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RESEARCH ARTICLE

Advanced spatial knowledge of target location eliminates age-related differences in early sensorimotor learning

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Abstract

Motor learning has been shown to decline in healthy aging, particularly in the early stages of acquisition. There is now ample evidence that motor learning relies on multiple interacting learning processes that operate on different timescales, but the specific cognitive mechanisms that contribute to motor learning remain unclear. Working memory resources appear to be particularly important during the early stages of motor learning, and declines in early motor learning have been associated with working memory performance in older adults. We examined whether age differences in the early stages of motor learning could be reduced or eliminated by reducing the spatial working memory demands during a force-field adaptation task. Groups of younger and older adults made center-out reaching movements to spatial targets either in a repeating four-element sequence, or in a random order. Participants also performed a battery of cognitive tests to further investigate the potential involvement of associative memory, spatial working memory, and procedural learning mechanisms in the early stage of motor learning. Although all groups adapted their movements equally well by the end of the learning phase, older adults only adapted as quickly as younger adults in the sequence condition, with the older adults in the random group exhibiting slower learning in the earliest stage of motor learning. Across all participants, early motor learning performance was correlated with recognition memory performance on an associative memory test. Within the younger random group, who were able to adapt as quickly as the sequence groups, early motor learning performance was also correlated with performance on a test of procedural learning. These findings suggest that age differences in early stages of motor learning can be eliminated if the spatial working memory demands involved in a motor learning task are limited. Moreover, the results suggest that multiple cognitive resources may be utilized during the early stage of learning, and younger adults may be more flexible than older adults in the recruitment of additional cognitive resources to support learning when spatial working memory demands are high.

Keywords Sensorimotor adaptation · Spatial working memory · Associative memory · Aging · Implicit memory

Introduction

One of the hallmark characteristics of the human motor system is the ability to adapt motor output to changes in the environment. Numerous sensorimotor adaptation tasks have been developed to study the learning processes involved in adaptive motor behavior. There is now ample evidence that such learning involves multiple learning processes that operate on different timescales (McDougle et al. 2015, 2016; Smith et al. 2006; Taylor et al. 2014; Trewartha et al. 2014; Trewartha and Flanagan 2016; Wolpert and Flanagan 2016). The multi-process framework proposes that trial-to-trial sensorimotor learning arises from the complementary contributions of a fast process that adapts quickly, but decays quickly, and a slow process that adapts and decays more gradually (e.g., Smith et al. 2006).

The focus of recent research has been on delineating the nature of the cognitive mechanisms underlying the fast and slow processes for motor learning. This line of work has suggested a link between the fast process and explicit memory resources (Keisler and Shadmehr 2010; McDougle et al. 2015; Taylor et al. 2014). Additional work has

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highlighted an important association between working memory resources—especially spatial working memory resources—and the fast process that is thought to dominate early stages of motor learning (Anguera et al. 2010, 2011; Fernández-Ruiz et al. 2011; Seidler et al. 2012; Trewartha et al. 2014). Additional evidence suggests that the slow process for motor learning—thought to dominate later stages of learning—is associated with implicit memory resources (McDougle et al. 2015; Taylor et al. 2014).

These findings have significantly advanced our understanding of the cognitive contributions to motor learning, but there is yet no consensus about either the precise nature, or number of cognitive mechanisms that underlie motor learning (McDougle et al. 2015, 2016). In fact, a number of other cognitive mechanisms are thought to be involved, including explicit strategies, decision-making processes, performance monitoring, and associative memory processes (Anguera et al. 2009; Bock and Girgenrath 2006; Mazzoni and Krakauer 2006; Taylor et al. 2010; Taylor and Ivry 2011; Trewartha et al. 2014). However, the precise way in which multiple cognitive mechanisms interact during the course of learning a new motor skill is not yet clear. Moreover, the majority of the studies investigating the cognitive contributions to motor learning have used visuomotor rotation paradigms, with fewer using force-field adaptation tasks. It is unclear whether these two types of tasks rely on the same or different underlying cognitive processes. It is important to note that there is some evidence that the computational and neural mechanisms involved in these two tasks differ (Kalaska et al. 1990; Diedrichsen et al. 2005).

A number of approaches have been employed to delineate the nature of the multiple mechanisms underlying motor learning, including mathematical modeling (e.g., Lee and Schweighofer 2009; Smith et al. 2006), verbal reports of aiming direction (e.g., McDougle et al. 2015; Taylor et al. 2014), experimental manipulations of cognitive resources available during motor learning (e.g., Keisler and Shadmehr 2010; Lee and Schweighofer 2009), and comparisons of motor learning performance between groups of individuals that differ in the putative cognitive mechanisms underlying motor learning (e.g., Anguera et al. 2011; Bock and Girgenrath 2006; Fernández-Ruiz et al. 2000; Trewartha et al. 2014).

