

## Contributions of Spatial Working Memory to Visuomotor Learning

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## **Abstract**

Previous studies of motor learning have described the importance of cognitive processes during the early stages of learning; however, the precise nature of these processes and their neural correlates remain unclear. The present study investigated whether spatial working memory (SWM) contributes to visuomotor adaptation depending on the stage of learning. We tested the hypothesis that SWM would contribute early in the adaptation process by measuring i) the correlation between SWM tasks and the rate of adaptation, and ii) overlap between the neural substrates of a SWM mental rotation task and visuomotor adaptation. Participants completed a battery of neuropsychological tests, a visuomotor adaptation task, and a SWM task involving mental rotation, with the latter two tasks performed in a 3.0T MRI scanner. Performance on a neuropsychological test of SWM (two dimensional mental rotation) correlated with the rate of early, but not late, visuomotor adaptation. During the early, but not late, adaptation period, participants showed overlapping brain activation with the SWM mental rotation task, in the right dorsolateral prefrontal cortex and the bilateral inferior parietal lobules. These findings suggest that the early, but not late phase of visuomotor adaptation engages SWM processes.

## Introduction

Skill learning has been defined as an increase in spatial and temporal accuracy of movements with practice (Willingham, 1998). It is characterized by at least two stages: an initial learning stage (“fast/early learning”) in which within-session improvements can be induced through a limited number of trials on a time scale of minutes (Adams, 1971; V. Brooks, Hilperath, Brooks, Ross, & Freund, 1995; V. B. Brooks, Kennedy, & Ross, 1983; Fitts & Posner, 1967; Karni et al., 1998; Puttemans, Wenderoth, & Swinnen, 2005; Smith, Ghazizadeh, & Shadmehr, 2006; Willingham, 1998), and a “slow/late learning” stage, where improvement occurs incrementally over hours or even days of practice (Doyon, Penhune, & Ungerleider, 2003; Karni et al., 1998; Willingham, 1998). In general, the early learning stage is described as being cognitively demanding, while the late learning stage is described as being more automatic (e.g. Fitts & Posner, 1967).

A specific type of skill learning, visuomotor adaptation, has provided important insights into how humans represent and interact with their environment. Visuomotor adaptation requires the modification of a well-learned sensorimotor transformation, based in part on neural maps which encode and mediate visuomotor information for use by the motor control system (Cunningham, 1989).<sup>1</sup> There is evidence that modification of these neural maps requires the engagement of cognitive resources for processes such as error encoding and updating visual measurements to motor

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<sup>1</sup> The terms learning and adaptation each describe a relatively enduring change in performance, with adaptation being more relevant to the present study. The phrase ‘neural map’ describes the central nervous system’s correspondence, or mapping, between observed movements encoded visually and direction of movement as incorporated into motor commands for the hand-arm system (Cunningham & Welch, 1994), with ‘visuomotor map’ being specific to the task in the present study.

space (i.e. visuomotor mapping). For example, Taylor and Thoroughman (2007) found that performance of a secondary tone counting task during visuomotor adaptation led to divided attention, which in turn disrupted the encoding of errors during adaptation. Similarly, Eversheim and Bock (2001) found that performing secondary tasks requiring spatial resources, including sensory transformations, interfered with the early phase of adaptation. However, the need for these resources was diminished later in learning, when movement preparation processes were instead called upon to a greater extent. These results indicate that early stages of motor adaptation benefit from the engagement of cognitive resources with other processes playing a greater role later in learning. However, the specific nature of these cognitive contributions remains uncertain.

Consistent with a potential role for cognition in visuomotor adaptation, neuroimaging studies have shown that early learning engages prefrontal brain regions (Anguera, Russell, Noll, & Seidler, 2007; Clower et al., 1996; Hikosaka et al., 1999; Inoue et al., 1997; Sakai et al., 1998; Seidler, Noll, & Chintalapati, 2006; Toni, Krams, Turner, & Passingham, 1998). Although the contribution of prefrontal cortex to adaptation is unknown, the activated site is similar to regions reported in neuroimaging studies of spatial working memory (SWM); more specifically, the right prefrontal cortex and inferior parietal lobule (Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Jonides et al., 1993; McCarthy et al., 1994; McCarthy et al., 1996; Reuter-Lorenz et al., 2000). One intriguing possibility suggested by this neuroanatomical correspondence is that SWM is engaged during visuomotor adaptation.

Indeed, McNay and Willingham (1998) hypothesized that SWM plays a role in visuomotor adaptation, and the purpose of the present study is to test this idea by examining behavioral and imaging measures of SWM and visuomotor adaptation in the same group of participants. SWM involves the online maintenance and active manipulation of spatial information (Baddeley, 1986; Miyake & Shah, 1999). Both behavioral and neural evidence indicates that SWM is dissociable from verbal working memory (Miyake & Shah, 1999; Nagel, Ohannessian, & Cummins, 2007; Reuter-Lorenz et al., 2000), and that individuals differ in SWM capacity (Luck & Vogel, 1997; Vogel & Machizawa, 2004). Furthermore, it has been argued that the storage and processing functions of SWM are essential to mental rotation ability (Cohen, Kosslyn, Breiter, DiGirolamo, Thompson, Anderson, Brookheimer et al., 1996; Jordan, Heinze, Lutz, Kanowski, & Jancke, 2001; Logie, Della Sala, Beschin, & Denis, 2005; Suchan, Botko, Gizewski, Forsting, & Daum, 2006), which is the particular application of SWM that may be most relevant to visuomotor adaptation performance.

Seminal work by Metzler & Shepard (1974) and Just & Carpenter (1976) described the following steps thought to underlie mental rotation: the active maintenance of a visual configuration, its transformation, and a subsequent comparison to a target image. These functions require not only SWM, but also the more general cognitive processes that several groups have associated with sensorimotor adaptation such as attention (Anguera et al., 2007; Eversheim & Bock, 2001; McNay & Willingham, 1998; Seidler et al., 2006; Taylor & Thoroughman, 2007, 2008). We hypothesize that visuomotor adaptation engages overlapping

neural processes related to mental rotation while proceeding through a similar set of steps: understanding that the original visuomotor mapping (where initiated movements directly corresponded with the visual feedback) requires updating to produce accurate movements in this new environment, mentally rotating this neural map with SWM resources, and then using this updated map to perform subsequent movements in the rotated environment.

In the current study, behavioral and neural measures were used to test more precisely the nature and time course of SWM contributions to visuomotor adaptation. Participants performed a joystick-controlled visuomotor adaptation task that required them to make manual aiming movements to targets under veridical and rotated visual feedback in an fMRI environment. Furthermore, they also performed a test of SWM involving mental rotation in the scanner, as well as a battery of neuropsychological assessments of several cognitive processes. We hypothesized that SWM would play a role during early, but not late, adaptation, evidenced by correlations between the rate of early adaptation and SWM measures, as well as overlapping neural substrates for the performance of SWM and visuomotor adaptation tasks.

