Neurocognitive Contributions to Motor Skill Learning: The Role of Working Memory

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Abstract

Researchers have begun to delineate the precise nature and neural correlates of the cognitive processes that contribute to motor skill learning. Here, we review recent work from our laboratory designed to further understand the neurocognitive mechanisms of skill acquisition. We have demonstrated an important role for spatial working memory in two different types of motor skill learning, sensorimotor adaptation and motor sequence learning. We have shown that individual differences in spatial working memory capacity predict the rate of motor learning for both sensorimotor adaptation and motor sequence learning. We have also reported neural overlap between a spatial working memory task and the early, but not late, stages of adaptation, particularly in the right dorsolateral prefrontal cortex and bilateral inferior parietal lobules. We propose that spatial working memory is relied upon for processing motor error information to update motor control for subsequent actions. Further, we suggest that working memory is relied upon during learning new action sequences for chunking individual action elements together.

Introduction

We have ample opportunities as adults to learn new motor skills, whether it is for work or leisure, or re-learning of a skill during rehabilitative training following an injury. Thus it is perhaps not surprising that motor neuroscientists devote a substantial amount of effort to understanding the neurocognitive processes of motor skill learning. Early neuroscience experiments of human skill learning focused predominantly on motor cortical plasticity (Karni et al., 1995; Grafton et al., 1992). More recent studies have shown that cognitive processes such as working memory (Anguera et al., 2010) and error detection (Anguera et al., 2009) play a role in motor skill learning, particularly early in the learning process. In the current review we provide an overview of the literature investigating time varying contributions of cognitive processes to motor skill learning and their neural substrates, with a particular emphasis on the role of working memory in the early stages of learning.

Skill acquisition (used interchangeably with the term "motor learning" in this review) has been defined as "…a set of processes associated with practice or experience leading to

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relatively permanent changes in the capability for responding" (Schmidt 1976). This review addresses cognitive contributions to two specific categories of skill acquisition: sensorimotor adaptation and sequence learning. In sensorimotor adaptation paradigms, participants modify movements to adjust to changes in either sensory input or motor output characteristics. A real-world example is learning to drive a new car; the magnitude of vehicle movement in response to the amount of wheel turn and accelerator depression varies across vehicles. Thus, the driver must learn the new mapping between his or her actions and the resulting vehicle movements. Another example of sensorimotor adaptation is learning the relationship between the size and speed of hand movements of the mouse and cursor movements on the computer display screen. Conversely, motor sequence learning refers to the progressive association between isolated elements of movement, eventually allowing for a multi-element sequence to be performed quickly. Real-world examples include learning to dial a new phone number or rehearsing the multiple components of a tennis serve.

In my recent work, I have obtained behavioral and neural evidence that working memory plays a role in the early stages of both visuomotor adaptation and motor sequence learning (Anguera et al., 2010; Bo & Seidler 2009; Seidler et al., in press). Working memory refers to the processes used for temporarily storing and manipulating information in the mind (Baddeley 1986; Miyake & Shah 1999). Dissociated processing for spatial and verbal information was proposed by Baddeley and Hitch in their classic model of working memory (Baddeley & Hitch 1974). Current views suggest that working memory may not be as process-pure as once thought (Cowan 1995; Cowan 2005; Jonides, Lewis et al. 2008), but the idea of separate modules for processing different types of information still holds (Goldman-Rakic 1987) (Shah & Miyake 1996; Smith, Jonides et al. 1996) (Volle, Kinkingnéhun et al. 2008). Variation exists in the number of items that individuals can hold and operate upon in working memory (cf. Vogel & Machizawa 2004), making it particularly amenable to individual differences research approaches. For example, individual differences in working memory capacity have been found to be predictive of learning categorization tasks and math problem solving (Beilock & Carr 2005; Decaro et al., 2008). Inter-individual variation in performance is often treated as noise, with measures averaged across participants to wash out these effects. However, the study of individual differences in brain structure, function and performance is becoming more widely recognized as a productive approach for understanding human behavior (Kanai & Rees, 2011). The work reviewed here relies on such approaches in an effort to determine how individual variations in cognitive capacity affect skill acquisition.

