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Age differences in spatial working memory contributions to visuomotor adaptation and transfer

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Abstract

Throughout our life span we encounter challenges that require us to adapt to the demands of our changing environment; this entails learning new skills. Two primary components of motor skill learning are motor acquisition, the initial process of learning the skill, and motor transfer, when learning a new skill is benefitted by the overlap with a previously learned one. Older adults typically exhibit declines in motor acquisition compared to young adults, but remarkably, do not demonstrate deficits in motor transfer (Seidler, 2007). Our recent work demonstrates that a failure to engage spatial working memory (SWM) is associated with skill learning deficits in older adults (Anguera et al., 2011). Here, we investigate the role that SWM plays in both motor learning and transfer in young and older adults. Both age groups exhibited performance savings, or positive transfer, at transfer of learning for some performance variables. Measures of spatial working memory performance and reaction time correlated with both motor learning and transfer for young adults. Young adults recruited overlapping brain regions in prefrontal, premotor, parietal and occipital cortex for performance of a SWM and a visuomotor adaptation task, most notably during motor learning, replicating our prior findings (Anguera et al., 2010). Neural overlap between the SWM task and visuomotor adaptation for the older adults was limited to parietal cortex, with minimal changes from motor learning to transfer. Combined, these results suggest that age differences in engagement of cognitive strategies have a differential impact on motor learning and transfer.

Keywords

Spatial Working Memory; Aging; Visuomotor Adaptation; Skill Acquisition; Transfer

1. Introduction

The ability to adapt to changes in the world around us is an essential life skill. Learning a new skill (“motor learning”) and modifying it to meet new task demands (“motor transfer”) are both important for adaptive motor behavior (reviewed in Seidler, 2010) at all stages of

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life. A large number of studies have documented age-related reductions in the rate and magnitude of motor skill acquisition (cf., Ruch 1934; Harrington and Haaland 1992; Pratt and Abrams 1996; McNay and Willingham 1998; Seidler-Dobrin and Stelmach 1998; Seidler 2006). One form of motor learning that has been widely studied is sensorimotor adaptation, in which the learner modifies their 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.

Both young and older adults demonstrate positive motor transfer of sensorimotor adaptation (Bock and Schneider 2002; Bock and Gigenrath 2006; Seidler 2007). That is, prior experience with one form of adaptation results in better performance of another, regardless of age. Given this age dissociation, with older adults exhibiting impairments in initial motor learning but preserved motor transfer, the underlying neural and cognitive processes of motor learning and transfer may be distinct (Seidler and Noll, 2008).

We have recently investigated the mechanisms underlying age impairments in sensorimotor adaptation. We administered a battery of neuropsychological assessments to both young and older adults. In addition, participants performed a manual sensorimotor adaptation task and a spatial working memory (SWM) task while functional magnetic resonance images were acquired. We found that performance on the card rotation task, a measure of SWM, was correlated with the rate of early, but not late, learning of a visuomotor adaptation task for young adults (18 participants, mean age 21.1 ± 2.5 yrs, Anguera et al., 2010). There were no correlations between verbal working memory measures and either early or late learning. Moreover, the neural correlates of early learning overlapped with those that participants engaged when performing a SWM task, notably in the right dorsolateral prefrontal cortex and bilateral inferior parietal lobules (Anguera et al; 2010). There was no neural overlap between late learning and SWM. Thus we found that early but not late learning engages SWM processes in young adults, compatible with other work documenting greater cognitive demands during early learning (Taylor and Thoroughman 2007; 2008; Eversheim and Bock 2001).

In contrast, in a companion study we found that older adults (18 participants, 71.4 ± 4.2 yrs old) had a significantly reduced rate of early but not late learning in comparison to young adults (18 participants, 21.1 ± 2.5 yrs old, Anguera et al., 2011). Measures of working memory did not correlate with either the early or late learning period for older adults. In addition, although older adults recruited the right dorsolateral prefrontal cortex and bilateral inferior parietal lobules in a comparable fashion to young adults during the SWM task, they did not engage these regions during either early or late learning. These findings suggest that older adults do not effectively recruit available SWM resources to support early motor learning processes.