## **Methods**

### *Participants*

Eighteen participants ( $21.1 \pm 2.5$  yrs; 9 males) were recruited from the University of Michigan student population and were paid for their participation. Each participant signed an IRB-approved informed consent document and filled out a

health history questionnaire prior to the experiment. All participants were right-handed as assessed using the 20-item version of the Edinburgh Inventory (Oldfield, 1971); mean handedness score =  $.83 \pm .10$ ).

### *Experimental setup and procedure*

Testing occurred on two separate days. On day one, participants performed a battery of neuropsychological tests to assess the following cognitive processes: 1) mental rotation and spatial relation abilities were tested using Thurston's card rotation (2D) and cube rotation (3D) tasks (Ekstrom, French, & Harman, 1976); 2) short term visuospatial memory was assessed by the forward Corsi Block tapping test (Corsi, 1972); 3) sensorimotor processing speed was determined by the digit-symbol substitution task from WAIS-R (Wechsler, 1997); 4) short-term verbal memory was evaluated by the forward digit span tasks from WAIS-R (Wechsler, 1997) and the reading span task (Daneman & Carpenter, 1980); 5) verbal working memory was assessed by the backward digit span task from WAIS-R (Wechsler, 1997), while serial visuospatial working memory was assessed through the backward Corsi Block tapping task (Corsi, 1972); 6) The DEX questionnaire (dysexecutive syndrome; Wilson et al., 1996) is a self report measure used to determine whether individuals have difficulty with abstract thinking, planning, or other tasks associated with executive functioning. Participants also practiced three blocks of joystick aiming movements made under veridical feedback conditions, as well as one block of a SWM control task (detailed below), to familiarize them with basic task requirements before subsequent testing in the fMRI scanner.

The second day of testing was completed within 1 week of the first testing day. During the second testing session, participants performed the visuomotor adaptation task, the SWM control task (SWMc), and the SWM task which involved mental rotation. For these tasks, participants lay supine in a 3.0 Tesla MRI scanner (General Electric) with their head comfortably restrained to prevent excess head movement. Task presentation and response collection were accomplished with custom Labview 6.1 software (National Instruments) for the visuomotor adaptation task, and E-prime 1.1 software for the SWM tasks (Psychology Software Tools, Inc.). Stimuli were presented through a mirror mounted on a set of specialized goggles, reflecting a video projection screen placed at the rear of the scanner. For the SWM tasks, E-prime recorded participants' responses (“matching” = thumb press, “different” = index finger) via a right-handed button-glove.

[Figure 1 about here]

The SWM task, modeled after the task employed by Reuter-Lorenz et al. (2000), required participants to memorize a three target set (three solid circles) in a 500 ms period (Figure 1). Following presentation of the target set, participants saw a blank screen for 3000 ms (retention interval, RI). During this period, they were instructed to mentally ‘connect the dots’ of the target set, and then mentally rotate this shape by 30° clockwise. Following the RI, participants were given 3000 ms to decide whether the subsequently presented probe set of open circles formed the same configuration as the target set that they had mentally rotated. There was a 30

second visual fixation baseline period before and after each set of 10 trials.

Participants performed 2 runs of this task, with 30 trials within each run. 70% of the trials were 'match' trials in which the probe set was rotated 30° clockwise; the remaining 'non-match' trials had two of the three probe circles displaced by 1.1cm (hard), 1.5cm (medium), and 1.9cm (easy) from the original target dot configuration.

Participants also performed a SWMc task (1 block of 40 trials; see Figure 1) modeled after the control task used by Reuter-Lorenz et al. (2000). This task involved the presentation of three solid circles for 500 ms, followed by a 200 ms RI; this shortened RI, in theory, requires immediate matching without providing sufficient time to engage working memory processes. Following this, participants were presented with a single circle for 2500 ms and asked to determine whether its spatial location matched that of a previously observed dot. This control task included all of the cognitive components of the SWM task (e.g. perceptual encoding, response selection, preparation, and initiation) except for the working memory and mental rotation components. Thus, the subtraction of images from the control condition should reveal areas actively involved with SWM and mental rotation (Reuter-Lorenz et al. 2000).

For the visuomotor adaptation task, targets (0.8 cm in diameter) appeared for four seconds in one of four locations: 4.8 cm to the right, left, above, or below the centrally-located home position (0.8 cm in diameter). Participants controlled a cursor with a dual potentiometer joystick placed on their lap. Participants held the joystick with their thumb and index finger, and made small wrist and finger movements to control the joystick, with real-time feedback displayed as a cursor on

the projection screen. Participants were asked to move the cursor into the target circle as quickly and accurately as possible, and to maintain the cursor within the circle until the target disappeared. Upon target disappearance, they were told to release the spring-loaded joystick handle so that it would re-center for the subsequent trial. The next trial began one second later, resulting in an inter-trial interval (from one target presentation to the next) of five seconds. Participants performed 13 blocks (B) as separate fMRI runs of the task (24 trials per block), with 30 second visual fixation baseline periods at the beginning and end of each block. An initial practice block (P) performed in the scanner was not included in the analysis. The first experimental block (B1) was performed under normal visual feedback conditions (control condition), while the subsequent 11 blocks (B2-B12; adaptation period) were performed with visual feedback rotated 30° clockwise about the center of the screen.

#### *fMRI acquisition parameters*

Functional images were acquired using a single-shot gradient-echo reverse spiral pulse sequence (Börnert, Aldefeld, & Eggers, 2000). The field of view was 220 x 220 mm, voxel size was 3.2 x 3.2 x 3.2 mm, TR (repeat time to accomplish a full volume) was 2 seconds, and TE (echo time) was 30 ms. Forty contiguous axial slices were acquired, encompassing the whole brain, including the cerebellum. Structural images were acquired using a T1-weighted gradient echo pulse sequence (TE/TR/FA = 3ms/250ms/25 degrees) with a field of view of 240 x 240 mm, voxel size = 1.4 mm x 1.4 mm x 3.2 mm.

### *Behavioral data processing*

For both the SWMc and SWM task, the response time and percentage of correct responses were calculated. For the adaptation task, the X and Y coordinates from the joystick were recorded at a rate of 100 Hz. These data were analyzed offline using custom Labview 6.1 software (National Instruments) to track behavioral changes with learning. The data were first filtered with a dual low pass Butterworth digital filter (cf. Winter, 1990), using a cutoff frequency of 10 Hz. The resultant joystick path was calculated by computing the square root of the sum of the squared X and Y coordinate data at each time point. The tangential velocity profile was then calculated through differentiation of the resultant position data. Movement onset and offset were computed through the application of Teasdale, Bard, Fleury, Young, & Proteau's (1993) optimal algorithm to the velocity profile for each movement. Learning was assessed by measuring direction error (DE), which is the angle between a straight line from the start to the target position and the position at peak velocity.