Working Memory Contributions to Visuomotor Adaptation

Visuomotor adaptation involves the recalibration of a well-learned spatial-motor association. The study of motor performance under transformed spatial mappings spans over one hundred years. Helmholtz (1866) originally used prisms to invert the visual world to study adaptation, while more recent investigations make use of computer displays to transform visual feedback of movement (Cunningham, 1989; Ghilardi et al., 1995; Krakauer et al., 2000; Seidler et al., 2006). These studies have demonstrated that sensorimotor adaptation occurs when movements are actively made in the new environment, with updated visuomotor mappings believed to be stored as an internal model within the cerebellum (Imamizu et al., 2000, 2003; Wolpert & Miall, 1996; Shadmehr & Mussa-Ivaldi, 1994; Wolpert & Ghahramani, 2000).

Visuomotor adaptation clearly involves sensorimotor processes, but whether or not cognitive strategies play a role remains a topic of debate. Mazzoni and Krakauer (2006) demonstrated that explicit cognitive strategies were unconsciously overridden during the adaptation process. That is, when participants were given instructions to aim at a neighboring target to

counteract an applied visual feedback rotation, they still made implicit performance adjustments as well. Thus, the combination of the explicitly instructed strategy and implicit adaptive processes resulted in over-correction for the rotation. Recent work by Taylor and Ivry (2011) demonstrates, however, that, with extensive practice, participants can flexibly combine such instructed strategies with implicit adaptive processes to optimize performance. Patients with cerebellar damage are able to utilize strategies without interference from implicit processes during adaptation (Taylor et al., 2010), suggesting that differing neural pathways underlie the two components. We have also shown that participants can make use of explicit instruction to virtually eliminate performance errors during the adaptation process, but these individuals show less adaptive recalibration than those that proceed under purely implicit conditions (Benson et al., 2011). Regardless of whether sensorimotor adaptation is predominately implicit, cognitive processes may still play a role. For example, it has been shown that motor sequence learning can occur in the absence of explicit awareness, yet learning is still degraded by the performance of a secondary, attention distracting task (Hartman et al., 1989). Similar processes may be at play in visuomotor adaptation, with learning in the absence of awareness reliant on cognitive processes.

There is evidence to support that visuomotor adaptation is cognitively demanding (Eversheim & Bock, 2001; Taylor & Thoroughman, 2007, 2008). For example, Eversheim and Bock (2001) used dual task paradigms to demonstrate that cognitive resources are engaged in a time-dependent fashion during adaptation: resources related to spatial transformations and attention were highest in demand early in adaptation, while those related to movement preparation were more in demand later in learning. Subsequent studies also describe the adaptive process as having two potentially overlapping stages: a cognitively driven "fast/early learning" stage characterized by rapid performance improvements and an autonomous "slow/late learning" stage with smaller performance gains evolving over longer time periods (Smith et al., 2006; Keisler & Shadmehr, 2010).

Stage theories have also been incorporated into studies of the neural bases of motor learning, which posit that there are distinct neural correlates associated with each stage (early versus late; Doyon et al., 2003; Willingham, 1998). For example, PET studies of force-field adaptation demonstrate bilateral activation at the dorsolateral prefrontal cortex (DLPFC) and parietal regions early in learning, while later in learning activation shifts towards left premotor and right cerebellar regions (Krebs et al., 1998; Shadmehr & Holcomb, 1997). Similarly, fMRI studies of visuomotor adaptation have reported activation in the right DLPFC, basal ganglia, premotor, and parietal regions during the early stages of adaptation (Anguera et al., 2007; Hikosaka et al., 1999; Inoue et al., 1997; Sakai et al., 1998; Seidler et al., 2006; Toni et al., 1998), with late learning activation observed at the cerebellum, visual, parietal and temporal cortices (Graydon et al., 2005; Imamizu et al., 2000; Inoue et al., 2000; Krakauer et al., 2004; Miall et al., 2001).