The purpose of the current study is to investigate the contribution of SWM to motor *transfer* for young and older adults. It may be that older adults do not experience difficulties at transfer of learning (Bock and Schneider 2002; Bock and Gigenrath 2006; Seidler 2007) because performance at transfer does not require SWM engagement. Therefore, we hypothesize that SWM performance measures will be *less* correlated with motor transfer than with motor learning for both age groups. Further, we hypothesize that both age groups will show reduced activation of brain regions that contribute to SWM such as prefrontal and parietal cortex at transfer of adaptation versus learning. Determining the mechanisms underlying conditions in which older adults exhibit preserved performance is an important first step towards designing targeted interventions to improve motor performance.

2. Material and Methods

2.1 Participants and Procedure

Young (N=18, 20.8 ± 2.5 yrs old, 14.6 ± 2.0 yrs education, 10 female) and older adults (N=18, 72.3 ± 4.7 yrs old, 15.9 ± 2.5 yrs education, 12 female) were recruited from the University of Michigan (UM) community and through the UM NIH Claude D. Pepper Older American's Independence Center human subjects and assessment core. All participants signed an Internal Review Board (IRB) approved consent form prior to entrance into the study. Participants were right handed (Edinburgh Handedness Inventory, Oldfield 1971, mean handedness scores: young adults 88.6 ± 11.4 , older adults 80.4 ± 13.8), free of contraindications for an fMRI study and scored a minimum of 26/30 on the Mini Mental State Exam (Folstein 1975) and a minimum of 123/144 on the Mattis Dementia Rating Scale (Mattis 1976). These participants were separate cohorts from those that participated in similar experiments in the lab (Anguera et al., 2010, 2011; Seidler 2007).

On day one of testing cognitive abilities were assessed through a battery of neuropsychological tests. Spatial working memory was assessed with Thurston's card rotation task (Ekstrom et al; 1976) and forward and backward Corsi Block tapping tests (Corsi 1972). A brief description of these tests appears in Table 1. Following this, participants practiced the baseline condition for the visuomotor adaptation task and the control condition for the spatial working memory task in a mock MRI scanner to become familiar with the MRI environment and the experimental protocols. For the adaptation task, participants moved a joystick with the dominant hand, and real-time feedback was presented as a cursor moving on the display screen. The starting position of the cursor for a given trial was the center of the screen. Targets would appear randomly above, below, right or left of the original cursor position. Participants were instructed to move the cursor as quickly and accurately as possible to the target, hold the cursor in the target until the target disappeared and then release the spring-loaded joystick allowing the cursor to return to the original centered position. A trial was defined as the time between the appearance and disappearance of the target (2.5 seconds). In a single run participants were given two blocks of 12 trials (20 seconds visual fixation, block of 12 trials, 20 seconds visual fixation, block of 12 trials, 22 seconds visual fixation). Participants practiced three runs of the task in the mock scanner.

In the spatial control task participants were presented with three closed circles on the screen for 500 msec. Following a brief retention interval of 250 msec, an open circle would appear. Participants responded with a button box, pressing the index finger if the open circle was in the same location as one of the closed circles and pressing the middle finger if the circle was in a different location. The open circle was presented for 2500 msec followed by a fixation screen for 500 msec and a blank screen for another 500 msec. Participants practiced one block of 10 trials of the spatial control task in the mock scanner.

The second day of testing was conducted at the UM Functional MRI Laboratory. A series of scans were performed using a 3.0 T MRI scanner (General Electric, Waukesha, WI). Participants' heads were comfortably restrained to reduce head movement. They wore fMRI compatible mirrored goggles to view a screen for the visual stimuli. Participants completed 17 runs of the joystick task during scanning. Some of the runs included visual rotation of online feedback requiring visuomotor adaptation to reach the target (Supplemental Materials Table S1). Three rotation magnitudes, 15° , 30° and 45° clockwise rotations of the feedback display about the center of the screen, were presented to participants. Each magnitude of visual rotation was given for three consecutive runs. Following each magnitude of visual rotation the display returned to baseline conditions for two consecutive runs for washout of the adaptation (cf., Seidler 2007; Seidler and Noll 2008). Participants were presented the visual rotations in one of two orders. Presentation order 1 (9 young adults and 9 older adults)

received the visual rotations in the order of 30°, 15° and 45°. Presentation order 2 (a separate group of 9 young adults and 9 older adults) received the visual rotations in the order of 45°, 15° and 30°. Using two presentation orders allowed us to compare participants that received the 30° rotation first (order 1) to participants that received the 30° rotation last (order 2) and likewise for the 45° rotation.