We made the assumption based on previous literature that the learning process in visuomotor adaptation contains an “early” and “late” phase (cf. Krebs et al., 1998), with the early phase reflected by a period of rapid improvement, and the late phase showing slower incremental performance gains. To identify which adaptation blocks comprised the early learning period, we searched for the optimal number of consecutive adaptation blocks which resulted in the steepest rate of learning from the first adaptation block (i.e. the slope across the 1st two adaptation

blocks, the slope across the 1st three adaptation blocks, etc) for each subject. This point was identified as the block whose inclusion led to a significant decrease in the rate of learning slope. Early learning was defined using the most frequently occurring breakpoint in order to keep the number of trials and the amount of practice time consistent across participants. Late learning was then defined as the equivalent consecutive number of adaptation blocks, counting backwards from the final adaptation block. Rate of learning was used as the primary adaptation measure. Mean DE was also examined to provide a within-block index of learning; we performed a block x trial repeated measures analysis of variance (RM ANOVA) on DE to test for differences across blocks and trials. Significant interactions were followed up with simple contrasts. The Huynh-Feldt epsilon (Huynh & Feldt, 1970) was evaluated to determine whether the repeated measures data met the assumption of sphericity ( $\epsilon > 0.75$ ). Pearson correlations were also computed between performance on each of the neuropsychological tests and accuracy and reaction time for each SWM task, as well as the rate of learning for each adaptation period for DE.

### *fMRI data processing*

The first three volumes of each run were discarded to allow the MRI signal to reach its steady state. Head motion correction was performed using the Automated Image Registration (AIR) package (Woods, Grafton, Holmes, Cherry, & Mazziotta, 1998). Structural images were skull-stripped using FSL's Brain Extraction Tool (<http://www.fmrib.ox.ac.uk/fsl>). fMRI data were processed and analyzed using

Statistical Parametric Mapping 2 (SPM2; Wellcome Department of Cognitive Neurology, London, UK). We computed a mean functional image for each participant. Then we coregistered the structural image to this mean image and then spatially normalized images to the Montreal Neurological Institute (MNI) template (Evans, Kamber, Collins, & Macdonald, 1994). These images were then spatially smoothed with a Gaussian kernel with a full width at half maximum (FWHM) of 8mm. In addition, head movement parameters were added as covariates of no interest to correct for potential confounding effects induced by head movement.

Boxcar models time-locked to the effect of interest were created and convolved with an estimate of the canonical hemodynamic response function. Analyses were performed at the single participant and group levels through SPM2 to determine regions activated in association with task performance. Significant areas of activation were then localized using the automated anatomical atlas (AAL; (Tzourio-Mazoyer et al., 2002) and confirmed with the Talairach atlas (Talairach & Tournoux, 1988). Medial motor areas were identified as in Picard & Strick (1996) and Mayka, Corcos, Leurgans, & Vaillancourt (2006), and cerebellar regions as in Schmahmann et al. (1999).

#### *fMRI contrasts*

Different contrasts were designed to examine the visuomotor adaptation task and the SWM task. The *SWM contrast* searched for regions of statistically greater activation for the two SWM blocks in comparison to the SWM control block. The first adaptation contrast (*early adaptation*) searched for regions of statistically greater

activation across the first 3 adaptation blocks (defined as the early learning phase by the breakpoint analysis) versus the first control block (B1). The second adaptation contrast evaluated the late adaptation period using the final 3 adaptation blocks (*late adaptation*) versus B1. As the neural correlates of SWM, early, and late adaptation have been previously reported in other studies, we utilized a more lenient threshold (p-value of .005 and cluster magnitude  $\geq 10$  voxels) to replicate and display these findings.

In order to evaluate overlapping regions of SWM activation for each task, an inclusive mask of the *SWM contrast* was applied to both the *early* and *late* adaptation activation maps. The threshold for this mask to exclude non-SWM related voxels was set at a liberal p-value of .05 uncorrected; however, all statistical inferences utilized a more stringent False Discovery Rate (FDR)-corrected threshold p-value of .05 (Genovese, Lazar, & Nichols, 2002). Furthermore, conjunction analyses (using an uncorrected threshold p-value of .01, given that each contrast involved had already been subjected to a more stringent threshold ( $p < .005$ )) were also performed to support any mask-related findings and provide evidence of areas being equally engaged during the SWM task and the corresponding stage of adaptation. Whole brain activation correlations were also performed between the following behavioral performance measures and activation at their corresponding scanning blocks: DE early average block score and rate of early adaptation, DE late average block score and rate of late adaptation.

## Results

fMRI data from two participants were excluded due to complications with the collection process. This left 18 participants for the behavioral analysis, and 16 for the imaging portion (8 males).

### *Behavioral dependent measures*

Table 1 shows the group mean and standard deviation for performance on each of the neuropsychological tests, as well as performance on the SWM tasks. As expected, the SWM task was more difficult than the SWMc as indicated by lower accuracy ( $t_{(1, 17)} = 6.85$ ,  $p < .0001$ ) and a longer reaction time ( $t_{(1, 17)} = -7.27$ ,  $p < .0001$ ).

[Table 1 about here]

[Figure 2 about here]

Figure 2 illustrates performance by block for DE. A repeated measures ANOVA (RM ANOVA) with block (12) and trial (24) for DE resulted in a significant main effect for block ( $F_{(11, 187)} = 30.40$ ,  $p < .0001$ ), so follow up tests were conducted. Within-participants polynomial contrasts across block for the adaptation period (11 blocks) for each measure showed a significant linear fit ( $F_{(1,17)} = 151.38$ ,  $p < .001$ ), indicating improvements with practice. Following the calculation of slopes for each combination of consecutive adaptation blocks, a RM ANOVA with a repeated contrast of the slopes revealed that the 1st 3 adaptation blocks had the steepest rate of learning versus all other combinations (see Table 2).

[Table 2 about here]

Evidence that the 1st 3 adaptation blocks comprised the early adaptation period was established by a difference between the 3 and 4 block slopes ( $F_{(1,17)} = 10.49, p < .01$ ), and leveling off indicated by a lack of difference between the 4 and 5 block slopes ( $F_{(1,17)} = .32, p > .50$ ). Because the slope across the final 8 adaptation blocks and the final 3 adaptation blocks did not differ ( $t_{(1,17)} = -1.40, p > .15$ ), we designated the final 3 adaptation blocks as the late period. Imaging analyses were thus based on an equal number of blocks for the early and late learning periods. Importantly, there was a difference in the 3 block adaptation slopes between the early and late periods ( $t_{(1,17)} = 7.08, p < .0001$ ).

### *Behavioral Correlation Analysis*

Table 3 shows the results of the correlation analyses between the neuropsychological tests, measures of accuracy and RT for the SWM task, and the rate of adaptation for each stage of learning. The card rotation task correlated with both accuracy and RT on the SWM task ( $r = .63, p < .05$  and  $r = -.52, p < .05$ , respectively). The card rotation task also correlated with the DE rate of learning during the early adaptation period ( $r = .57, p < .05$ ; see Figure 3), but not during the late period ( $r = -.42, p > .05$ ; z-score difference = 3.00,  $p < .005$ ), supporting the hypothesis that SWM processes underlying 2D mental rotation play a role in early visuomotor adaptation<sup>2</sup>. The digit symbol task, which tests sensorimotor processing speed, also showed a correlation with the DE rate of learning during the early

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<sup>2</sup> Fitts & Posner's (1967) theory of skill learning also included an intermediate stage, where aspects of both early and late learning were present. While considerable change in performance occurred during the 'intermediate stage' of the current study, the rate of learning during this period (B5-B9) did not correlate with any of the neuropsychological measures ( $p > .05$  in each case), suggesting distinct neural processes were utilized here (versus early learning).

adaptation period ( $r = .50, p < .05$ ), but not during the late ( $r = .30, p > .05$ ). Tests of verbal working memory (i.e. forward digit span and reading span) did not show a correlation with the SWM task (forward digit span:  $r = .12, p > .05$ ; reading span:  $r = .01, p > .05$ ), the card rotation task (forward digit span:  $r = .08, p > .05$ ; reading span:  $r = .34, p > .05$ ), or the rate of early learning of the visuomotor adaptation task (forward digit span:  $r = -.29, p > .05$ ; reading span:  $r = .20, p > .05$ ).