The extant evidence that spatial working memory resources contribute to early stages of motor learning comes primarily from correlative approaches to associating performance on independent spatial working memory tasks with early motor learning performance (Anguera et al. 2010, 2011; Christou et al. 2016; Trewartha et al. 2014). These findings are important in showing that individual differences in working memory capacity are related to the ability to learn motor skills. However, it is difficult to draw causal inferences about the role of spatial working memory resources in early motor learning with correlational evidence. Some experimental evidence has been provided in the form of dual-task studies that divide attention between a motor learning task and an unrelated secondary task. This research demonstrates that early stages of motor learning require cognitive resources, particularly when making spatial transformations during visuomotor adaptation (Eversheim and Bock 2001; Taylor and Thoroughman 2007, 2008; Seidler et al. 2012), corroborating the correlative data mentioned above.

Motor learning is typically impaired in later adulthood, particularly during the early stages of acquisition of a new motor task (Anguera et al. 2011; Buch et al. 2003; Fernández-Ruiz et al. 2000; Huang and Ahmed 2014; King et al. 2013; Seidler 2007). A few recent studies have highlighted the correlation between spatial working memory resources and age-related declines in early stages of motor learning (Anguera et al. 2011; Trewartha et al. 2014). An important prediction arising from these findings is that experimentally reducing the working memory resources required to perform a sensorimotor adaptation task should limit or eliminate age differences in the early stages of motor learning. Given that previous work on motor learning impairments in older adults has predominantly relied on visuomotor adaptation tasks, it is also important to verify the role of spatial working memory resources in early stages of learning in older adults in the context of force-field adaptation tasks. To this end, the current study manipulated the spatial working memory demands involved when younger and older adults performed a force-field adaptation task. Younger and older adults were split into groups who adapted to a force-field while reaching to four different spatial targets either in a repeating four-element sequence, or in a random order. Performing the task in the context of a repeating sequence provides advanced spatial information about the location of the target on each trial, whereas the random condition does not. In multi-target force-field adaptation studies, the movement and forces required (e.g., the specific direction the participant will have to push) to compensate for the perturbation differs for each spatial location. Having advance spatial information reduces the extent to which that information would have to be retrieved into working memory during the trial. Thus, the goal of this manipulation in the sequence condition is to minimize the spatial working memory resources required to maintain, and recall a mental representation of the perturbation—and the required compensatory actions—from trial to trial to facilitate learning.

In this study we tested the hypothesis that age differences in the early stages of motor learning would be eliminated if the working memory demands of the adaptation task were reduced in the sequence condition compared to the random condition. Additionally, to further specify the nature of the cognitive processes underlying age differences in motor learning, we also administered a battery of cognitive tasks to assess the relationship between early stages of motor learning and spatial working memory, associative memory, and procedural learning processes, all of which have been shown to contribute to motor learning (Anguera et al. 2010; Mazzoni and Krakauer 2006; McDougle et al. 2015; Taylor et al. 2014; Trewartha et al. 2014).

Methods

Participants

Thirty-one younger adults ($M = 20.4$, SD = 2.3, 17 women) and 30 older adults ($M = 68.7$, SD = 7.2, 18 women) were recruited to participate in this experiment. Younger adults were recruited from the undergraduate and graduate student populations at Michigan Technological University, and the older adults were recruited from the Houghton, Michigan community. Importantly, the older adults were all very high functioning adults living independently. A health questionnaire was administered to the older participants to ensure that they were in good self-reported health and had no significant medical or neurological conditions. All participants were right-handed and had normal, or corrected-to-normal vision. The experimental protocol was reviewed and approved by the institutional review board at Michigan Technological University.

Materials

While seated in a comfortable chair, participants made out and back reaching movements while grasping a handle attached to a robotic device capable of applying forces to the handle (Endpoint KINARM; BKIN Technologies). A circular cursor (5 mm radius), representing the position of the handle in the horizontal plane, and circular targets (10 mm radius) were projected on a horizontally oriented display mirror located halfway between the display and the plane of handle motion. Sensors in the manipulandum recorded the position of the hand in the plane of motion, as well as forces applied by the participant to the handle.

On each trial, a starting circle appeared at the center of the screen and participants were required to move the cursor to the center of the starting position and hold for 250 ms, at which point a target circle appeared. The targets could appear in one of four locations: 15 cm toward (near target), away from (far target), to the left, or to the right of the starting circle (Fig. 1a). During the outward reaching movements to the targets, the manipulandum applied no force (null field trial), a clockwise (CW force-field trial) or a counterclockwise (CCW force-field trial) viscous curl field, or a force channel (error-clamp trial). In the curl-field trials, the robot applied a force that was proportional to the velocity of the handle, but perpendicular to the instantaneous direction of motion. The relation between force (F), and velocity (V) was defined by the equation $F = CV$, where C is the matrix $C = 20[0\ f(n);\ -f(n)\ 0]$ Ns/m. The task parameter on the nth trial was $f(n) = 0$ for the null field, $f(n) = +1$ for the CW force field, and $f(n) = -1$ for the CCW force field. Generally, the force fields perturbed the hand in the rightward (CW) or leftward (CCW) direction, relative to the direction from the start to the end target. In the error-clamp trials, the manipulandum simulated a channel from the start to the end target. In these trials, any movements perpendicular to the direction of movement to the target were countered by opposing forces from the robot, compelling the hand to move in a straight line to the target, effectively eliminating kinematic errors. Specifically, the channel was implemented as a damped spring with 6000 N/m stiffness and 1 Ns/m viscosity.