One cognitive process that may play a role in visuomotor adaptation is spatial working memory. Baddeley (1986) proposed the existence of a working memory subsystem specialized for processing visuo-spatial information ("a visuo-spatial sketch pad"). Revised versions of this model (Logie, 1995; Cornoldi & Vecchi, 2003) suggest working memory tasks which require information manipulation ('active'; i.e. mental rotation) have greater processing demands than 'passive' storage tasks (Cornoldi & Vecchi, 2003). Interestingly, a number of imaging studies targeting the neural correlates of spatial working memory have shown involvement of the right prefrontal cortex, specifically the right DLPFC, along with the right premotor and parietal cortices (Courtney et al., 1998; Jonides et al., 1993; McCarthy et al., 1994; McCarthy et al., 1996; Reuter-Lorenz et al., 2000), areas which overlap with the regions engaged during the early stages of visuomotor adaptation. Given that increased cognitive distraction has been shown to compromise motor adaptation (Taylor

& Thoroughman, 2007, 2008), the contributions of 'active' spatial working memory may be important for visuomotor adaptation.

In our recent work, we investigated whether individual differences in spatial working memory capacity relate to the speed of adaptive performance changes in a visuomotor adaptation paradigm (Anguera et al., 2010). We investigated the contribution of cognitive processes to sensorimotor adaptation by administering a battery of neuropsychological assessments which measured abilities in attention, processing speed, verbal and spatial working memory to 18 participants (average age 21.1 years). We then had them perform a manual visuomotor adaptation task and a spatial working memory task in a 3.0 T MRI scanner. Participants adapted manual aiming joystick movements to a 30° clockwise rotation of the visual feedback display about the central start location. We divided the learning curve into "early" and "late" components for each individual. We found that performance on the card rotation task (Ekstrome et al., 1976), a measure of spatial working memory, was correlated with the rate of early, but not late, learning on the visuomotor adaptation task (R = .57, p < .05, see Figure 1). The card rotation task requires participants to maintain and manipulate shapes in working memory, and then decide whether a given shape matches a previously presented target. Importantly, there were no correlations between measures of verbal working memory and either early or late learning, suggesting this effect was specific to the early period and spatial working memory. Moreover, the neural correlates of early learning overlapped with those that participants engaged when performing a spatial working memory task, notably in the right dorsolateral prefrontal cortex and in the bilateral inferior parietal lobules (see Figure 1). In addition, there was no neural overlap between the late stages of adaptation and spatial working memory. Given that individual differences in spatial working memory were predictive of the rate of early, but not late adaptation, these findings suggest a specific reliance on spatial working memory for the early stages of visuomotor adaptation.

In a follow up study with older adults we obtained further support for the role of spatial working memory in visuomotor adaptation (Anguera et al., 2011). It is known that older adults exhibit deficits in visuomotor adaptation (Seidler, 2006; Bock, 2005) and have reduced spatial working memory performance (cf. Reuter-Lorenz et al., 2001; Hale et al., 2011; Piefke et al., 2010). We evaluated whether reduced working memory contributes to age declines in adaptation using an individual differences approach. Across 18 older adult participants (average age 71.4 years), we observed a lack of correlation between the rate of early adaptation and spatial working memory performance. These older adults exhibited similar brain activation patterns for performance of a spatial working memory task as young adults, including engagement of the right DLPFC and bilateral inferior parietal lobules. However, when we used the spatial working memory activation as a limiting mask, young adults showed neural activation that overlapped with the early adaptation period as described above (Anguera et al., 2010), whereas older adults did not (Anguera et al., 2011). Furthermore, a partial correlation controlling for age revealed that the rate of early adaptation correlated with the amount of activation at the right DLPFC, a structure known to play a role in spatial working memory. These findings suggest that a failure to effectively engage spatial working memory processes and the right DLPFC during learning contributes to age-related deficits in visuomotor adaptation. Moreover, they provide additional support for the important role that spatial working memory plays in the early phases of visuomotor adaptation.