Following the visuomotor adaptation task participants were presented with the same spatial control task that they practiced in the mock scanner. In a single run, participants were given four blocks of 10 trials interspersed with 20 second visual fixation periods. Eighty percent of the trials were 'match' trials in the control task. Participants were also given a SWM task in the scanner, (similar to those used in Anguera et al., 2010, Reuter-Lorenz et al. 2000). Three closed circles appeared on the screen for 500 msec. After the three second retention interval the probe set was presented on the screen for 3000 msec. Participants responded with the index finger using the button box if the target and probe set were in the same configuration, but rotated (match). If the configuration was different, participants pressed the middle finger (non match). Participants performed three runs of this task (two blocks of 10 trials separated by 20 second visual fixation periods). Seventy percent of the trials were 'match' trials. A single-shot gradient-echo reverse spiral pulse sequence was also used to acquire the fMRI data. Pulse sequence parameters were TR/TE/FA/FOV of 2000ms/30ms/80/220mm respectively. Forty, 3.2 mm thick slightly oblique axial slices (no gap) were acquired. High resolution anatomical images were also acquired using a T1- weighted gradient echo pulse sequence with the following parameters TR/TE/FA/FOV 200ms/3.7ms/90/220mm and a voxel size of 1mm × 1mm × 1.2mm.

2.2 Behavioral data analysis

Custom Labview 6.1 software (National Instruments) was used to analyze the joystick data offline. A dual pass Butterworth digital filter (Winter 1997) using a cutoff frequency of 10 Hz was used to filter the raw data. 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. The optimal algorithm of Teasdale (Teasdale et al. 1993) was used to determine movement onset and offset. Performance on the task was measured by reaction time (RT), direction error (DE) and initial endpoint error (IEE). RT was computed by subtracting the time of the stimulus presentation from the time of the onset of movement. DE is determined by the angle between a direct line to the target and the spatial position of the cursor at peak velocity. IEE represents the distance from the joystick controlled cursor and the target at the end of the first ballistic movement. The algorithm used to calculate IEE identifies a period of acceleration following a period of deceleration or a change in the sign of the velocity. These variables were calculated for each trial. To assess rate of change in performance, the slopes of DE across initial learning trials (run 3) and motor transfer trials (run 13) were determined. For both the spatial control task and the SWM task the average percent accuracy and RT for the run was calculated.

The amount of learning that occurred during the first experience with the visuomotor adaptation task was quantified since total learning may impact the amount of transfer. We computed the amount of learning as the amount of actual correction that occurred as a percentage of the magnitude of correction necessary to return to baseline. The mean of run 13 (initial transfer) was divided by the mean of run 3 (initial learning). A score below 1 would represent that learning during the first visuomotor adaptation positively generalizes to the last visuomotor adaptation. Scores greater than 1 indicate negative transfer (interference), while 1 represents equivalent performance at transfer and learning.

2.3 MRI data analysis

fMRI data—The first three volumes per run were discarded to allow for signal equilibration. High-pass filtering was used to remove low-frequency drift. Motion correction was performed using MCFLIRT and the Brain Extraction Tool (BET) was used to strip the skull from images (using FSL toolboxes, <http://www.fmrib.ox.ac.uk/fsl>). Statistical Parametric Mapping version 5 (SPM5) was used for subsequent analyses. A mean functional image was created for each participant. All functional and structural images were aligned to this functional mean image. The Montreal Neurological Institute (MNI) template was used for spatial normalization (Mazziotta et al. 1995). The structural image was normalized to MNI space first and the resulting parameters were applied to the functional images. Functional images were spatially smoothed using a full width at half-maximum 8mm Gaussian smoothing kernel. Four participants were removed from the fMRI analyses due to poor co-registration (leaving testing order 1: 9 young and older adults; testing order 2: 8 young and 7 older adults). Boxcar models synchronized to the effect of interest and convolved with an estimate of the hemodynamic response function were used for statistical analyses. A general linear model analysis was first conducted at an individual level for motor learning (run 3) and motor transfer (run 13) contrasting periods of movement with rest. Second level random effects analyses were run for single group whole brain contrasts (uncorrected $p=.001$). Imaging data for older adults in orders 1 and 2 were combined to increase power as they demonstrated similar behavior. Similarly, young adults in orders 1 and 2 were also combined (see Seidler and Noll 2008 for justification of this approach). Contrasts identified regions of greater or less activation during motor learning versus transfer for both young and older adults. To identify regions involved in both spatial working memory and visuomotor adaptation, masks of spatial working memory activation established with separate cohorts of young and older adults in our previous studies (Anguera et al. 2010; Anguera et al. 2011) were applied to the visuomotor adaptation activation for both learning and transfer. Applying the mask, within-group analyses were used to identify regions where activation was greater at motor learning compared to transfer and vice versa (uncorrected $p<.001$). Between group analyses distinguished regions in which young or older adults demonstrated greater or less activation during motor learning and transfer (uncorrected $p<.001$). The Talairach atlas (Talairach and Tournoux 1988) was used to localize significant areas of activation.