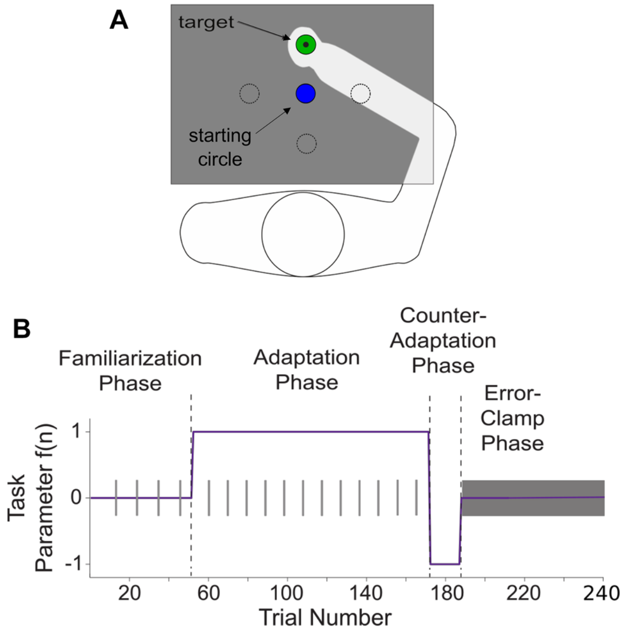

Fig. 1 **a** Top-down participant's view of the experimental paradigm with a central starting circle and four radial targets presented on a horizontally oriented display mirror. A single target is illuminated, depicting what would be displayed on the screen in an example trial. The positions of the other three potential targets would be invisible during a given trial, but are depicted here as dotted circles for demonstration. **b** Schedule for force-field perturbations applied across outward reaching movements during the experiment (purple trace). Vertical gray lines denote trials in which a force channel was applied to track the participant's memory for the load. In the final error-clamp phase, all outward reaches were performed in a force channel

Procedure

Sensorimotor adaptation task

Participants made alternating out and back reaching movements to four targets from a central starting position

(Fig. 1a). At the start of each trial, participants moved the cursor to the start position and were required to hold within 5 mm of the center of the start target for 200 ms. At that time, the starting circle turned from green to red, and a green target circle appeared at one of the four target locations, serving as a go signal. Participants were then free to initiate their movement to the target at any time, but were required to move the cursor to within 5 mm of the center of the target in 350–500 ms. Upon acquiring the target it turned red, and the green start target appeared once again, signaling a movement back to the start position. Feedback was displayed on the screen after each movement to inform the participant if the movement was "too slow," "too fast," or "good." Participants were instructed to obtain a "good" feedback by reaching the target in the time allowed as often as possible during the experiment.

The experiment consisted of four blocks of trials that differed in terms of the forces applied during the outward reaching movements to the targets (Fig. 1b). In the first familiarization phase of the experiment, 52 outward reaching movements were performed in a null field. The second adaptation phase consisted of 128 trials performed either with a CW or CCW force field, counterbalanced across participants in each group. The third, counter-adaptation phase included 12 trials performed in a force-field opposite to the one experienced in the adaptation phase. Finally, the fourth phase was an error-clamp phase that consisted of 36 trials performed in a force channel. For all inward movements back to the starting position, a force channel was implemented so that participants would not experience any kinematic errors. The entire experiment included 480 trials, but all analyses were focused on the 240 outward trials. During the course of the experiment, a number of error-clamp trials were included in the outward movement trials to measure the state of adaptation (Smith et al. 2006; Trewartha et al. 2014). Specifically, trials 15, 26, 37, and 48 in the familiarization phase, and trials 67, 78, 89, 100, 111, 122, 133, 144, 155, 166, 177, and 188 in the adaptation phase were performed in a force channel.

Groups of younger and older adults were randomly assigned either to a sequence group or a random group. All groups performed the same procedures described above, with the only difference being the order in which the targets were displayed. In the sequence groups, participants received the same repeating four-element sequence for the entire experiment (i.e., right target, far target, left target, and near target). For the random groups, the order of targets was randomly determined, with the only constraint being that all four targets were equally represented across the experiment.

Cognitive tasks

A battery of three cognitive tasks was also administered to all participants using the Psychology Experiment Building Language (PEBL; Mueller and Piper 2014) to provide measures of spatial working memory, associative memory, and procedural learning, respectively.

Corsi test

A computerized version of the traditional Corsi blocks test (Corsi 1972) for assessing spatial working memory capacity was administered. Briefly, an array of nine squares is presented on the screen on a given trial. Participants observe as a subset of those squares changes color in a predetermined order. Participants are then required to repeat the sequence in the same order by clicking on the squares with the computer mouse. The task starts with a sequence size of two, and increases by one as long as the participant continues to correctly repeat the sequence that was presented. Once participants make three consecutive errors at a given sequence length, the task ends. The longest sequence correctly repeated is recorded as the participant's block span.