[Table 3 about here]

[Figure 3 about here]

#### *fMRI results- SWM, early, and late activation*

The SWM > SWMc contrast revealed significant bilateral brain activation in a number of frontal, parietal, temporal, and cerebellar regions, including the right and left DLPFC, consistent with previous investigations of similar tasks (see Table 4; (Courtney et al., 1998; Jonides et al., 1993; McCarthy et al., 1994; McCarthy et al., 1996; Nystrom et al., 2000; Reuter-Lorenz et al., 2000; Walter et al., 2003). Early adaptation was also associated with significant bilateral brain activation in the inferior/middle frontal gyrus (IFG/MFG) and inferior parietal lobule (IPL), in addition to a number of other areas (see Table 5), consistent with previous investigations of visuomotor 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). No regions at late adaptation showed significantly greater activation than the adaptation control

condition<sup>3</sup>. Using the SWM activation as a limiting mask resulted in early adaptation activation in the right DLPFC and bilateral IPL, among other regions (see Table 6 and Figure 4). A conjunction analysis between SWM and early adaptation revealed activation only at the right DLPFC (Table 6). There were no regions which reached significance when this mask was applied to the late adaptation period, nor for the conjunction analysis involving these contrasts.

[insert Table 4 about here]

[insert Table 5 about here]

[insert Table 6 about here with Figure 4]

#### *fMRI- Individual correlations with whole brain activation*

Individual differences in activation for each visuomotor adaptation measure at the early and late periods were examined using a whole brain correlation analysis. Table 7 shows activation in the left MFG/DLPFC and caudate obtained from a whole brain correlation analysis of early visuomotor activation with the rate (slope) of early adaptation. Using the same analysis with the rate of late adaptation resulted in activation in the left middle temporal gyrus, left superior temporal gyrus, as well as the left cerebellum (H IX; Table 7). Right precuneus and superior parietal lobule activation was observed when the early mean DE score was correlated with early adaptation activation (Table 7).

[Table 7 about here]

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<sup>3</sup> Another approach to measuring adaptation is a direct contrast of the early and late adaptation periods. The early > late adaptation contrast revealed comparable frontal and parietal regions of activation to the early > control contrast (noted in Table 5), while the late > early contrast did not result in any significant activation. These findings provide further support of the early adaptation period selectively utilizing SWM regions.

## Discussion

The present study tested the hypothesis that SWM contributes to visuomotor adaptation, with the results supporting the proposal that early, but not late, adaptation engages SWM. Support for this proposal was evidenced by the findings that: i) individual differences on Thurston's card rotation task predicted the rate of early but not late adaptation, and ii) brain activation associated with the SWM mental rotation task overlapped with that of the early, but not late, adaptation period. Despite recent assertions that this task is largely implicit (Mazzoni & Krakauer, 2006), these findings are consistent with the hypothesis that SWM processes are involved in the early stages of acquiring new visuomotor mappings.

### *Correlations between cognitive measures and visuomotor adaptation*

In agreement with previous studies of visuomotor adaptation (Anguera et al., 2007; Cunningham, 1989; Ghilardi et al., 2000; Krakauer et al., 2004; Seidler et al., 2006; Smith et al., 2006), as well as motor learning theories (Doyon et al., 2003; Willingham, 1998), more rapid improvement was observed at the early adaptation stage than the late adaptation stage. Furthermore, the finding that the rate of early, but not late, visuomotor adaptation correlates with the card rotation task and the digit symbol task suggests distinct cognitive contributions to the early stages of learning. This pattern is also consistent with less cognitive and more 'automatic' influences in later learning (Adams, 1971; Eversheim & Bock, 2001; Fitts & Posner, 1967; Karni et al., 1998; Taylor & Thoroughman, 2007, 2008). In addition, there were no correlations between the early or late rate of adaptation and verbal working memory

measures (i.e. digit span, reading span), suggesting that the observed correlations do not reflect a general executive effect. It is important to note that all of the reported correlations no longer reach significance after correcting for multiple comparisons ( $p < .0005$ ). However, one could argue that because certain correlations were predicted a priori (e.g. the card rotation-rate of early adaptation, card rotation-SWM accuracy), a post-hoc correction for significance could be considered unnecessary. Regardless, the strength of these correlations is modest and these findings should be replicated with larger samples in the future.

The selectivity of the correlations between our neuropsychological measures and early adaptation performance is consistent with the idea that specific cognitive operations contribute to motor learning (see also Bock, 2005). That is, the significant correlation between card rotation and early adaptation suggests that 2-D rotation ability may be a critical shared process, whereas the lack of correlation with backward Corsi block and cube rotation argues that neither general spatial working memory abilities nor 3-D rotation ability are significantly related to visuomotor adaptation. While this interpretation suggests that the observed correlation results are both task- and environment- dependent, a clear behavioral distinction between these working memory resources has not been observed (Carroll, 1993; Lohman, 1988; Miyake, Friedman, Rettinger, Shah, & Hegarty, 2001). A concern with the present study is that we did not find a significant correlation between SWM accuracy (fMRI task) and the rate of early learning. This result was unexpected given i) the card rotation/SWM task accuracy correlation, and ii) the card rotation/rate of early adaptation correlation. While it is unclear why this correlation was non-significant,

the significant correlations between the card rotation task and the cube & SWM tasks do support that these tasks share similar processes related to mental rotation.

The early visuomotor adaptation period, the card rotation task, and the SWM task all require 'active' SWM (involving manipulation and transformation) as opposed to 'passive' SWM (involving maintenance and/or comparison). The null correlations between the rate of early adaptation and i) the cube rotation task, or ii) the Corsi backward task suggest that the type of SWM process utilized may be specific to the task at hand. We speculate that a spatial n-back task would not show a correlation with adaptation due to the absence of the mental rotation component. Furthermore, it may be that learning a visuomotor adaptation in 3D space would correlate with a 3D mental rotation task (i.e., cube rotation). One may question whether the observed relationship between visuomotor adaptation and SWM is task-specific, or whether SWM plays a role in other motor learning tasks as well. We have recently shown that visuospatial working memory capacity predicts the organization of explicitly acquired motor sequences (Bo & Seidler, 2009), supporting the possibility that the current findings may generalize to other motor tasks.

