Behavioral/Cognitive

Fast But Fleeting: Adaptive Motor Learning Processes Associated with Aging and Cognitive Decline

Kevin M. Trewartha,[1,2] Angeles Garcia,[1,2,3] Daniel M. Wolpert,[4] and J. Randall Flanagan[1,2]

[1]Centre for Neuroscience Studies and Departments of [2]Psychology and [3]Medicine, Queen's University, Kingston, Ontario, Canada, K7L 3N6, and [4]Department of Engineering, University of Cambridge, Cambridge, CB2 1PZ, United Kingdom

Motor learning has been shown to depend on multiple interacting learning processes. For example, learning to adapt when moving grasped objects with novel dynamics involves a fast process that adapts and decays quickly—and that has been linked to explicit memory—and a slower process that adapts and decays more gradually. Each process is characterized by a learning rate that controls how strongly motor memory is updated based on experienced errors and a retention factor determining the movement-to-movement decay in motor memory. Here we examined whether fast and slow motor learning processes involved in learning novel dynamics differ between younger and older adults. In addition, we investigated how age-related decline in explicit memory performance influences learning and retention parameters. Although the groups adapted equally well, they did so with markedly different underlying processes. Whereas the groups had similar fast processes, they had different slow processes. Specifically, the older adults exhibited decreased retention in their slow process compared with younger adults. Within the older group, who exhibited considerable variation in explicit memory performance, we found that poor explicit memory was associated with reduced retention in the fast process, as well as the slow process. These findings suggest that explicit memory resources are a determining factor in impairments in the both the fast and slow processes for motor learning but that aging effects on the slow process are independent of explicit memory declines.

Key words: aging; explicit memory; human; motor control; motor learning; state-space model

Introduction

The ability to adapt our motor output to changes in the environment is critical for successful performance. For example, to transport a grasped object, we must tailor our motor commands to the dynamics of the object specifying the mapping between applied force and motion. To investigate motor learning, numerous studies have examined how people adapt their motor output, from trial to trial, when transporting a grasped object with novel dynamics (Shadmehr et al., 2010; Wolpert et al., 2011). Recently, it has been shown that such adaptation involves two memory processes: (1) a fast process that both adapts and decays quickly; and (2) a slow process that adapts and decays more gradually (Smith et al., 2006).

Each process has an internal state, and the two states adapt independently at different rates (one fast, one slow) and sum to produce the motor command (an estimate of the perturbation), thereby compensating for the perturbation. Each state is updated based on the error from the previous trial, weighted by a learning

rate, and also decays from trial to trial as specified by a retention factor. Together, these two processes enable the motor system to respond to changes in the environment that occur on different timescales (Smith et al., 2006; Kording et al., 2007). Thus, the fast process allows the system to respond effectively to sudden and transient changes in the environment, whereas the slow process allows the system to respond effectively to more stable changes in the environment, even in the face of short-term fluctuations.

A recent study by Keisler and Shadmehr (2010) provides evidence for a link between the fast memory process and declarative memory. These authors showed that performing a declarative memory task after motor adaptation disrupts the fast but not the slow process, consistent with observations that fast adaptation is associated with explicit learning processes, including spatial working memory and/or explicit strategies (Anguera et al., 2010; Fernández-Ruiz et al., 2011; Taylor and Ivry, 2011).

Older adults usually exhibit impairments in sensorimotor adaptation (Fernández-Ruiz et al., 2000; Anguera et al., 2011). However, it is unknown whether these impairments are related to alterations of the fast or slow process or whether aging has a differential effect on the learning rates or retention. Predictions about the influence of aging on these parameters can be made on the basis of known changes in cognitive functioning in later adulthood. One prediction is that the fast process is altered in aging because declarative memory systems are particularly diminished in healthy older adults (Craik, 2000; Hoyer and Verhaeghen, 2006). However, alterations in the slow process are also possible because age-related changes have been observed in pro-

Table 1. Means ± SEs of the neuropsychological tests and the t test results of the age group comparisons for each test

Age group	Age	Years of education	Letter–number sequencing	Stroop interference score	Trails difference score
Younger adults	23.1 ± 4.2	17.4 ± 2.5	13.4 ± 3.0	0.64 ± 0.09	8.4 ± 6.5
Older adults	71.1 ± 7.8	16.4 ± 2.4	10.8 ± 3.2	0.45 ± 0.13	24.4 ± 25.2
Age difference		NS	$p < 0.05$	$p < 0.001$	$p < 0.01$

Mean scores are presented with SEs for the number of sequences remembered correctly (maximum of 21) in the Weschler Adult Intelligence Scale letter–number sequencing subtest, the ratio between the seconds per item completed on the congruent and incongruent versions of the color Stroop test, and the difference in time (seconds) to complete versions B and A of the trail-making test.

cedural motor tasks thought to involve nondeclarative memory systems (Rodrigue et al., 2005).

Here, we tested the hypothesis that the fast learning process would be affected by aging and, among older individuals, would be correlated with performance on an explicit memory task. We also tested whether the slow learning process, which may involve nondeclarative memory systems, is affected by aging.