Paired associates

Participants performed a verbal paired-associates learning task that included assessment of both recognition and recall memory in three blocks of trials each. In each block, during the learning phase, participants passively viewed 12 pairs of words presented in the center of the computer screen. For the recall tests, participants were shown one of the words from each word pair in the center of the screen one at a time, paired with a response entry box into which participants typed the second word they recalled being part of the pair. In the event that participants could not recall the second word, they were asked to guess. In the recognition tests, one of the words from each learned pair was presented in the center of the top of the screen, along with 12 possible word pairs presented in a 4 × 3 grid in the center of the screen. Participants were asked to identify the word that they recognized as part of the original pair by clicking on their selection. In both the recall and recognition test phases, the accuracy and reaction time for each response were recorded.

Pursuit rotor task

A computerized version of the classic pursuit rotor task was administered to provide a measure of procedural learning. On a given trial, participants are shown a dark gray ring (15 cm radius), with a small red target circle (1 cm radius) located on the ring. At the beginning of the trial, the red circle began to travel around the ring, completing two revolutions in each 15 s trial. The participants were instructed to use the mouse to guide the cursor so that it stayed on the target circle as much as possible throughout each trial. Participants performed four consecutive trials of the pursuit rotor task and the amount of time spent on the target was recorded for each trial. A procedural learning score was calculated by subtracting the average time spent on the target on the first two trials from the average time spent on the target on the last two trials for each participant.

Data analysis

Sensorimotor adaptation task

The x and y positions of the handle, in the horizontal plane, and the x and y forces exerted by the handle were recorded at 1000 samples/s. The raw position and force data were digitally smoothed using a fourth-order, low-pass Butterworth filter with a cutoff frequency of 14 Hz. The x and y velocities of the handle were computed from the smoothed position data using a first-order central difference equation. The counterbalanced groups who experienced different force fields (CW and CCW) in the different stages of the experiment were combined for all analyses by flipping the sign for those subjects who had experienced the CCW force field first in the adaptation phase. To assess learning during the course of the experiment, we calculated deviation scores for non-channel trials, and an adaptation index for force-channel trials. Deviation scores were defined as the deviation perpendicular from a straight line connecting the start position and the target at the moment of peak velocity in the direction of movement to the target. For analysis, we created epochs by averaging the deviation scores across every four consecutive trials, including one movement to each target. To quantify the level of adaptation in the force-channel trials, we first determined, based on the velocity of the handle along the channel, the time-varying force that would have had to be generated to perfectly compensate for force field throughout the movement, had the force field been applied. Using a least-squared regression (without an intercept), we computed an adaptation index defined as the slope of the relation between the ideal force and the actual force that was produced in the channel (Smith et al. 2006; Trewartha et al. 2014).

Statistical analyses

For all of the statistical analyses presented below, pairwise comparisons to assess simple effects were reported with a Bonferroni correction.

Results

Cognitive task performance

The cognitive test battery provided us with individual difference measures of spatial working memory, associative memory, and procedural learning. To assess group differences in performance of each of the cognitive tasks (Table 1), we conducted a univariate ANOVA on each dependent variable with age group (younger vs. older adults) and experimental group (sequence vs random) as independent variables. For the block span measure in the Corsi test, there was a significant effect of age group such that older adults exhibited a significantly shorter block span than younger adults [$F(1, 57) = 6.1$, $p < 0.05$, $\eta^2 = 0.10$], but the main effect of the experimental group and the interaction were not significant ($p > 0.3$).

For the paired-associates task, the same pattern was observed for all dependent measures. There was a significant main effect of age group such that older adults performed worse than younger adults for recognition accuracy [$F(1, 57) = 17.8$, $p < 0.001$, $\eta^2 = 0.24$], recognition reaction time [$F(1, 57) = 61.1$, $p < 0.001$, $\eta^2 = 0.52$], recall accuracy [$F(1, 57) = 25.1$, $p < 0.001$, $\eta^2 = 0.32$], and recall reaction time [$F(1, 57) = 15.5$, $p < 0.001$, $\eta^2 = 0.21$]; however, no other comparisons were significant ($p \geq 0.056$).

Table 1 Cognitive test scores summarized across groups

Group	Corsi blocks test	Pursuit rotor task	Paired-associate memory task			
	Block span	Learning score (ms)	Recall accuracy (%)	Recall RT (ms)	Recognition accuracy (%)	Recognition RT (ms)
Younger sequence group	6.6 (±0.4)	819.5 (±472.1)	50.5 (±0.04)	5031.6 (±457.0)	78.1 (±0.03)	4321.5 (±513.2)
Older sequence group	5.3 (±0.4)	1197.6 (±400.9)	28.6 (±0.04)	9333.2 (±1075.9)	60.0 (±0.03)	7346.0 (±771.2)
Younger random group	6.5 (±0.4)	1227.1 (±363.2)	46.7 (±0.05)	6628.6 (±538.2)	76.0 (±0.03)	4774.0 (±531.8)
Older random group	5.6 (±0.4)	980.0 (±347.3)	30.00 (±0.03)	8104.3 (±731.3)	66.0 (±0.04)	7156.0 (±762.1)

For the pursuit rotor task, the learning score was calculated as the difference in the time spent on target (ms) between the last trial and the first trial. For all measures, mean scores are presented with standard error in parentheses

Finally, for the pursuit rotor task we conducted a trial (4) by age group (younger vs older adults) by experimental group (sequence vs random) ANOVA to assess group differences in implicit learning. There was a significant main effect of age group [$F(1, 57) = 156.9$, $p < 0.001$, $\eta^2 = 0.73$] such that older adults spent less time on the target than younger adults overall. There was also a significant main effect of trial [$F(1, 57) = 156.9$, $p < 0.001$, $\eta^2 = 0.73$] such that the time spent on the target was lowest in the first trial compared to trials 2 through 4 (all $p < 0.001$), but no other comparisons were significant ($p > 0.4$). Thus, older adults generally spent less time on the target, but both older and younger adults learned to a similar extent across the experiment.