#### *SWM, early, and late activation*

Activation associated with the SWM > SWMc contrast was observed bilaterally in the IFG/ MFG and IPL, including the right DLPFC. These findings are in accord with other imaging studies of SWM and mental rotation (Cohen, Kosslyn, Breiter, DiGirolamo, Thompson, Anderson, Bookheimer et al., 1996; Courtney et al., 1998; Gauthier et al., 2002; Jonides et al., 1993; McCarthy et al., 1994; McCarthy et

al., 1996; Milivojevic, Hamm, & Corballis, 2008; Nystrom et al., 2000; Reuter-Lorenz et al., 2000; Suchan et al., 2006; Walter et al., 2003). The observed activation in premotor, prefrontal, temporal, and parietal regions during the early adaptation phase also agrees with previous imaging studies of visuomotor adaptation (Anguera et al., 2007; Clower et al., 1996; Krakauer et al., 2004; Seidler et al., 2006). No regions reached significance at late learning, an outcome which also agrees with prior studies of this and similar tasks.

It is important to note that the early and late learning periods were defined relative to a total learning duration of approximately 40 minutes. Thus, it is unclear whether our findings would generalize to visuomotor adaptation that spans multiple days or learning sessions (Della-Maggiore & McIntosh, 2005; Graydon, Friston, Thomas, Brooks, & Menon, 2005). Regardless of the length or number of sessions, an exact breakpoint between early and late learning processes is less likely than a gradual transition occurring from one to the other.

#### *Neural overlap between SWM and visuomotor adaptation*

When both the early and late adaptation periods were masked with the activation from the SWM task, only the early adaptation period showed significant activation. In particular, the right DLPFC and bilateral IPL, regions which have previously been associated with mental rotation in SWM tasks (Gill, O'Boyle, & Hathaway, 1998; Jordan et al., 2001; Suchan et al., 2006), were engaged. The overlapping engagement of the right DLPFC for the SWM task and early adaptation period was supported by the conjunction analysis. In addition, masked overlapping

activation was also observed in the right IFG and right PMC, supporting previous work from this laboratory which suggested that these right lateralized regions comprise a network that contributes to spatial cognitive processes of adaptation, specifically SWM and spatial attention (Seidler, Noll, & Chintalapati, 2006). Other studies have also reported right lateralized activation with the same visuomotor adaptation task (Ghilardi et al., 2000; Inoue et al., 1997; Krakauer et al., 2004), but have not interpreted this activation as supporting SWM processes.

The present findings suggest that prefrontal activation during the early stage of adaptation reflects engagement of SWM processes underlying mental rotation. These data support previous work suggesting that cognitive processes play a role in the adaptation process (Eversheim & Bock, 2001; Taylor & Thoroughman, 2007, 2008), and are also in line with theories of motor learning regarding the engagement of distinct neural correlates at different stages of learning (Doyon, Penhune, & Ungerleider, 2003; Smith et al., 2006; Willingham, 1998).

#### *Neural correlates of visuomotor adaptation*

There was a correlation between the rate of early adaptation and activation in the left MFG/DLPFC. This region was also active in the SWM contrast, indirectly supporting the function of SWM processes during early adaptation. During late learning, left middle temporal gyrus activation was correlated with the rate of late adaptation. Activation in this region was previously observed during late learning for a sensorimotor adaptation task (Krebs et al., 1998). Individual mean early DE score correlated with activation at right precuneus and superior parietal lobule, both

regions we have previously observed during the early adaptation period for this task (Anguera et al., 2007; Seidler, Noll, & Chintalapati, 2006).

Unfortunately, the design of the present study prevented discerning strategic online corrections from gradual visuomotor recalibration, both of which have been shown to influence sensorimotor adaptation. However, strategic control is quickly engaged following awareness of the altered visuomotor mapping, with recalibration occurring over an extended period of exposure to the perturbation (cf. Richards et al. 2007). This transition to a more autonomous stage is reflected by a shift in activation away from the prefrontal cortex towards regions like the cerebellum, which is hypothesized to reflect the storage and refinement of the new internal model for this task (Graydon et al., 2005; Imamizu et al., 2000; Seidler & Noll, 2008). In the present study, cerebellar activation (H IX), but not prefrontal activity, correlated with the rate of late adaptation, supporting this interpretation.

#### *How is SWM used in the motor learning process?*

How does SWM contribute to visuomotor adaptation? We propose that it is recruited to support mental rotation used to modify visuomotor maps. We suggest that the learner recalls the original, congruent visuomotor map, mentally rotates this map with SWM resources, and then uses this updated map to plan the subsequent movement in the rotated environment. While the maintenance of error information in WM likely contributes to the adaptation process, we believe the manipulation of the contents in WM for a given trial is critical for adaptation to take place. This interpretation agrees with Abeele and Bock's (2001) proposal that adaptation

progresses in a gradual fashion across the learning period from small angles of transformation through intermediate values until the prescribed angle of rotation is reached. Thus, the engagement of these SWM resources late in adaptation is markedly diminished, as compared to early adaptation, when the new mapping has been formed and is in use. These proposals also agree with electrophysiological data demonstrating an interaction between motor areas and a fronto-parietal network for information processing in motor adaptation (Wise, Moody, Blomstrom, & Mitz, 1998). It should be noted that other cognitive processes such as error detection and monitoring (Anguera, Seidler, & Gehring, 2009) are also likely contributing to the early phase of visuomotor adaptation.

Recent dual-tasking studies of motor adaptation and executive function have provided a framework for when SWM would most likely be recruited during the early adaptation period. Taylor and Thoroughman (2007, 2008) have shown that the adaptation process is most affected when attentional resources are distracted by a secondary task imposed late in the trial, when error information becomes available. These authors suggest that cognitive resources are engaged between trials so that error information can be integrated to update visuomotor maps for the subsequent trial, because a secondary task performed early in the trial did not produce interference. Direct testing of this theory was not possible in the current study due to the use of a block design to image the visuomotor adaptation task. Nevertheless, our findings are consistent with the idea that participants are utilizing SWM to transform their motor plan for subsequent trials based on information held in WM

comparing performance between previous accurate and current deviated movements.

## **Conclusions**

The early, but not late, stage of visuomotor adaptation is related to SWM processes. This relationship was evidenced by behavioral performance correlations and by overlapping neural activation patterns between early stages of adaptation and a SWM task involving mental rotation. These findings point to a role for spatial cognition early in the motor learning process, and provide insight into the potential functions served by prefrontal and parietal regions that are selectively engaged during the visuomotor adaptation process.

