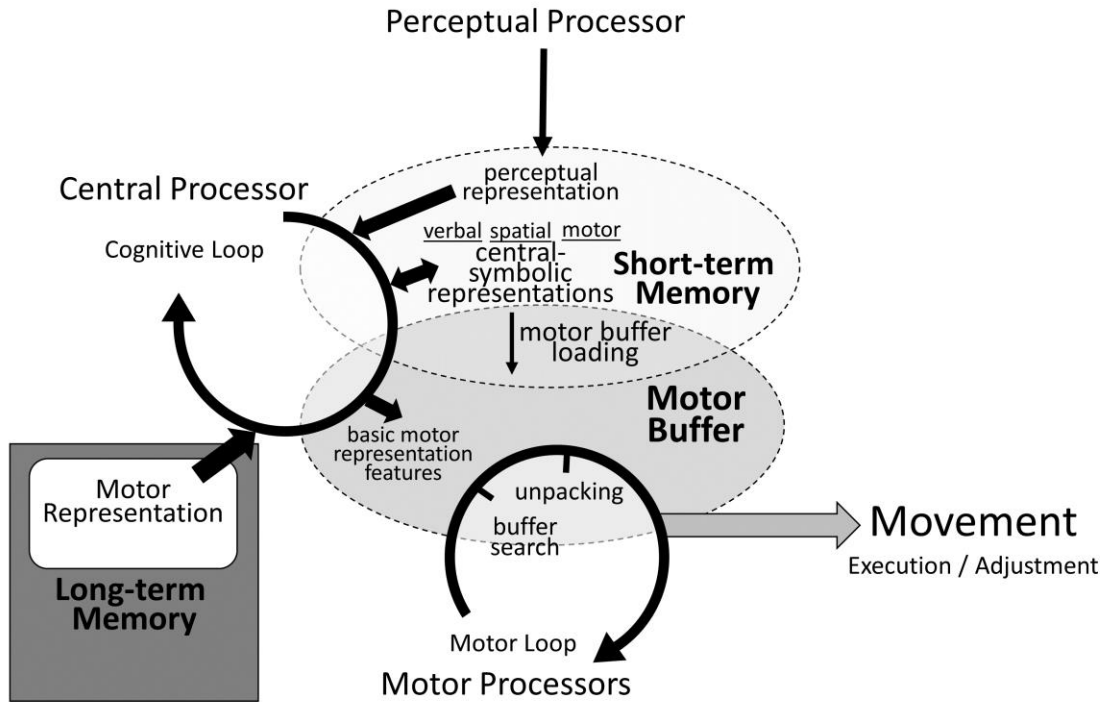


Figure 11.1. Key components of cognitive framework of sequential motor behavior (C-SMB; Verwey et al., 2015). This model describes the collaboration of perceptual, central, and motor processors in using (spatial, verbal) central-symbolic, and motor representations to execute motor sequences.

FIGURE 11.2

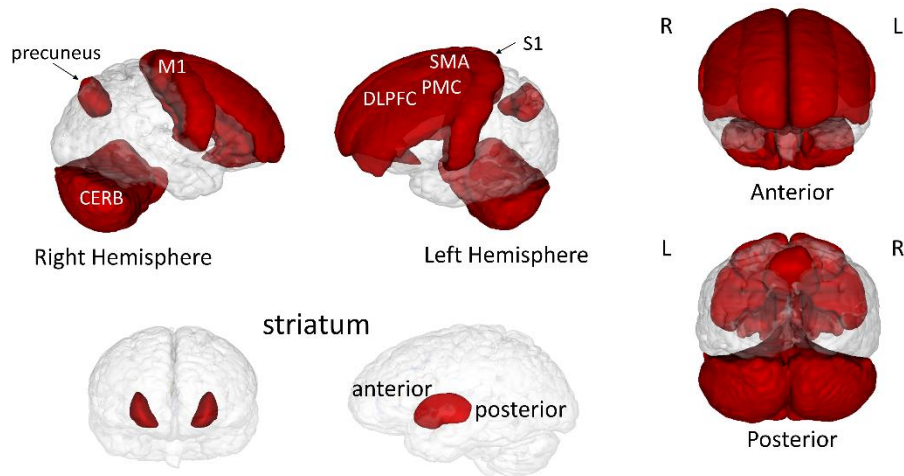


Figure 11.2. Key regions associated with early motor skill practice. M1 = primary motor cortex, CERB = cerebellum, DLPFC = dorsolateral prefrontal cortex, SMA = supplementary motor area (proper and preSMA), PMC = premotor cortex, S1 = somatosensory cortex.