2.4 Statistical Analyses

Statistical analyses were conducted in SPSS. Independent t-tests (using the mean of trials for each participant) were used to assess differences between age groups and transfer orders for the second baseline run (the first run was treated as practice and not included in statistical analyses). Levene's test for equality of variances was conducted and corrected t-tests were used if equal variances were not assumed. To ensure that participants had returned to baseline levels of performance (run 2) between each set of adaptation runs, the last 4 trials of the baseline run immediately preceding the last adaptation run (run 12) were compared to the last 4 trials of run 2 using a paired t-test. We compared performance at learning to performance during transfer for the 30° and 45° visual rotations using a linear mixed model design with a compound symmetric residual covariance structure. Age group, presentation order and trial were treated as fixed effects, and all 2- and 3-way interaction terms were considered. Correlation analyses were used to assess the relationship between motor learning, transfer, neuropsychological test performance and spatial working memory task performance. Scores that were greater than 2.5 standard deviations outside of the mean were considered as outliers and removed from the analysis.

3. Results

3.1 Visuomotor Adaptation Task Performance

At baseline (run 2), young adults performed better than older adults in terms of RT and IEE ($p < .01$); there was no difference between groups in DE ($t = .98$, $df = 34$, $p = .34$, Supplemental Materials Table S2). The two testing order groups within young and older adults performed similarly on RT, DE and IEE at baseline ($p > .10$).

To determine whether baseline performance was similar prior to the first and last visuomotor adaptations, the last four trials of runs 2 and 12 were compared. Young adults in orders 1 and 2 returned to baseline performance for all variables ($p > .10$ between runs 2 and 12), indicating that the first and last adaptive experiences had similar starting points. Older adults in order 1 and 2 did not return to baseline in terms of RT ($t = 2.68$, $df = 8$, $p = .03$, $t = 4.13$, $df = 8$, $p < .01$). Older adults in order 2 also failed to return to baseline in terms of DE ($t = 3.70$, $df = 8$, $p = .01$). We corrected for this by subtracting the baseline DE from adaptation runs to account for older adults not returning to baseline levels. Statistical analyses to identify age differences in learning and transfer were run on both the original and the baseline-corrected data. Since there was no difference in the pattern of age, learning, or transfer effects, data without baseline correction are reported for both young and older adults for ease of interpretation.

To examine transfer of motor learning, we evaluated differences in performance during the first and last exposures to a visual rotation. Analogous to our previous work, experience with a visuomotor adaptation was beneficial to subsequent performance (Seidler 2007). Benefits were most consistently found for both the 30° and 45° visual rotations when comparing initial learning (run 3) to initial transfer (run 13). That is, transfer benefits diminished with additional task practice. Thus, the following behavioral and imaging statistics reported are based on the initial learning and transfer runs (runs 3 and 13, respectively).

3.2 Amount of Learning

Older adults demonstrated a lower amount of learning compared to young adults (mean learning percentages across conditions for older adults ranged from 9 – 27% and for young adults 33 – 64%, DE ($t = 2.4$, $df = 33$, $p = .02$), IEE ($t = 2.30$, $df = 34$, $p = .03$)). It is notable that, although older adults demonstrated less learning than young adults, they exhibited equivalent, or even greater, savings at transfer of learning on some of the performance variables (see below). Thus it appears that the magnitude of learning that occurred did not directly influence transfer performance.