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**Table 1. Group mean (M) and standard deviation (SD) for each behavioral measure**

<b>Task</b>	<b>Units</b>	<b>M</b>	<b>SD</b>
<b>Neuropsych test</b>			
Card rotation	# of correct-incorrect cards (3 min)	52.3	20.4
Cube rotation	# of correct-incorrect cubes (3 min)	8.4	6.4
Digit symbol	# of correct symbols (2 min)	79.6	16.2
Corsi forward	# of correct trials	8.7	1.9
Corsi backward	# of correct trials	8.5	1.9
Digit span forward	# of correct trials	11.8	2.6
Digit span backward	# of correct trials	7.8	2.5
Reading span	# of words recalled	30.2	6.3
Edinburgh inventory	handedness index	.83	.11
DEX	executive impairment	19.8	8.4
<b>SWMc</b>			
Spatial control accuracy	% correct	93%	3%
Spatial control RT	ms	905	147
<b>SWM</b>			
Spatial rotation accuracy	% correct	81%	7%
Spatial rotation RT	ms	1257	209
<b>VMA</b>			
DE (early)	linear slope at early	3.4	1.0
DE (late)	linear slope at late	1.3	0.9

**VMA = visuomotor adaptation.**

**Table 2. Adaptation slopes for each combination of adaptation blocks**

<b>Adaptation slope</b>	<b>M</b>	<b>SD</b>
1st 2 ** (2)	1.71	1.26
1st 3 (11)	3.42	1.03
1st 4 ** (1)	2.80	0.56
1st 5 * (2)	2.88	0.57
1st 6 * (2)	2.69	0.47
1st 7 **	2.55	0.42
1st 8 **	2.13	0.27
1st 9 **	1.88	0.20

**\* p < .05, \*\* p < .005**

**Each comparison is with regards to the slope for the 1st 3 blocks (highlighted). Numbers in parentheses indicate the number of participants whose adaptation slope was steepest at that particular breakpoint.**

**Table 3. Behavioral Correlations**

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. Card rotation	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2. Cube rotation	0.52*	-	-	-	-	-	-	-	-	-	-	-	-	-
3. Digit symbol	0.49*	0.11	-	-	-	-	-	-	-	-	-	-	-	-
4. Corsi forward	0.16	0.29	-0.04	-	-	-	-	-	-	-	-	-	-	-
5. Corsi backward	0.13	0.22	0.22	0.68**	-	-	-	-	-	-	-	-	-	-
6. Digit span forward	0.08	0.11	-0.08	0.42	0.50*	-	-	-	-	-	-	-	-	-
7. Digit span backward	0.29	0.02	0.24	0.43	0.38	0.42	-	-	-	-	-	-	-	-
8. Reading span	0.34	0.25	-0.08	0.52*	0.50*	0.51*	0.47	-	-	-	-	-	-	-
9. Edinburgh inventory	-0.41	-0.3	-0.48*	0.35	0.29	0.33	0.02	0.01	-	-	-	-	-	-
10. Dex	0.29	0.18	-0.08	0.26	-0.16	-0.20	0.05	0.25	-0.04	-	-	-	-	-
11. Spatial rotation accuracy	0.63**	0.25	0.17	0.14	0.12	0.01	0.34	0.38	-0.01	0.16	-	-	-	-
12. Spatial rotation RT	-0.52*	-0.41	0.19	-0.14	0.08	-0.19	-0.01	-0.30	0.20	-0.38	-0.44	-	-	-
13. DE early slope	0.57*	0.15	0.50*	-0.10	-0.29	0.04	0.20	0.08	-0.43	0.44	0.29	-0.34	-	-
14. DE late slope	-0.42	0.01	0.30	-0.22	0.02	-0.22	-0.02	-0.41	-0.09	-0.15	-0.43	0.45	-0.09	-

\* Correlation is significant at the 0.05 level (2-tailed).

\*\* Correlation is significant at the 0.01 level (2-tailed).

**Table 4. SWM > SWMc activation**

<b>Anatomic location</b>	<b>BA</b>	<b>Coordinates of peak</b>	<b>Z score</b>
<b>Frontal/Motor</b>			
R IFG	44	48, 6, 28	3.2
L IFG	44	-50, 10, 34	3.7
L DLPFC	46	-48, 34, 18	2.8
R DLPFC	46	38, 36, 14	3.1
<b>Parietal</b>			
R IPL	40	40, -50, 46	2.9
L IPL	40	-34, -56, 44	3.0
R SPL	7	32, -62, 50	2.8
<b>Temporal/Occipital</b>			
R ITG	37	56, -52, 14	2.7
L ITG	37	-44, -56, -6	2.9
L MOG	39	-50, -74, 6	4.2
L SOG	19	-28, -72, 38	3.2
L IOG	18	-40, -88, -10	3.2
R IOG	18	38, -90, -4	3.5
<b>Cerebellum</b>			
R Cerebellum (H V)	-	6, -54, -28	2.7
L Cerebellum (H V)	-	-6, -50, -30	2.7

**BA = Brodmann area; R = right, L = left; IFG = inferior frontal gyrus; DLPFC = dorsolateral prefrontal cortex; IPL = inferior parietal lobule; SPL = superior parietal lobule; ITG = inferior temporal gyrus; MOG = middle occipital gyrus; SOG = superior occipital gyrus; IOG = inferior occipital gyrus; H V = hemisphere 5 of the cerebellum.**

**Table 5. Early VMA > control condition activation**

<b>Anatomic location</b>	<b>BA</b>	<b>Coordinates of peak</b>	<b>Z score</b>
<b>Frontal</b>			
R MFG*	9	52, 8, 36	3.5
L IFG*	44	-38, 44, 2	3.7
R IFG	47	50, 38, -2	4.4
L IFG*	47	-32, 14, -16	3.8
R IFG*	46	40, 38, 8	3.6
L MeFG	6	-4, 4, 54	3.4
<b>Motor</b>			
R VPMc	6	48, -4, 32	3.6
R DPMc	6	36, -10, 58	3.6
L DPMc*	6	-30, -8, 58	3.1
<b>Parietal</b>			
R IPL*	40	54, -42, 43	3.3
L IPL*	40	-56, 44, 42	4.0
L SPL*	7	-32, -50, 58	3.2
R Prec*	7	24, -64, 38	3.7
<b>Others</b>			
R Lingual Gyrus	19	22, -56, -8	3.3
L Lingual Gyrus	18	-8, -86, 2	4.0
R MTG	21	54, -46, -6	3.4
R Putamen	-	16, 2, 6	4.5
L Putamen	-	-20, 0, 10	4.4
L VL Thalamus	-	-18, -16, 12	3.1

**BA = Brodmann area; R = right, L = left; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; MeFG = medial frontal gyrus; VPMc = ventral premotor cortex; DPMc = dorsal premotor cortex; IPL = inferior parietal lobule; SPL = superior parietal lobule; Prec = precuneus; MTG = middle temporal gyrus; VL = ventral lateral.**

**\* These regions were also found for the Early Adaptation > Late Adaptation contrast.**

**Table 6. Early adaptation > baseline masked with SWM**

<b>Anatomic location</b>	<b>BA</b>	<b>Coordinates of peak</b>	<b>Z score</b>
<b>Frontal/Motor</b>			
R LPMC	6	52, 8, 36	3.6
R IFG	46	40, 38, 10	3.4
R DLPFC	46	46, 40, 16	3.4
R DLPFC <sup>1</sup>	46	42, 34, 14	2.7
<b>Parietal</b>			
R IPL	40	48, -40, 44	3.2
L IPL	40	-46, -38, 50	4.1
R Prec	22	22, -72, 50	3.4
L SPL	7	-32, -50, 58	3.9
R SOG	19	24, -64, 38	3.9

**BA = Brodmann area; R = right, L = left; IFG = inferior frontal gyrus; DLPFC = dorsolateral prefrontal cortex; LPMC = lateral premotor cortex; IPL = inferior parietal lobule; SPL = superior parietal lobule; Prec = precuneus; SOG = superior occipital gyrus.**