FIGURE 11.3

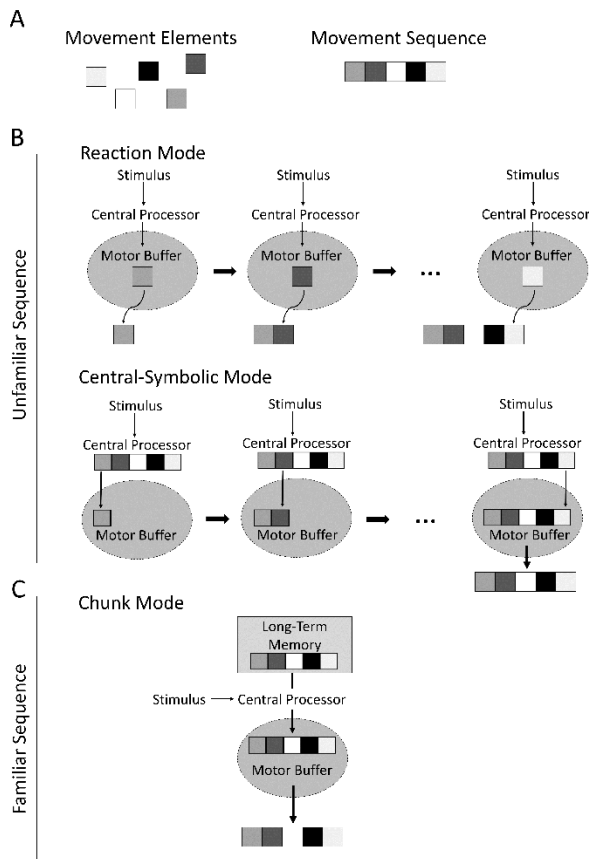


Figure 11.3. The cognitive framework for sequential motor behavior (C-SMB; Verwey et al., 2015) describes how movement elements can be organized into a target motor sequence (panel A). Initially, performance of an unfamiliar sequence (panel B) occurs via a reaction mode, where the target is reproduced based on presentation of a fixed series of movement element-specific stimuli. With practice, central-symbolic representations of the unfamiliar target sequence are developed allowing for motor buffer loading of the target sequence based on iterative translation of the symbolic representation. Both reaction and central-symbolic modes are relatively slow and place high demands on cognitive resources. Further practice allows for familiar sequences to be represented in long-term memory as an internal model of the target sequence (panel C). This enables the sequence to be performed via a chunk mode. The chunk mode is relatively fast and incurs little cognitive resource costs due to reduced central-cognitive processing requirements.

FIGURE 11.4

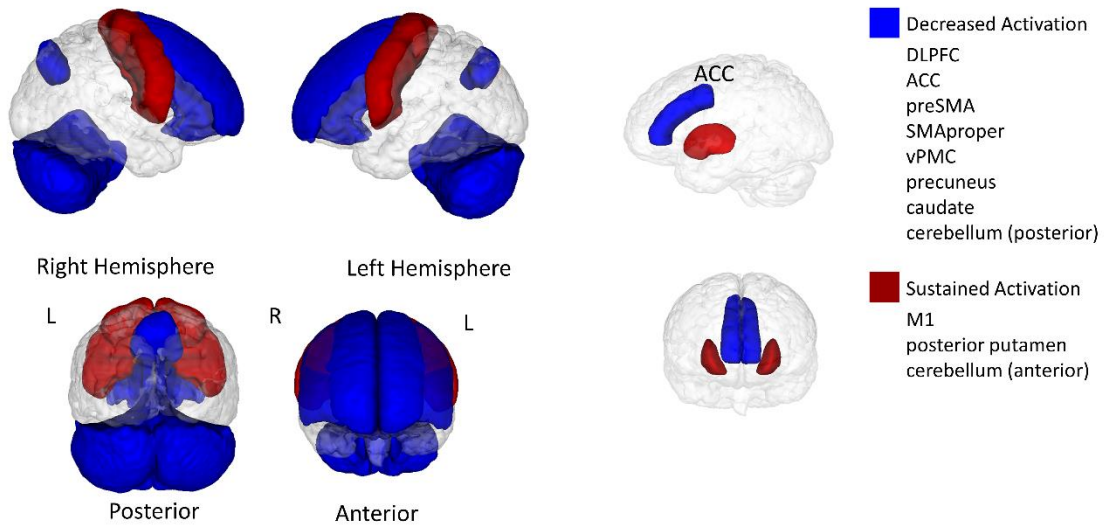


Figure 11.4. Decreased and sustained functional region activation when early and automatic stages of skill learning are contrasted. DLPFC = dorsolateral prefrontal cortex, ACC = anterior cingulate cortex, SMA = supplementary motor area (proper and preSMA), vPMC = ventral premotor cortex, M1 = primary motor cortex.