Taken together, these findings show that older adults performed worse than younger adults on our measure of spatial working memory and associative memory, but not procedural learning. These observations are consistent with the cognitive aging literature (Craik 2000; Hoyer and Verhaeghen 2006). Importantly, no systematic differences were observed between our experimental groups, on any of the cognitive dimensions, beyond the difference attributable to the age group.

Sensorimotor adaptation

Kinematics of the motor learning task

The data presented in Fig. 2a, b show the perpendicular deviation from a straight line connecting the start position and the target on each four-trial epoch. We specifically tested the hypothesis that manipulating the working memory demands during force-field adaptation would impact early learning rather than later learning. To assess differences between early and late learning, we defined early learning as the first half of the adaptation phase and late learning as the second half. To assess group differences in learning during the adaptation phase we conducted an epoch (32) by learning phase (early vs late) by age group (younger vs older adults) by experimental group (sequence vs random) ANOVA. This analysis revealed significant main effects of the learning phase [$F(1, 57) = 156.9$, $p < 0.001$, $\eta^2 = 0.73$], and epoch [$F(15, 43) = 39.2$, $p < 0.001$, $\eta^2 = 0.93$]. There were also significant interactions between epoch and experimental group [$F(15, 43) = 2.8$, $p < 0.01$, $\eta^2 = 0.49$], between epoch and learning phase [$F(15, 43) = 8.6$, $p < 0.001$, $\eta^2 = 0.75$], and between epoch, learning phase, and experimental group [$F(15, 43) = 2.7$, $p < 0.05$, $\eta^2 = 0.45$]. Importantly, there was also a significant four-way interaction between epoch, learning phase, age group, and experimental group [$F(15, 43) = 2.1$, $p < 0.05$, $\eta^2 = 0.42$]. Bonferroni corrected pairwise comparisons revealed that in older adults, the deviation was significantly larger for the random group compared to the sequence group for the first adaptation epoch ($p < 0.01$) and again for the eighth epoch in the early learning phase ($p < 0.01$). No epochs differed between groups in the late learning phase. In the younger adults, the deviation was significantly greater for the sequence group compared to the random group in the seventh epoch during early learning ($p < 0.01$), but no other epochs differed between groups in either learning phase. No other main effects or interactions were significant. This analysis revealed a small, but reliable effect of the sequence manipulation in the older adults, but not the younger adults, particularly in the earliest part of the adaptation phase.

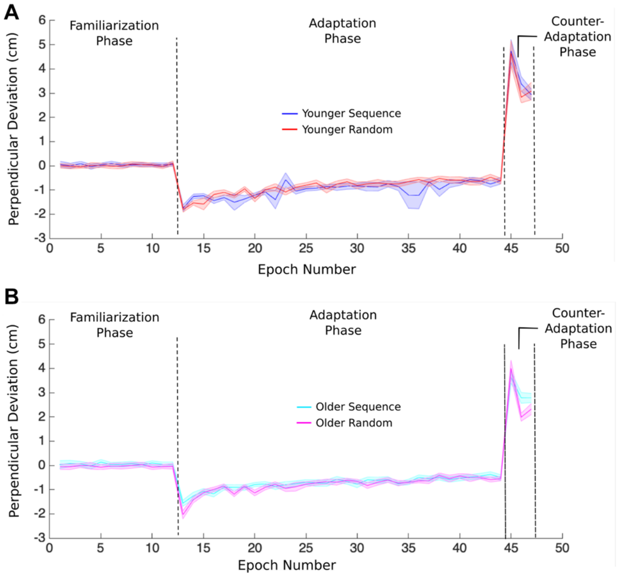

Fig. 2 Averages of the perpendicular deviation from a straight line between the starting circle and the target in the sequence and random conditions. Each epoch represents the average of four consecutive trials, including one movement to each target. The top panel (**a**) shows the perpendicular deviation for younger adult groups, whereas the bottom panel (**b**) shows the older adult groups. The heights of the shaded regions denote ± 1 standard error

To assess whether there were differences in performance during the counter-adaptation phase, we conducted an epoch (3) by age group (younger vs older adults) by experimental group (sequence vs random) ANOVA. There was a main effect of epoch [$F(2, 56) = 37.9$, $p < 0.001$, $\eta^2 = 058$] and a main effect of age group [$F(15, 43) = 39.2$, $p < 0.001$, $\eta^2 = 0.93$] such that younger adults exhibited larger deviations than older adults overall. There was also a significant epoch by experimental group interaction [$F(2, 56) = 3.9$, $p < 0.05$, $\eta^2 = 0.13$], but no other effects were significant. Pairwise comparisons revealed that the random groups exhibited smaller deviations during the second epoch of the counter-adaptation phase compared to the sequence groups ($p < 0.01$), but there was no difference in the other epochs.