**<sup>1</sup> Conjunction: Early Adaptation > Baseline & SWM > SWMc contrasts.**

**Table 7. Correlations with whole brain activation**

<b>Anatomic location</b>	<b>BA</b>	<b>Coordinates of peak</b>	<b>Z score</b>
<b>Parietal</b>			
R Prec <sup>3</sup>	7	4, -56, 58	3.2
R SPL <sup>3</sup>	7	24, -48, 64	2.7
<b>Temporal</b>			
L MTG <sup>2</sup>	21	-48, -48, 6	3.5
L STG <sup>2</sup>	22	-46, -34, 14	3.3
L STG <sup>3</sup>	28	-26, 8, -22	3.0
<b>Others</b>			
L MFG/DLPFC <sup>1</sup>	45/46	-52, 32, 16	3.1
L Cerebellum (H IV) <sup>3</sup>		-18, -28, -28	3.2
L Cerebellum (H IX) <sup>2</sup>		-14, -58, -44	3.3
L Caudate <sup>1</sup>		-8, 8, 4	3.2
L Hippo <sup>3</sup>		-34, -28, -8	3.3

**BA = Brodmann area; R = right, L = left; Prec = precuneus; SPL = superior parietal lobule; MTG = middle temporal gyrus; STG = superior temporal gyrus; MFG = middle frontal gyrus; DLPFC = dorsolateral prefrontal cortex; H VI = hemisphere 6 of the cerebellum; IX = hemisphere 9 of the cerebellum; Hippo = Hippocampus.**

<sup>1</sup> DE early slope correlation with 1st 3 adaptation blocks activation.

<sup>2</sup> DE late slope correlation with final 3 adaptation blocks activation.

<sup>3</sup> DE average early score with 1st 3 adapt blocks activation.

Figure 1. Spatial rotation (SWM) and spatial control (SWMc) tasks schematic.

RI = retention interval.

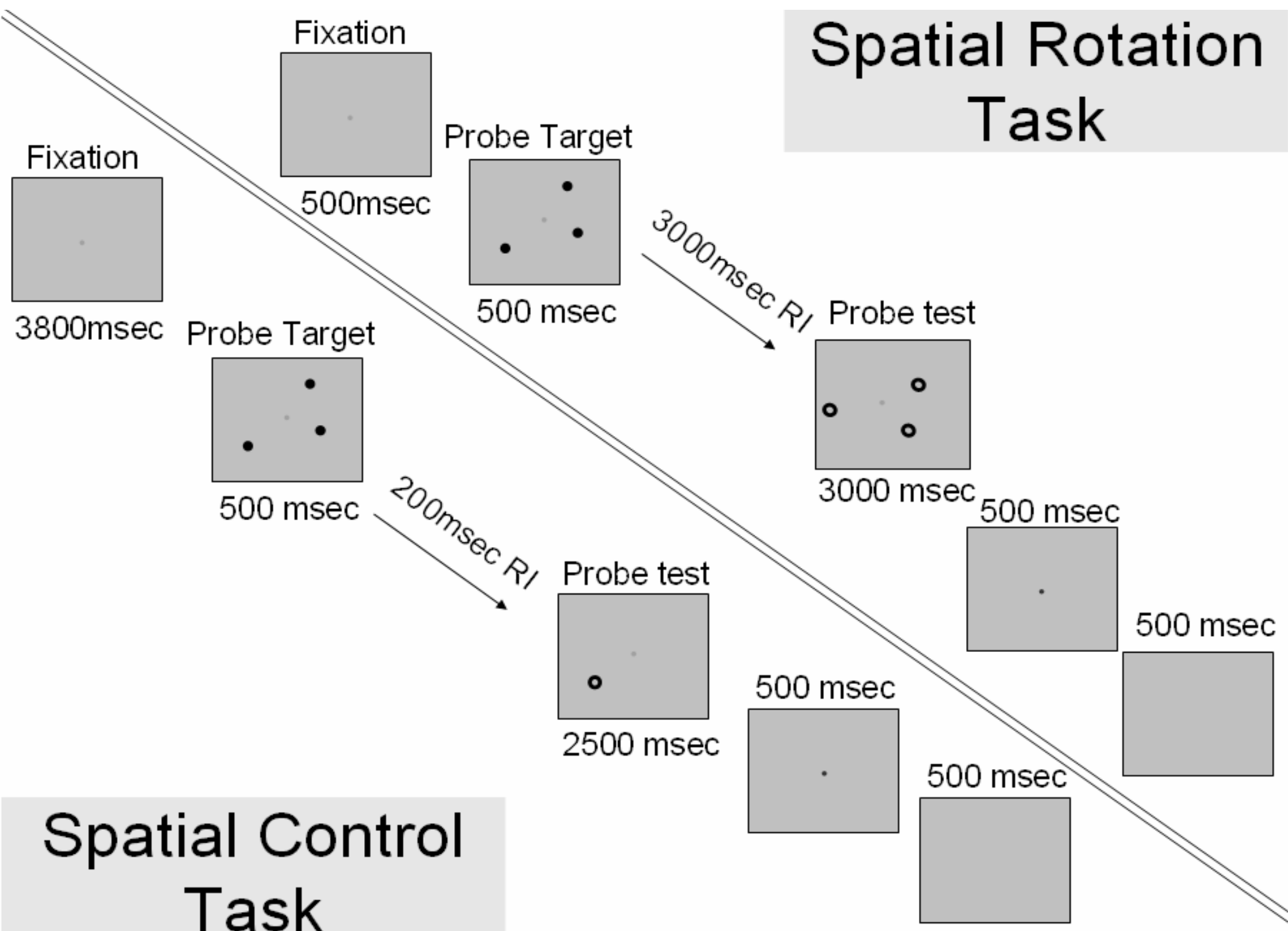
Figure 2. Visuomotor adaptation task performance across all blocks. Each block reflects performance averaged across trials and participants (group mean  $\pm$  SD).

Blocks 1 was performed under veridical visual feedback, while blocks 2-12 were performed under 30° clockwise rotation about the center of the screen.