If spatial working memory plays a role in motor learning, it stands to reason that augmenting working memory via training (Dahlin et al., 2008; Jaeggi et al., 2010) or degrading it via process-specific fatigue (Persson et al., 2007) would either boost or impair skill learning, respectively. We recently investigated this in two experiments (Anguera et al., in press). In

the first experiment, we selectively fatigued spatial working memory by having participants perform a demanding task for approximately 20 minutes. Spatial working memory performance was impaired as a result, but more general function was not, as speed of processing was not affected. Participants that showed the greatest working memory fatigue effects exhibited the slowest rate of learning on a subsequent visuomotor adaptation task, further supporting the importance of this process in skill learning. In contrast, a group of participants that performed an n-back training protocol (Jaeggi et al., 2010) over five weeks exhibited improvements in working memory relative to a control group but did not demonstrate transfer to faster visuomotor adaptation. Thus it appears that working memory capacity is not the rate limiting factor for visuomotor adaptation, at least in young adults.

We have found that individual differences in spatial working memory capacity and DLPFC engagement explain variations in the rate of learning. However, it is likely that other cognitive processes play an important role in motor learning as well. That is, although there is a significant correlation between spatial working memory performance and the rate of learning, the spread of points around the regression line in Figure 1 indicates that other factors contribute to learning rate. One likely process is performance monitoring, which has been associated with activity in the anterior cingulate cortex (ACC) in cognitive studies (Carter, Braver et al. 1998; Botvinick, Nystrom et al. 1999). Work on this topic has shown that performance errors-- or even an increased potential to commit errors--elicit an event related potential termed "event-related negativity", or ERN. Whereas these studies all evaluated errors on discrete, "yes/no" button press response tasks, we recently assessed whether this activity is sensitive to the magnitude of motor errors made during a sensorimotor adaptation task (Anguera et al., 2009). Forty individuals (average age 22.8 years) adapted manual aiming movements under either a small (30°, N = 20 participants) or large (45°, N = 20 participants) clockwise rotation of the visual feedback display. EEG waveforms from large error trials were significantly different from those of small error trials (main effect of error magnitude $P < .001$). That is, the observed ERP component reflected differences in error magnitude, with the amount of activity corresponding to the size of the error experienced (Anguera et al., 2009). The waveforms also changed as a function of practice as early adaptation waveforms were larger than late adaptation waveforms. These data help to elucidate the role of the ACC during motor learning, which is typically activated in the early stages of sensorimotor adaptation (Seidler, Noll et al. 2006; Anguera et al., 2007; Contreras-Vidal & Kerick 2004).

We have developed a model of how spatial working memory is used during visuomotor adaptation based on our recent findings (Anguera et al., 2010; Anguera et al., 2009). Error information for a single aiming movement is processed late in the trial and during the intertrial interval. We propose that motor error information is loaded into spatial working memory during this timeframe to update the motor plan accordingly for subsequent actions (Seidler et al., in press). It remains yet to be confirmed, however, whether spatial working memory is relied upon for within-trial corrective submovements, or rather is relied upon for corrections made from one trial to the next, which is a reflection of visuomotor adaptation. These questions could be investigated for example with protocols that do not allow participants to make within-trial corrections, and by having participants perform precisely timed secondary tasks that interfere with working memory processes to examine the impact on learning rates.