Adaptation revealed by channel trials

Figure 3 presents the adaptation index data from channel trials in the null field, adaptation, and error-clamp phases for the younger adult groups (Fig. 3a) and older adult groups (Fig. 3b). The adaptation index provides a way of quantifying the level of adaptation across the experiment by relating the actual forces exerted into the channel to the ideal force that would be required for perfect compensation on each channel trial ("Methods"), effectively providing an estimate of the memory of the load developed over the course of the experiment. From Fig. 3, it is clear that all four groups adapted to the perturbation during the adaptation phase and exhibited residual memory of that learning in the error-clamp phase. To test the hypothesis that reduced working memory load would improve early motor learning in older adults, and given that differences in deviation scores between the random and sequence groups only occurred during the first half of the adaptation phase, we conducted a trial (6) by experimental group (sequence vs random) by age group (younger vs older adults) ANOVA on the first half of the channel trials from the adaptation phase. This analysis revealed a significant main effect of trial [$F(5, 52)=30.6$, $p<0.001$, $\eta^2=0.75$]. There were also significant interactions between the trial and experimental group [$F(5, 52)=3.2$, $p<0.05$, $\eta^2=0.24$], between the trial and age group [$F(5, 52)=5.4$, $p<0.001$, $\eta^2=0.34$], and, importantly, between the trial, age group, and experimental group [$F(5, 52)=3.5$, $p<0.01$, $\eta^2=0.25$]. Pairwise comparisons revealed that for older adults, the adaptation index was significantly lower in the first channel trial for the random compared to the sequence group ($p<0.05$), but no other trials reached significance. For younger adults there were no significant differences between the experimental groups for any of the trials. Similar to the deviation scores, this analysis of the channel trials during early learning revealed that the random group in the older adults performed worse than the sequence group, but only for the earliest stage of motor learning. Despite those early differences, the older random group quickly caught up to the older sequence group by the second channel trial in the adaptation phase.

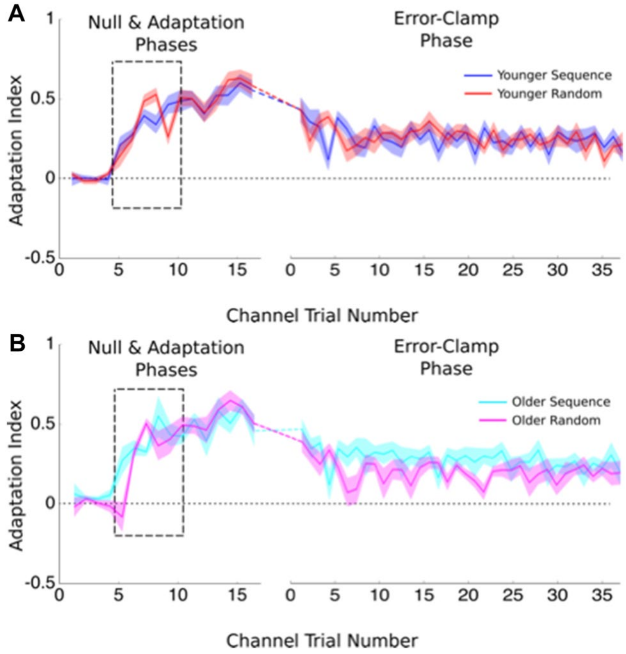

Fig. 3 **a**, **b** The average adaptation index for all channel trials in the younger sequence (blue trace), younger random (red trace), older sequence (cyan trace), and older random (magenta trace) groups across all experimental phases. The heights of the shaded regions denote ±1 standard error. The dotted squares denote the channel trials within the early stage of learning, during which the experimental manipulation of working memory demands was hypothesized to have the largest effect

From visual inspection of Fig. 3b, it appears that there could be a difference between the older adult random and sequence groups in the retention of initial learning during the error-clamp phase. To test for group differences in retention, we conducted a trial (36) by experimental group (sequence vs random) by age group (younger vs older adults) ANOVA on the error-clamp phase. This analysis revealed a main effect of trial [$F(35, 23)=4.2$, $p<0.001$, $\eta^2=0.87$], and an interaction between trial and age group [$F(35, 23)=3.8$, $p<0.01$, $\eta^2=0.85$], but no significant interactions with experimental group. Pairwise comparisons revealed that the adaptation index was larger for older adults on error-clamp trial 4 ($p<0.05$), but smaller for older adults on trials 5, 6, 7, 17, 21, and 27 compared to younger adults (all $p<0.05$). This general pattern of reduced retention during the error-clamp phase in older compared to younger adults is consistent with previous observations using a force-field adaptation task (Trewartha et al. 2014). This analysis shows that manipulating the working memory resources involved in motor learning did not have a systematic effect on the retention of initial learning in the error-clamp phase for either age group.