FIGURE 11.5

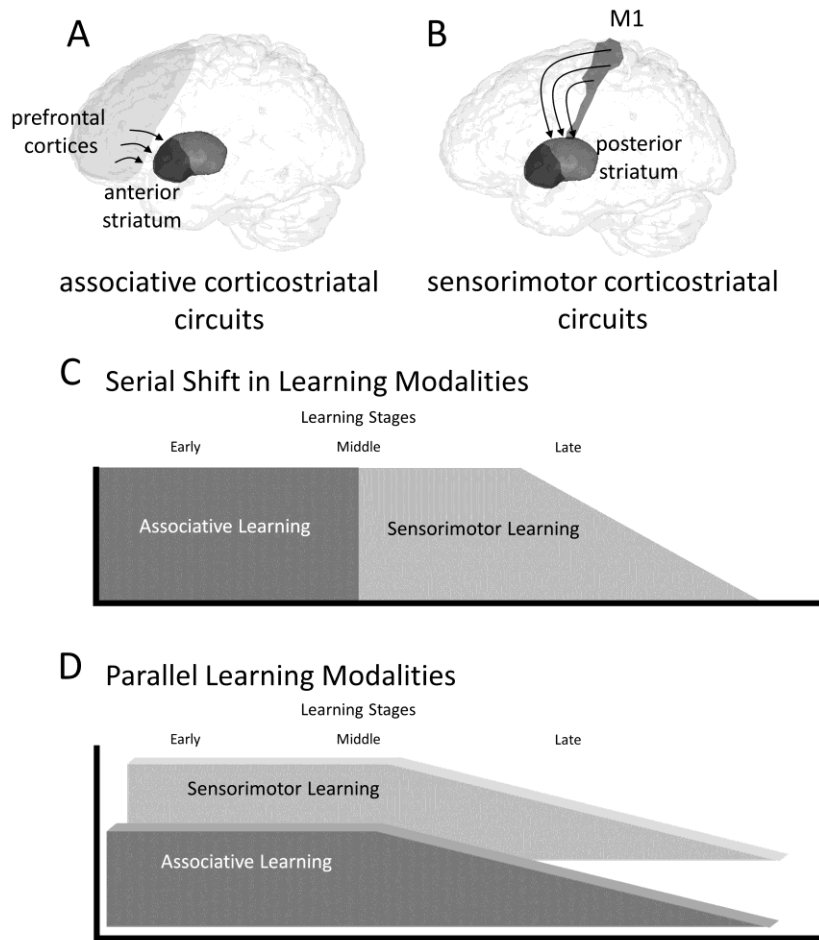


Figure 11.5. The dorsal and posterior putamen are functionally differentiated according to associative and sensorimotor forms of learning. Associative learning (panel A) is based on circuits between the prefrontal cortices and the dorsal striatum while sensorimotor learning (panel B) is based on circuits between the motor cortices and the posterior putamen. Motor skill learning has been described as involving a serial shift from associative to sensorimotor processes (panel C) or alternatively, parallel implementation of associative and sensorimotor processes (panel D).

FIGURE 11.6

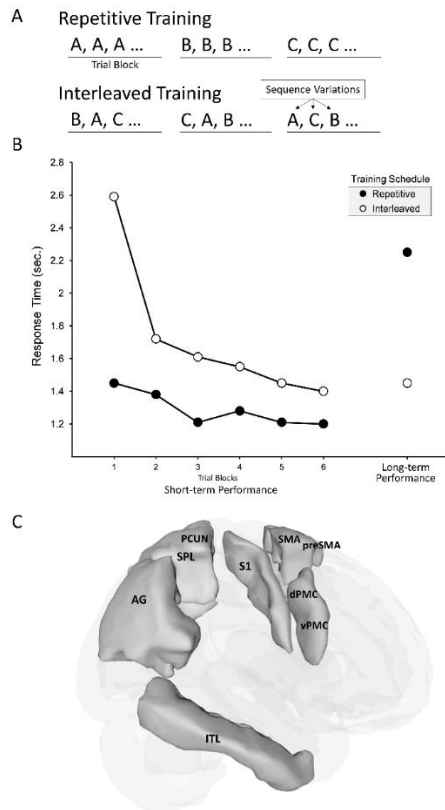


Figure 11.6. Under the contextual interference (CI) effect, practice scheduling of motor sequence variations under repetitive and interleaved schedules (panel A) results in distinct short-term and long-term performance profiles (panel B) as well as differences in neural region recruitment (panel C). As illustrated in panel B, repetitive training affords short-term performance gains but then results in long-term performance costs, particularly when long-term performance is tested under interleaved schedules (data is based on the seminal study by Shea & Morgan, 1979). Panel C illustrates neural regions that have been associated with the CI effect. There is reduced recruitment of these regions under repetitive training in comparison to interleaved training. However, when long-term performance is tested following repetitive training, these neural regions exhibit increased activity when compared to those previously exposed to interleaved training. ITL = inferior temporal lobe, AG = angular gyrus, SPL = superior parietal lobe, PCUN = precuneus, S1 = somatosensory cortex, SMA = supplementary motor area proper, preSMA = pre supplementary motor area, dPMC = dorsal premotor cortex, vPMC = ventral premotor cortex.

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