Working Memory Contributions to Motor Sequence Learning

The ability to learn new action sequences is fundamental for everyday motor behaviors such as typing, playing a musical instrument, or participating in sport. Motor sequence learning is known to be affected by key task parameters such as sequence length (Turcotte et al. 2005;

Verwey 2001), rate (Bove et al., 2007) and complexity (Howard et al. 2004), and whether the sequence is acquired implicitly or explicitly (Brown & Robertson 2007; Moisello et al., 2011). A number of studies have reported that motor sequence learning is supported by activation in primary motor cortex, supplementary motor cortex, premotor cortex, dorsolateral prefrontal cortex, parietal cortex, and the basal ganglia (Ghilardi, Ghez et al. 2000) (Hikosaka, Nakahara et al. 1999) (Jueptner, Stephan et al. 1997a; Jueptner, Frith et al. 1997b) (Seidler, Purushotham et al. 2005), (Seidler, Purushotham et al. 2002), with activation in these areas shifting across the time course of learning (cf. Ashe et al., 2006).

Lashley (1951) first proposed that action sequences do not need to be triggered element by element but rather can be preplanned in advance as a "chunk". Such grouping of action elements together may rely on cognitive processes such as working memory. Preliminary support for this notion comes from a study by Pascual-Leone et al. (1996) in which it was reported that transcranial magnetic stimulation (TMS) applied to the contralateral DLPFC, a structure involved in working memory (Jonides et al. 1993), markedly impairs the ability to learn a sequence of finger movements. In another TMS study,Robertson et al. (2001) reported that repetitive inhibitory TMS applied to the DLPFC disrupted sequence learning only when responses were cued by the spatial location of stimuli. These authors suggest that the role played by the DLPFC in sequence learning is exclusively related to the processing of spatial cues in working memory.

Conceptual models of sequence learning have also supported the importance of cognitive processes (Hikosaka 2002; Verwey 2001). In particular, Verwey (1996, 2001) has proposed that motor sequence learning includes two components: buffer loading, and a dual-processor. Buffer loading refers to a kind of short term memory that allows sequence chunks to be programmed in advance of their execution. The dual processor comprises a cognitive and a motor processor (Verwey 2001). Participants rely on the cognitive processor to select individual sequence elements one by one when learning a new sequence, resulting in slow execution speeds. The learning process involves forming a motor chunk representation, which can be selected by the cognitive processor while the motor processor is running in parallel to execute the sequence. Evidence for chunk breakpoints in the sequence is seen as an uneven distribution of the timing between each movement element following practice (Shea et al. 2006; Verwey 1996, 2001). Longer inter-response times between elements represent the division points between chunks, whereas shorter inter-response times imply strong associations within each chunk.

We have recently investigated contributions of working memory to the formation of motor chunks during explicit sequence learning using an individual differences approach (Bo & Seidler 2009). Twenty-five participants (average age 20.9 years) performed a visuospatial working memory task (a modified version of Luck & Vogel's (1997) change detection test) and learned a sequence of finger movements. We examined whether individual differences in working memory abilities relate to learning new motor sequences under explicit (instructed) conditions. Consistent with the model proposed by Verwey (2001), these participants developed an unevenly distributed temporal pattern (i.e. clear chunks) when learning the sequence. In addition, we found that visuospatial working memory capacity correlated with both the rate of early motor sequence learning and the chunking pattern observed in the learned sequence (see Figure 2). It is interesting to note that most of the participants (20 out of 25) created chunks of three or four button presses, given that recent estimates of working memory capacity in the visual and verbal domains is approximately four items (Cowan 2001; Jonides et al., 2008; Luck & Vogel 1997; Vogel & Machizawa 2004). Thus, we found that individual differences in short-term visuospatial working memory capacity predict the temporal structure of explicitly acquired motor sequences.