Additional behavioral analysis

To further characterize the behavioral performance of younger and older adults during the motor learning task, we measured reaction time and movement time, and averaged across channel and non-channel trials, respectively (Table 2). To confirm that participants in the sequence groups were able to acquire the repeating sequence, we compared average reaction times between groups for non-channel trials across each phase of the experiment. We conducted an experimental phase (familiarization, adaptation, counter-adaptation) by experimental group (sequence vs random) by age group (younger vs older adults) ANOVA. There

Table 2 Averaged reaction time (RT) and movement time (MT) data for non-channel trials

Group	RT familiarization trials	RT adaptation trials	RT counter-adaptation trials	MT familiarization trials	MT adaptation trials	MT counter-adaptation trials
Younger sequence group	392.7 (±38.6)	367.0 (±42.3)	384.7 (±124.4)	435.2 (±28.9)	528.8 (±209.0)	721.6 (±274.2)
Older sequence group	520.1 (±92.8)	512.5 (±174.8)	503.3 (±206.3)	438.3 (±52.7)	488.8 (±50.6)	608.1 (±106.0)
Younger random group	454.2 (±157.2)	448.3 (±124.3)	470.1 (±146.8)	432.4 (±30.4)	482.7 (±52.0)	648.4 (±171.1)
Older random group	574.8 (±162.4)	575.0 (±158.8)	619.9 (±177.7)	480.0 (±113.5)	490.0 (±64.6)	650.1 (±258.0)

Mean scores are presented with standard deviation in parentheses

were significant main effects of age group [$F(1, 57) = 17.0$, $p < 0.001$, $\eta^2 = 0.23$] such that older adults exhibited slower RT than younger adults overall, and a main effect of experimental group [$F(1, 57) = 5.8$, $p < 0.05$, $\eta^2 = 0.09$] such that the sequence groups exhibited faster RT than the random groups overall. No other effects were significant. These results provide behavioral evidence that participants were able to acquire the repeating sequence, it benefited their performance, and the sequence was acquired equally by both age groups.

For movement times, we conducted the same experimental phase (familiarization, adaptation, counter-adaptation) by experimental group (sequence vs random) by age group (younger vs older adults) ANOVA. There was a main effect of experimental phase [$F(2, 56) = 33.2$, $p < 0.001$, $\eta^2 = 0.54$], but no other effects were significant. Pairwise comparisons revealed that overall, MT was fastest in the familiarization phase, slower in the adaptation phase, and slowest in the counter-adaptation phase (all $p < 0.01$). These movement time data demonstrate that there were no systematic differences between age groups or experimental groups in the speed with which participants moved from the start position to the target.

Association between cognitive performance and motor learning

Given the established link between early stages of motor learning and various cognitive processes, including spatial working memory and associative learning, an important aim of the current study was to investigate the contributions of both processes to early motor learning. Specifically, we assessed the relationship between the adaptation index on the first channel trial in the adaptation phase, and performance on a Corsi block, spatial working memory test, and a verbal paired-associate learning test. Implicit memory resources have also been implicated in motor learning, albeit in later stages of learning, we also assessed correlations between early adaptation and performance on the pursuit rotor task as a measure of procedural learning. To assess the overall associations between motor learning and cognitive variables, we conducted a stepwise linear regression with the adaptation index on the first channel trial in the adaptation phase as the dependent variable, and performance on each of the cognitive tasks as independent variables across all participants. The only cognitive variable entered into the model was the paired-associate recognition accuracy measure [$F(1, 59) = 5.0$, $p < 0.05$, $R^2 = 0.08$], but no other cognitive variables were entered into the regression model ($p > 0.4$). Thus, irrespective of group membership, the early stage of motor adaptation was associated with associative memory performance across all participants, but not with any other cognitive variables.

Spatial working memory performance—as assessed by the Corsi test—was not correlated with early motor learning. However, our experimental manipulation of the spatial information available prior to each trial in the sequence and random groups showed a clear difference in early motor learning in the older, but not younger adults. To further explore cognitive explanations for this difference, we conducted the same stepwise linear regression analysis described above for each of the four groups separately. For the older adult sequence and random groups, and for the younger adult sequence group, none of the cognitive variables were included in the regression model as significant predictors of early motor learning. However, in the young adult random group the procedural learning score on the pursuit rotor task was entered as a significant predictor of early motor learning [$F(1, 13) = 19.2$, $p < 0.01$, $R^2 = 0.60$]. Moreover, the addition of paired-associate recall accuracy significantly improved the model [$F(1, 12) = 4.9$, $p < 0.05$, $R^2 = 0.71$]. Thus, the young adult random group was unique in exhibiting an association between early motor learning and procedural learning processes, in addition to associative memory.

As a final pass, we also investigated whether there were age group differences, irrespective of experimental group membership, in the cognitive variables that predict early motor learning. Separate stepwise regression analyses within each age group revealed that no cognitive variables were entered as significant predictors of early motor learning.

Discussion

The primary aim of this study was to examine whether reducing the spatial working memory demands required to perform a sensorimotor adaptation task would limit or eliminate age differences in the early stage of motor learning. To this end, we tested whether providing advance information about target location on each trial would facilitate motor learning in older adults. A separate groups of younger and older adults performed a force-field adaptation experiment with either a repeating sequence of target locations, or a random order. Our first finding was a small, but significant effect of the sequence manipulation in the older adult group such that older adults in the sequence condition were faster to adapt in the earliest stages of motor learning than the older adults in the random group. Younger adults exhibited similar performance during early learning regardless of the order of target locations, and neither group's performance differed from the older sequence group. These data show that having advance knowledge of the spatial location of the target on each trial conveyed an initial benefit for early motor learning in older adults, suggesting that spatial working memory resources are important for initial adaptation. However, all groups adapted equally well by the end of the adaptation phase, so the effect on early learning may be relatively fleeting.