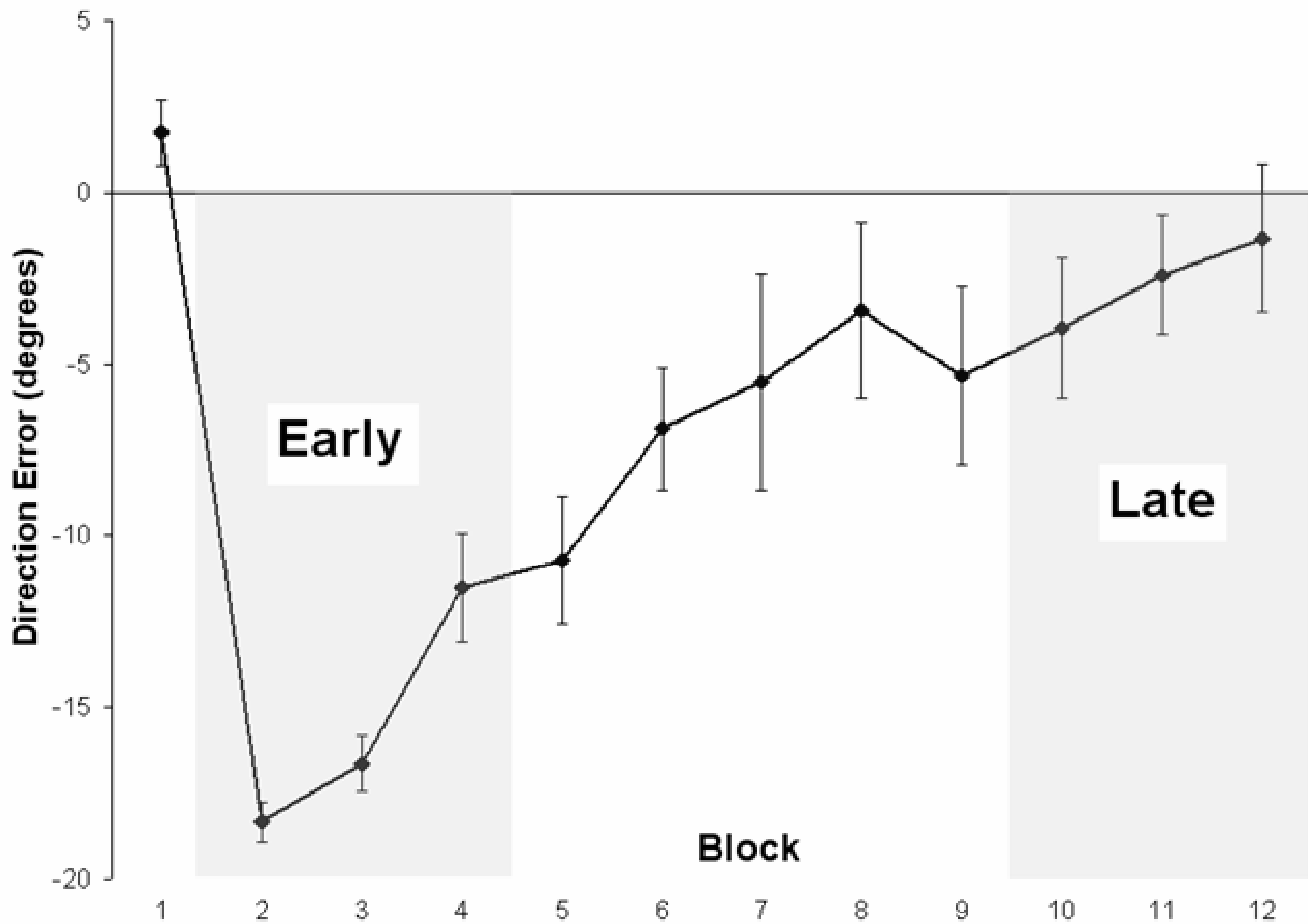
Figure 3. Performance correlation between card rotation task and early adaptation rate of learning,  $r = .53$ ,  $p < .05$ .

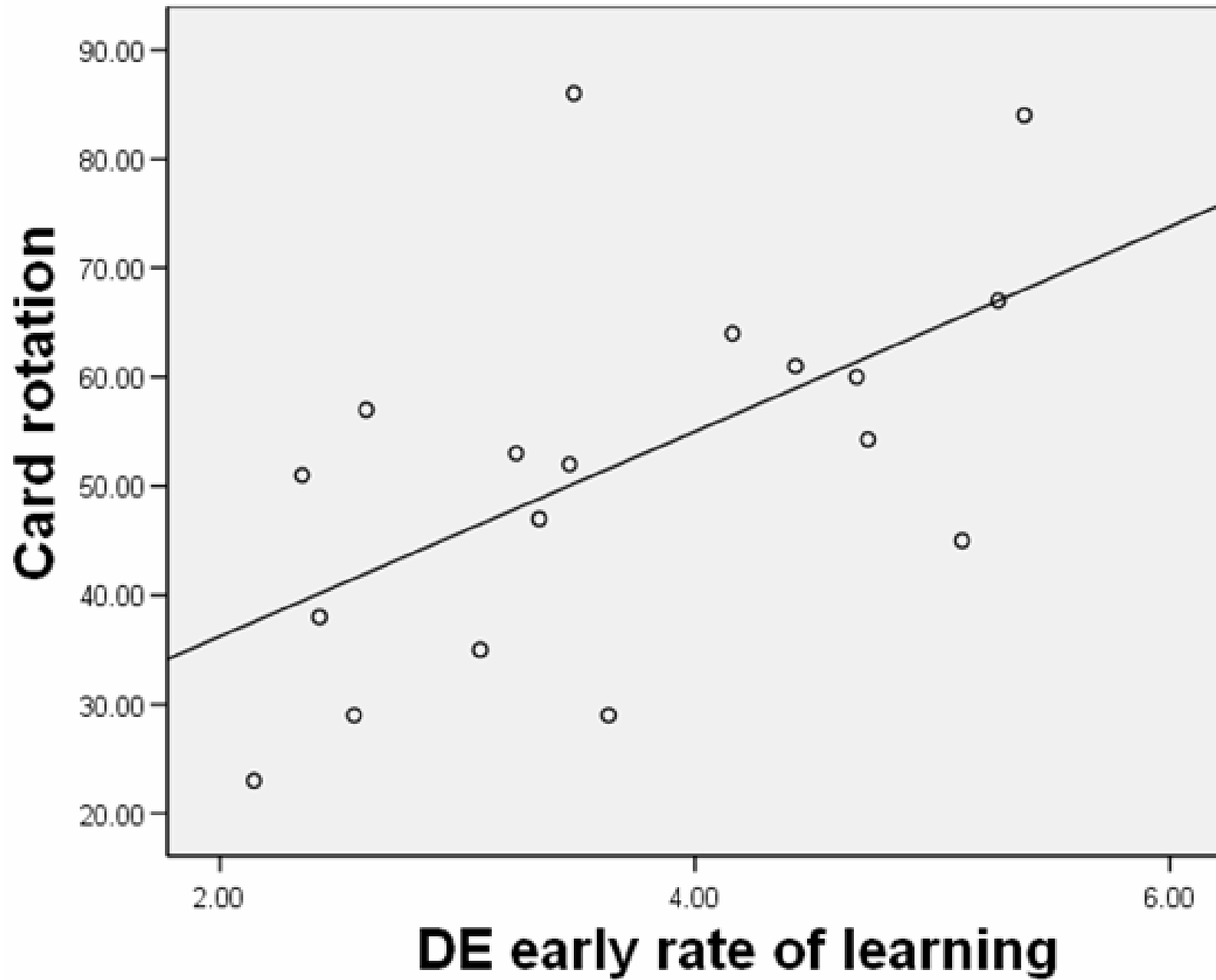
Figure 4. These images present activation from Table 7. The left image ( $z = 16$ ) depicts activation in the right dorsolateral prefrontal cortex (R DLPFC). The right image ( $y = -40$ ) depicts activity at the left and right inferior parietal lobule (IPL). Left in this image corresponds to participant's left.

# Spatial Rotation Task



# Spatial Control Task





**R DLPFC**



**Z = 16**

**R & L IPL**



**Y = - 40**