We reported further support for the contributions of working memory to motor sequence learning in a follow up study that we conducted with older adults (32 participants, average age of 70.6 years; Bo et al., 2009). Although normal aging does not appear to affect the acquisition of relatively simple motor sequences (e.g., Frensch & Miner 1994; Howard & Howard 1989; Seidler 2006), numerous studies have reported a decline in the ability of older adults to learn action sequences with complex structure under both implicit and explicit learning conditions (e.g., Curran 1997; Howard et al. 2004; Shea et al. 2006). Aging has a detrimental impact on many cognitive functions, including working memory (e.g., Reuter-Lorenz et al., 2000) and temporal processing (Rakitin & Malapani 2008; Rakitin et al., 2005; Vanneste et al., 2001). Therefore, in a design parallel to that described above (Bo & Seidler, 2009), we examined whether age-related declines in explicit motor sequence learning were related to individual differences in cognitive declines, particularly in terms of visuospatial working memory and temporal control (Bo et al., 2009). We found that older adults exhibited a correlation between visuospatial working-memory capacity and motor sequence chunk length, as we observed previously in young adults. In addition, older adults exhibited an overall reduction in both working memory capacity and motor chunk length compared to those of young adults. However, visuospatial working-memory capacity did not correlate with the rate of learning in older adults (Bo et al., 2009). These results indicate that working memory decline contributes to age differences in explicit motor sequence learning, and that individuals with poorer working memory have the greatest declines in sequence learning.

Previous work suggests that learning action sequences even under purely implicit conditions can be cognitively demanding. For example, Frensch and Miner (1994) found that verbal working memory performance is correlated with the magnitude of implicit sequence learning under dual task conditions. We have also recently shown that visuospatial working memory capacity is predictive of the rate of implicit performance change during the alternating serial reaction time sequence learning task (Bo et al., in press). Twenty individuals (average age 20.1 years old) performed a motor sequence learning task under implicit conditions, as well as verbal and visuospatial working memory tasks. Variations in performance across individuals on the visuospatial working memory task correlated with the rate of performance change during sequence practice. Thus it appears that working memory plays a role in motor sequence learning even when participants do not have explicit awareness of the learning process. Of interest for rehabilitation approaches, recent work has shown that patients with subcortical stroke continue to engage the dorsolateral prefrontal cortex even late in the process of implicit sequence learning (Meehan et al., 2011), suggesting that they may be relying on working memory for motor performance of even highly practiced actions.

Similar to Verwey's model of sequence learning (1996, 2001), we propose that working memory is relied upon for the progressive association of neighboring action elements into discrete chunks during explicit sequence learning (Bo & Seidler, 2009). It is not clear whether the same mechanisms are at play during implicit sequence acquisition, since evidence for grouping of elements into chunks has been consistently reported for explicit but not implicit sequence learning (Kennerley et al., 2004; Shea et al., 2006; Verwey 1996). Further investigation is needed to clarify this issue.

Temporal processing is another cognitive ability that has been proposed to underlie sequence acquisition (Ashe et al., 2006). Ivry and colleagues have proposed that a common timing mechanism underlies various timing tasks such as perception and motor production (Ivry & Hazeltine 1995). Such superordinate temporal control may act as a building block for a wide range of motor tasks that exhibit temporal structure. Brain imaging studies have shown that the DLPFC, inferior prefrontal cortices, presupplementary motor area (pre-SMA), supplementary motor area (SMA), and cerebellum may act as a general timing

network (Maquet et al., 1996; Smith et al., 2003). These areas are also engaged during motor sequence learning (Boyer et al., 2005; Doyon et al., 2002; Kennerley et al., 2004), making it plausible that temporal control processes contribute to motor sequence chunking patterns. Moreover, Kennerley et al. (2004) have shown that low frequency repetitive TMS to the pre-SMA disrupts the chunking pattern of acquired motor sequences. Thus, in addition to working memory, we have also investigated whether temporal processing plays a role in the temporal chunk patterns that are formed during explicit sequence learning (Bo & Seidler 2009). We found that temporal ability did not correlate with indices of sequence learning, however. Therefore, it seems that temporal processing does not play a role in sequence learning, at least within the context of the paradigms that we have used which do not require participants to learn sequences with an imposed temporal rhythm.