The second aim of this project was to further specify the nature of the cognitive mechanisms that contribute to early motor learning in younger and older adults. Participants performed a battery of cognitive tasks assessing spatial working memory, associative memory, and procedural learning. Across all participants, early motor learning was correlated with associative memory performance, suggesting that associative learning contributes to early motor learning, regardless of task condition or age group. Our second finding was that in addition to associative memory, early motor learning was uniquely related to procedural learning in the younger adults in the random condition, suggesting that younger adults capitalize on procedural learning processes for early motor learning when advance spatial knowledge of target location is not available. These findings suggest that age-related changes in early stages of motor learning may be related to reduced flexibility in engaging a number of cognitive mechanisms that contribute to initial learning.

Age differences in motor learning have been identified in both visuomotor rotation tasks (Anguera et al. 2011; Buch et al. 2003; Fernández-Ruiz et al. 2000; King et al. 2013; Seidler 2007) and force-field adaptation tasks (Huang and Ahmed 2014; Trewartha et al. 2014). Visuomotor adaptation experiments have frequently reported that younger adults learn faster during the early stage of acquisition, with steeper learning curves than older adults. This effect has not been observed in the limited number of force-field adaptation experiments that have investigated age differences in motor learning. One reason for this discrepancy could be that error processing and the computational and neural mechanisms involved in these two tasks differ (Kalaska et al. 1990; Diedrichsen et al. 2005). Although there are likely differences in those mechanisms, the current findings indicate that, like visuomotor adaptation (Anguera et al. 2011; Seidler et al. 2012; Christou et al. 2016), spatial working memory resources likely contribute to early learning in force-field adaptation tasks. When spatial working memory demands were higher in the random condition, older adults exhibited slower learning than younger adults. The extent to which older adults are slower to learn a novel motor task may depend on the spatial working memory resources required to perform the task.

A potentially related explanation for the discrepancy between previous visuomotor rotation and force-field adaptation findings is that there are differences in the experimental design in those tasks. Previous visuomotor rotation experiments typically required participants to make center-out reaching movements from a central home position to multiple radial targets. In the two force-field adaptation experiments mentioned above, participants simply moved back and forth between two targets, with the force field being applied either in both (Huang and Ahmed 2014), or only one direction (Trewartha et al. 2014). Age differences in the early part of the learning curve may be more evident when reaching movements are required to multiple targets in different directions. This explanation is consistent with previous work demonstrating that task complexity is an important factor in age differences in motor performance (Ketcham et al. 2002). Increasing the number of targets during a sensorimotor adaptation task likely increases the demands placed on working memory to learn, retain, and recall spatial transformations necessary to perform the task. Although yet to be tested directly, it may be that age differences in motor learning are magnified as the number of target locations increases.

As discussed above, the current evidence expands on previously reported correlations between spatial working memory and early stages of motor learning, but the data also suggest that other cognitive resources may be recruited to support that learning. Across all participants, the level of adaptation in the early stage of learning was correlated with performance on an associative memory test. This finding is consistent with our previous observation of a correlation between spatial paired-associate working memory performance and estimates of the fast process for motor learning in older adults (Trewartha et al.

2014). Interestingly, the current data revealed a correlation between early motor learning and recognition memory performance on the associative memory task in particular. This suggests that the ability to recognize the appropriate forces to apply on a given trial to counteract the load—the direction of which will depend on the location of the target—is an important cognitive resource underlying the initial stage of motor learning. Although this hypothesis will need further testing, these data help shed light on the cognitive mechanisms involved. A second important finding was that for younger adults in the random condition, procedural learning performance in a pursuit rotor task accounted for an additional portion of the variance in early motor learning, beyond associative memory performance. This suggests that multiple cognitive mechanisms may be flexibly recruited during the early stages of motor learning, depending on task context. This is consistent with previous assertions that multiple cognitive mechanisms may underlie motor learning (McDougle et al. 2015, 2016).

The current findings provide evidence that the factors underlying age-related changes in motor learning are multifaceted. Subtle differences in the early stage of force-field adaptation observed for older adults who learn to adapt to novel dynamics without advance knowledge of target locations adds to previous results identifying spatial working memory ability as an important contributor to age differences in early motor learning. However, associative memory resources also explain some of the variance in early motor learning, regardless of age or spatial working memory demands suggesting that impairments in multiple cognitive systems could ultimately explain individual differences in motor learning in later adulthood. Finally, the observation that procedural learning mechanisms are recruited by younger, but not older adults when advance information about target location is unavailable suggests that the flexibility with which individuals can recruit multiple cognitive resources may contribute to age differences in motor learning. It will be important to identify additional factors that contribute to individual differences in motor learning in later adulthood and factors that explain discrepancies in the sensitivity of visuomotor rotation and force-field adaptation tasks to aging.

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