3.3 Transfer to 30° Visuomotor Adaptation

Young and older adults demonstrated reduced DE at transfer to the 30° rotation compared to initial learning to the same extent (figures 1A and 1B, main effect for presentation order, $F_{(1, 32, 20)} = 5.83$, $p = .02$). Similarly, both groups decreased IEE at motor transfer (figures C and 1D, main effect for presentation order, $F_{(1, 31, 56)} = 3.35$, $p < .01$). However, young adults demonstrated greater transfer for IEE than older adults (age group $\times$ presentation order interaction, $F_{(1, 31, 56)} = 3.98$, $p = .05$). RT was similar for both groups and did not change at transfer compared to initial learning (figures 1E and 1F).

3.4 Transfer to 45° Visuomotor Adaptation

Older adults demonstrated a larger benefit from prior training compared to young adults in terms of reducing DE at motor transfer to the 45° rotation (figures 2A and 2B, age group $\times$ presentation order interaction, $F_{(1, 32, 12)} = 3.88$, $p = .05$). Overall, young adults demonstrated

smaller IEE than older adults (main effect for age, $F_{(1, 31.87)}=13.99$, $p<.01$). Neither group demonstrated a change in IEE at transfer with respect to initial learning (figures 2C and 2D; no significant main effect or interactions with presentation order). There was a trend for RT to diminish at transfer (figures 2E and 2F, main effect for presentation order, $F_{(1, 31.93)}=2.98$, $p=.09$).

3.5 Spatial Working Memory Contributions to Motor Learning and Transfer

Young adults performed better on the spatial working memory assessments than the older adults ($p<.05$: card rotation, forward and backward Corsi blocks (See Supplemental Materials Table 3). To better understand the contributions of spatial working memory to motor learning and transfer, we examined correlations between performance on the visuomotor adaptation task during runs 3 and 13 and spatial working memory test scores. At transfer of learning (run 13), young adults with higher scores on the Corsi block backwards demonstrated shorter RT ($r=-.70$, $df=16$, $p>.01$). Young adults with shorter RT at initial learning also had lower average IEE ($r=.54$, $df=18$, $p=.02$). Taken together, these results indicate that young adults with better spatial working memory performance as well as shorter RT performed better at both motor learning and transfer. There were no significant differences between these correlations at initial learning versus at transfer in the young adult group, suggesting that working memory plays a role in both processes for this age group. In contrast to young adults, better SWM performance in older adults was related to longer RT at transfer. That is, older adults that did well on the Corsi block forward or the Card rotation task progressively increased their RT (Corsi, $r=.55$, $df=17$, $p=.02$) or had longer average RT at initial transfer (Card, $r=.48$, $df=17$, $p=.05$). RT, however, was not related to other visuomotor adaptation performance measures for the older adults.

Previous work in our lab has shown that SWM skills are beneficial to young adults during early learning of a visuomotor adaptation task (Anguera et al. 2010). We used the same spatial control and SWM task as those used in the Anguera et al. (2010, 2011) studies to examine contributions of SWM to initial learning and transfer here. Young adults that had the greatest decline in IEE in the visuomotor adaptation task at transfer of learning demonstrated greater accuracy in the SWM task ($r=-.54$, $df=16$, $p=.03$). This reinforces the previous observation from the neuropsychological data that young adults with better SWM performance learn and transfer the visuomotor adaptation task faster.

3.6 fMRI Results

Both young and older adults demonstrated at least partial motor savings at transfer of learning. To determine the neural substrates of this effect, we first contrasted brain activation within each group between initial learning (run 3) and transfer (run 13). Young adults demonstrated greater activation in the right superior frontal gyrus, cingulate gyrus and superior parietal lobule at initial learning compared to transfer (figure 4A, table 2), similar to what we have reported previously with a separate cohort of young adults (Seidler and Noll 2008). Older adults demonstrated greater activation in the right superior parietal lobule (figure 4B, table 2) at initial learning compared to transfer. Neither age group demonstrated greater activation at transfer compared to initial learning.

Between groups contrasts revealed that young adults activated the left postcentral gyrus, right superior frontal gyrus and middle occipital lobule greater than older adults at initial learning (figure 5A, table 3). Older adults had greater activation in the right postcentral gyrus and paracentral lobule than young adults (figure 5B, Table 3). At transfer of learning, young adults demonstrated greater activation in the left putamen and cingulate gyrus and the right caudate nucleus than the older adults (figure 6, Table 4). There were no regions in which older adults exhibited greater activation than the young adults at transfer of learning.