Conclusions and Future Directions

In our recent work we have demonstrated an important role for spatial working memory in the two major types of motor skill learning: sensorimotor adaptation and motor sequence learning. We found that an individual's spatial working memory performance is predictive of the rate of motor learning for sensorimotor adaptation and both explicit and implicit sequence learning. We also observed significant neural overlap between a spatial working memory task and the early, but not late, stages of adaptation, with activation in the right DLPFC correlated with early learning rate. In contrast, despite showing comparable brain activation patterns for a spatial working memory task in comparison to young adults, older adults do not engage these brain regions as young adults do when learning new motor skills. Older adults exhibit no correlation between spatial working memory performance and the rate of sensorimotor adaptation, and reductions in both spatial working memory and motor sequence learning in comparison to young adults. These results demonstrate that older adults do not successfully recruit spatial working memory during the early stages of skill learning. Up until now, the literature on interactions between cognition and action across the lifespan has shown that older adults rely on cognitive processes *more* than young adults for single joint actions (cf. Heuninckx et al., 2005). In contrast, our recent data show that for manual skill learning tasks, older adults are *less* likely to engage the relevant cognitive processes.

In our recent work we have also developed a conceptual model of how spatial working memory is used during motor learning. We propose that motor error information is loaded into spatial working memory in order to update the motor plan accordingly for subsequent actions. It may be that older adults do not engage spatial working memory during motor learning due to degraded error signals. These hypotheses await future evaluation.