Using the masks of SWM activation for young and older adults that we obtained for each age group (with separate cohorts of participants) from Anguera et al. (2011), we identified brain regions that were active during visuomotor adaptation and transfer in the current study. Young adults demonstrated more active regions during initial learning compared to transfer that overlapped with the SWM network, including in the bilateral inferior frontal gyrus, bilateral superior and inferior parietal lobules, and regions of occipital cortex (Tables 5 and 6). Similarly, older adults demonstrated more active regions at initial learning compared to transfer that overlapped with their SWM network, suggestive of reduced cognitive contributions to motor transfer versus learning (Tables 7 and 8). Neither age group had any regions exhibiting greater activation at transfer (run 13) than learning (run 3) which overlapped with their respective SWM networks.

4. Discussion

The goal of the current study was to determine whether age affects the extent to which individuals rely upon spatial working memory for motor learning and transfer. Similar to our previous results, we found that older adults exhibited equal or even better transfer than young adults for some performance variables (Seidler, 2007). This is particularly striking given that older adults exhibited less learning than the young adults and therefore had a theoretically less well-formed motor representation to work with at motor transfer. We also found that the underlying cognitive and neural correlates of motor transfer differed for the two age groups.

Spatial working memory performance (card rotation, backward Corsi blocks) was related to better motor transfer for the young adults. These results parallel our previous finding of SWM contributions to visuomotor adaptation in young adults (Anguera et al., 2010) and other studies demonstrating cognitive contributions to early sensorimotor adaptation (Eversheim & Bock, 2001; Taylor & Thoroughman, 2007, 2008). Older adults demonstrated correlations between spatial working memory and performance at motor transfer but not for motor learning. This is consistent with our previous report of a lack of correlation between working memory performance and visuomotor adaptation in older adults (Anguera et al., 2011), suggesting that a failure to engage SWM may be related to motor learning deficits. Surprisingly, older adults with better spatial working memory performance demonstrated *longer* RTs at motor transfer. Additionally, longer reaction times were not correlated with better transfer performance. These results underscore the differential impact of cognitive contributions to motor learning and transfer in young versus older adults.

To better understand whether and how spatial working memory contributes to motor learning and transfer we used a mask based on brain activation associated with SWM task performance to identify brain regions exhibiting overlapping activation during both the SWM task and the visuomotor adaptation task. In our recent work, we found activation in early learning that overlapped with that associated with SWM for young adults (Anguera et al., 2010). This pattern is similar to other studies of visuomotor transformations (Blum et al., 2007, 2008). In contrast, we found that a failure to engage SWM networks during visuomotor adaptation by older adults was associated with learning deficits (Anguera et al., 2011). Similarly, in the current study, we found that young adults recruited many of the same brain regions for SWM as they do for initial learning of the visuomotor adaptation task, including the bilateral superior and inferior parietal lobules and inferior frontal gyri. At motor transfer, overlapping activation reduced and was limited to the right inferior frontal and inferior parietal gyri. These data suggest that working memory processes are engaged to a reduced extent for motor transfer versus learning. In the current study, neural overlap between the SWM task and visuomotor adaptation for the older adults was limited to the left

superior and inferior parietal lobules, with minimal change between initial motor learning and transfer.

Young adults engaged an extensive overlapping network of brain regions for motor learning and, to a reduced extent, for motor transfer including prefrontal, premotor, occipital, and parietal cortices. In contrast, overlapping activation for older adults was limited to the parietal cortex. The superior parietal lobule plays a role in working memory, specifically in the ability to manipulate and rearrange information (Koenigs et al. 2009). The lateral prefrontal cortex is thought to support mechanisms of attention, interference resolution, and retrieval mechanisms in working memory (Jonides et al., 2008). It is typical that older adults exhibit under-recruitment of the lateral prefrontal cortex in cognitive tasks (cf. Logan et al., 2002). The lack of prefrontal activation in older adults here may indicate that they are not engaging the appropriate attentional and strategic mechanisms required for motor learning.

Direct comparisons of young and older adults' brain activation patterns at initial motor learning revealed that young adults more strongly engaged the left postcentral gyrus, right superior frontal gyrus and right middle occipital lobule compared to older adults, whereas the older adults more strongly recruited the right postcentral gyrus and paracentral lobule. Finding greater activation in the right sensorimotor cortex for older adults is compatible with what has been reported for other motor tasks (Langan et al., 2010; Mattay et al. 2002; Talelli et al., 2008; for a recent review see Seidler et al., 2010). At motor transfer the young adults demonstrated greater activation in the basal ganglia and cingulate gyrus compared to older adults. Both of these regions have been reported to contribute to visuomotor adaptation (Seidler et al. 2006b), and to play a role in error detection and correction processes (Falkenstein et al. 2001; Botvinick et al. 2004). The present findings suggest that young adults may be better able to engage these processes to modulate performance at transfer of learning.

Both age groups exhibited transfer under the two rotation presentation orders, with the older adults exhibiting more transfer than the young to the 45° condition and the young exhibiting more than the old to the 30° condition. We have previously shown that transfer is greater for young adults when the final rotation reflects an addition of previously experienced rotation magnitudes (i.e. 30°, 15°, 45°) than when it requires a subtraction (i.e., 45°, 15°, 30°, Seidler, 2005). This is consistent with the notion that adaptation occurs as a gradual process starting with small angles of rotation and proceeding up to the desired rotation angle (Abeele & Bock, 2001a, 2001b). The current findings suggest that contrasting transfer mechanisms for additive versus subtractive processes are compounded by age.

5. Conclusions

In conclusion, we found that both age groups exhibited positive motor transfer for at least some variables. Young adults exhibited both neural and behavioral overlap between SWM and motor learning and transfer performance. For older adults, neural overlap between SWM and motor learning and transfer was restricted to the parietal cortex and showed minimal changes from motor learning to transfer.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Abbreviations

SWM	spatial working memory
RT	reaction time
DE	directional error
IEE	initial endpoint error

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Research Highlights

- Working memory correlates with motor learning and transfer in young adults.
- Young adults have neural overlap between spatial working memory and motor learning.
- Older adults (OA) exhibit reduced learning but equal transfer compared to young adults.
- OA show little neural overlap between spatial working memory and learning/transfer.
- Cognitive contributions to motor learning and transfer differ by age.

Figure 1. Performance measures for the 30° visuomotor adaptation for both young (YA) and older (OA) adults. 3A. YA DE, 3B. OA DE, 3C. YA IEE, 3D. OA IEE, 3E. YA RT, 3F. OA RT.

Figure 2. Performance measures for the 45° visuomotor adaptation for both young (YA) and older (OA) adults. 4A. YA DE, 4B. OA DE, 4C. YA IEE, 4D. OA IEE, 4E. YA RT, 4F. OA RT.

Figure 3. Correlations between kinematic variables (DE and IEE) and verbal working memory (Reading Span Score) for older adults.

Figure 4.

Areas exhibiting greater activation at motor learning than transfer (run 3>13). 4A. Young adults show greater activation in the right superior frontal gyrus, cingulate cortex and parietal lobe during motor learning compared to transfer (run 3>13). 4B. Older adults show greater activation in the right superior parietal lobe during motor learning compared to transfer (run 3>13).

Figure 5.

Age differences in brain activation at initial motor learning. 5A. Areas in which young adults (YA) exhibit greater activation than older adults (OA) during motor learning (run 3). YA demonstrated greater activation in the left postcentral gyrus, right superior frontal gyrus and middle occipital lobule compared to OA. 5B. Areas in which older adults (OA) exhibit greater activation than young adults (YA) during motor learning (run 3). OA demonstrated greater activation in the right postcentral gyrus and paracentral lobule compared to YA.

Figure 6. Areas in which young adults (YA) exhibit more activation than older adults (OA) during transfer of learning (run 13). YA demonstrated greater activation in the left putamen, right caudate nucleus, and left cingulate gyrus compared to OA.

Table 1

Brief description of spatial working memory assessments and measurement units.

Neuropsychological Assessment	Description	Measurement Unit
Thurston's Card Rotation	Timed task: Compare two 2D images then state if the reference image has been rotated without being turned over.	Number correct
Corsi Block Tapping	The experimenter taps a sequence of blocks and the participant must reproduce the sequence either in the same order (forward) or reverse order (backward).	Number of correct trials

Table 2

Regions with greater activation during initial learning (Run 3) compared to transfer (Run 13).