Acknowledgments

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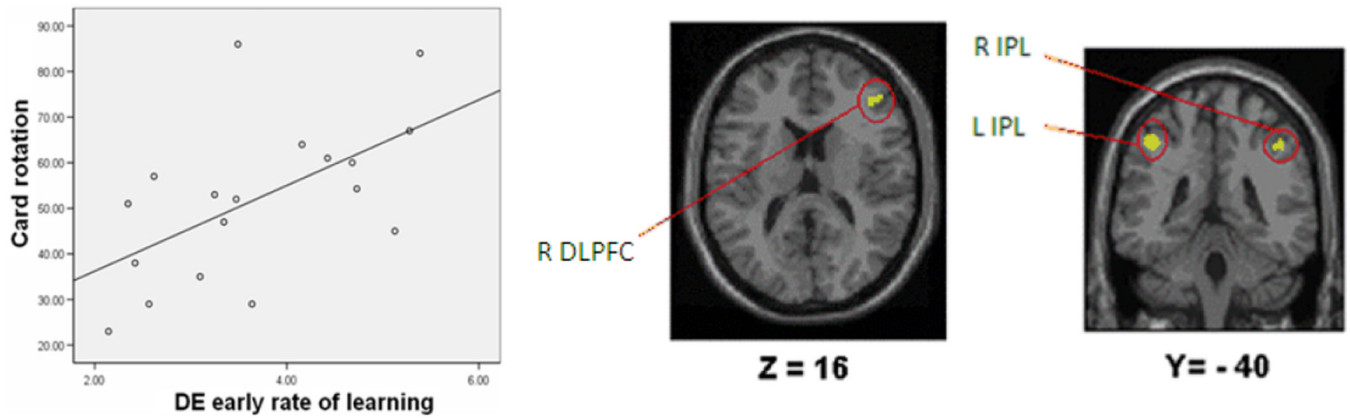
Figure 1.
Left panel, performance on the card rotation assessment of spatial working memory is correlated with the rate (slope) of early learning on the visuomotor adaptation task. Overlapping BOLD activation for the spatial working memory task and the early stage of the visuomotor adaptation task was observed in the right dorsolateral prefrontal cortex (middle panel) and the bilateral inferior parietal lobules (right panel). Figure adapted from Anguera, Reuter-Lorenz, Willingham & Seidler, 2010, J Cog Neuro 22: 1917–1930.
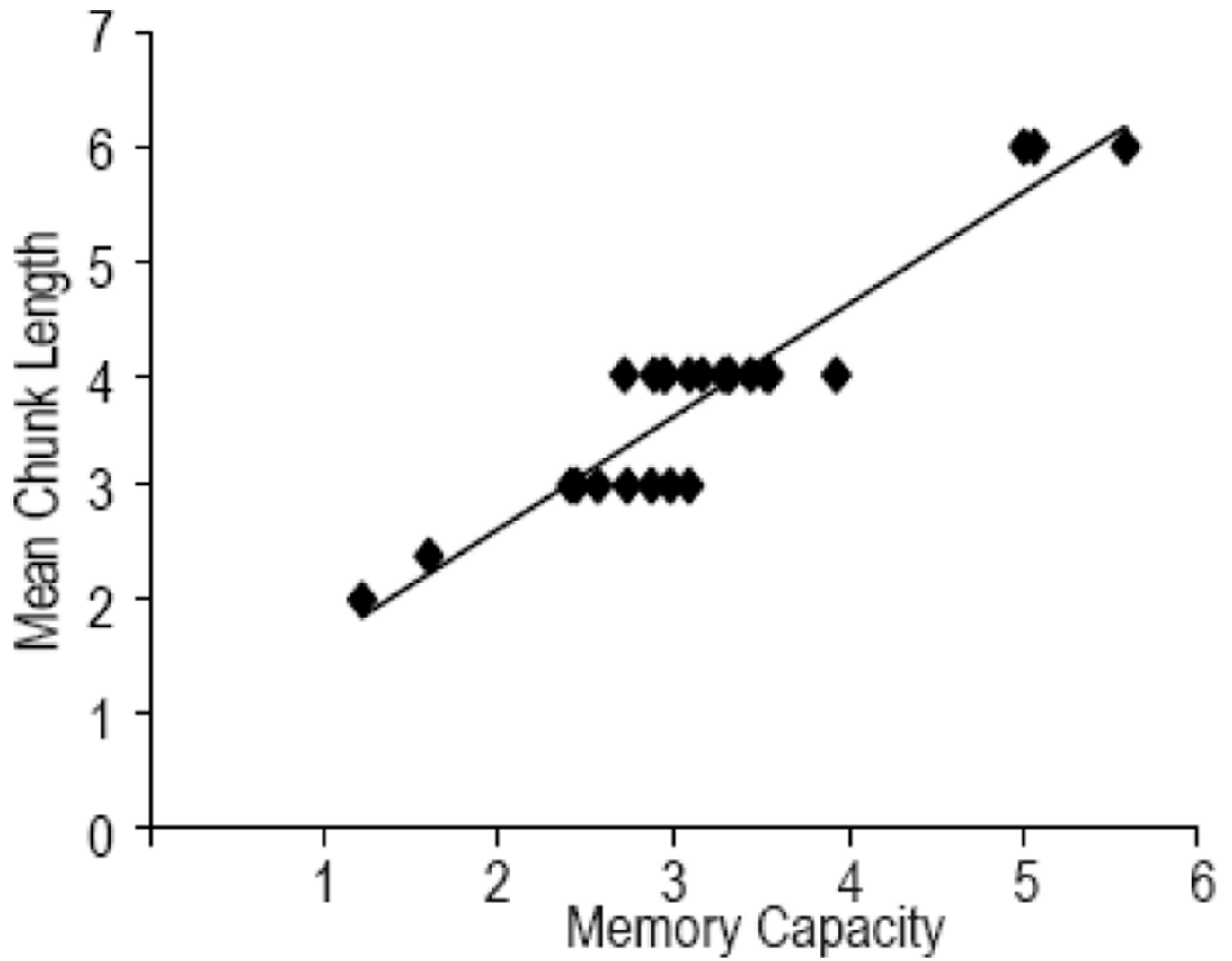
Figure 2.
Relationship between motor sequence chunk length and working memory capacity. Figure adapted from Bo & Seidler, 2009, J Neurophys 101: 3116–3125.