Anatomical Location	Brodmann's Area	Cluster Size	Coordinates of Peaks	Z score
YA				
Frontal Lobe				
R Superior frontal gyrus	BA9	103	28 42 28	3.91
R Cingulate gyrus	BA32	10	2 16 42	3.18
Parietal Lobe				
R Superior parietal lobule	BA7	47	14 -62 58	3.57
OA				
Parietal Lobe				
R parietal lobe	BA40	19	20 -38 58	3.43

Table 3

Age differences in initial learning activation (Run 3).

Anatomical Location	Brodmann's Area	Cluster Size	Coordinates of Peaks	Z score
YA>OA				
Frontal Lobe				
Pre Supplementary Motor Area	BA6	19	12 24 62	4.06
Parietal Lobe				
L Postcentral gyrus	BA2	53	-58 -24 46	4.03
Occipital Lobe				
R Middle occipital lobule	BA19	22	50 -60 -6	3.46
OA>YA				
Parietal Lobe				
R postcentral gyrus	BA43	14	42 -16 18	3.53
R Paracentral lobule	BA4	14	10 -28 76	3.57

Table 4

Regions exhibiting greater activation for YA than OA at transfer (Run 13).

Anatomical Location	Brodmann's Area	Cluster Size	Coordinates of Peaks	Z score
Frontal Lobe				
L Cingulate gyrus	BA32	51	-16 36 -6	3.68
Subcortical Regions				
L Putamen		95	-24 12 2	3.7
R Caudate nucleus		235	16 14 2	4.66

Table 5

YA Visuomotor adaptation activation during initial learning masked with SWM task activation.

Anatomical Location	Brodmann's Area	Cluster Size	Coordinates of Peaks	Z score
Frontal Lobe				
L Middle frontal gyrus	BA9	24	-54 8 38	4.68
L Inferior frontal gyrus	BA6	13	-52 6 24	4.75
R Inferior frontal gyrus	BA6	113	54 6 32	4.68
R Inferior frontal gyrus	BA6		50 4 22	4.34
R inferior frontal gyrus	BA6		46 2 32	4.23
Parietal Lobe				
L Superior parietal lobule	BA7	16	-18 -70 54	3.53
L Inferior parietal lobule	BA19	23	-48 -68 -2	5.02
L Inferior parietal lobule	BA40	17	-34 -48 44	3.61
R Superior parietal lobule	BA7	35	34 -62 54	5.24
R parietal lobule	BA40	98	42 -40 44	5.59
R Inferior parietal lobule	BA40		46 -44 54	5.41
Occipital Lobe				
L Middle occipital gyrus	BA19		-42 -76 -4	3.79
R Inferior occipital gyrus	BA18	40	40 -88 -8	3.78
R Inferior occipital gyrus	BA18		36 -94 -2	3.53
R Middle occipital gyrus	BA19/18		42 -86 2	3.63

Table 6

YA Visuomotor adaptation activation during transfer masked with SWM task activation.

Anatomical Location	Brodmann's Area	Cluster Size	Coordinates of Peaks	Z score
Frontal Lobe				
R Inferior frontal gyrus	BA44	99	54 6 32	4.45
R Inferior frontal gyrus	BA6		48 2 26	3.56
R Inferior parietal lobule	BA40	27	46 -44 54	4.25
Parietal Lobe				
R Inferior parietal lobule	BA40		42 -42 44	3.73

Table 7

OA Visuomotor adaptation activation during initial learning masked with SWM task activation.

Anatomical Location	Brodmann's Area	Cluster Size	Coordinates of Peaks	Z score
Parietal Lobe				
L Superior parietal lobule	BA7	82	-20 -64 56	3.49
L Superior parietal lobule	BA7		-28 -56 54	3.41
L Inferior parietal lobule	BA40	194	-36 -44 54	4.00
L Inferior parietal lobule	BA40		-48 -34 52	3.76

Table 8

OA Visuomotor adaptation activation during transfer masked with SWM task activation.

Anatomical Location	Brodmann's Area	Cluster Size	Coordinates of Peaks	Z score
Parietal Lobe				
L Superior parietal lobule	BA7	82	-30 -56 56	4.19
L Superior parietal lobule	BA7		-20 -64 56	3.59
L Inferior parietal lobule	BA40	194	-36 -46 54	5.11
L Inferior parietal lobule	BA40		-45 -35 50	4.85