Materials and Methods

Participants

Twenty-one young adults (13 women) and 21 older adults (10 women) participated after providing informed written consent. The mean ± SD age was 23.1 ± 4.2 years for the young adults and 71.1 ± 7.8 for the older adults. A health questionnaire was administered to the older adults to ensure that they were in good self-reported health with no significant medical and neurological conditions and had normal or corrected-to-normal vision. All participants were right handed. A Queen's University ethics committee approved the protocol. Participants completed a battery of neuropsychological tests to ensure that they are normally functioning for their age group. Those tests included the Stroop task (adapted from Spreen and Strauss, 2001), the letter–number sequencing subtest of the Wechsler Adult Intelligence Scale (Wechsler, 1997), and the Trails A and B [adapted from Reitan, 1958 and implemented with the Endpoint KINARM (BKIN Technologies)]. Typical age differences were observed between younger and older adults for all of the neuropsychological tests, and there was no significant difference between groups in terms of years of education (Table 1). The latter result is important because education level has been show in large-scale longitudinal studies to correlate with cognitive performance across the lifespan (Nyberg et al., 2012).

Materials

While seated, participants grasped a vertical cylindrical handle attached to a planar robotic manipulandum (Endpoint KINARM; BKIN Technologies) that allowed the handle to move in a horizontal plane and that could apply forces to the hand via the handle. A circular cursor (5 mm radius) representing the position of the handle and circular targets (10 mm radius) were displayed on a mirror located halfway between the plane of the handle motion and a monitor positioned above the mirror. Thus, the cursor and targets appeared in the plane of the handle, but participants could not see their hand or manipulandum. In addition to applying forces, the manipulandum recorded the position of the hand in the plane of motion and the forces applied by the participant to the manipulandum.

On a given trial, in which the participant moved the handle from the start target to the end target, the manipulandum applied no force (null trial), a clockwise (CW force-field trial) or counterclockwise (CCW force-field trial) viscous-curl force field, or a force channel (error-clamp trial). In the force-field trials, the applied force was proportional to the speed of the handle but perpendicular to the instantaneous direction of handle motion. Specifically, the relation between force (F) and velocity (V) was determined by the equation F = CV, where the matrix C = 20 [0 $f(n)$; $-f(n)$ 0] Ns/m. The task parameter $f(n)$ for the nth trial was 0 for the null field, +1 for the CW force field, and −1 for the CCW force field. Thus, relative to the direction from the start to the end target, the CW and CCW fields tended to perturb the hand rightward and leftward, respectively. In error-clamp trials, the manipulandum simulated a force channel that effectively prevented the handle from moving perpendicular to the straight line running from the start position to the target, thus compelling the handle to move in a straight line to the target and removing

kinematic movement errors. The channel was implemented as a damped spring (stiffness, 6000 N/m; viscosity, 1 Ns/m) that applied forces to the handle, perpendicular to the straight line between the targets, if the handle veered off this straight line.

Procedure

Motor adaptation task. The experimental procedure was based on that used by Smith et al. (2006), but the number of trials was reduced to accommodate elderly participants. On a given trial, the participant made either an inward (toward the body) and outward (away from the body) movement between two targets aligned with the participant's midsagittal plane and located 15 cm apart. At the start of each trial, the participants was required to align the handle at the start target and hold the center of the handle within 5 mm of the center of the target for 200 ms. At this point, the end target changed color to green, and this served as the go signal. Participants were free to initiate their movement at any time but were required to complete the movement by bringing the center of the handle within 5 mm of the end target in 350–500 ms. When the end target was reached, it turned red and became the start target for the next movement. Feedback was displayed on the screen after each trial for 1000 ms, indicating whether the participant's movement was "too slow," "too fast," or "good." Participants were instructed to try to obtain the "good" feedback as often as possible throughout the experiment.

The experiment consisted of four blocks of alternating inward and outward movements. For all outward movements, the force channel was applied such that participants did not experience kinematic errors. As described below, the conditions in which inward movements were made varied depending on the phase of the experiment (the trial structure is illustrated in Fig. 1A). In the familiarization phase, participants completed 52 inward trials in a null field (i.e., with no force applied by the handle). In the adaptation phase, participants completed 120 inward trials in the CW force field. In the counter-adaptation phase, participants completed 15 inward trials in the CCW field. Finally, in the error-clamp phase, they completed 25 inward trials in the force channel. Thus, the entire experiment included 424 movements, but the focus of all analyses is the 212 inward movement trials. During the familiarization phase, the force channel was turned on for two of the inward trials (trials 36 and 47), and during adaptation phase, the force channel was turned on for 10 of the inward trials (trials 63, 74, 85, 96, 107, 118, 129, 140, 151, and 162). These error-clamp trials were included so that we could measure the state of force-field adaptation (see below). Note that these error-clamp trials have been shown, in a number of contexts, to have little effect on overall adaptation (Scheidt et al., 2000; Smith et al., 2006; Ingram et al., 2010, 2011). The force fields were counterbalanced across participants such that half of each age group adapted to the CW force field and counter-adapted to the CCW force field, whereas the other half adapted to the CCW force field and counter-adapted to the CW force field.

Explicit memory task. Given that declarative (or explicit) memory resources are known to be involved in force-field learning (Keisler and Shadmehr, 2010), we asked our participants to perform an explicit memory task requiring both intentional encoding and intentional retrieval conditions. Keisler and Shadmehr (2010) showed that a verbal paired-associate learning task requiring explicit memory, and likely working memory resources, interrupted the fast process of motor learning. However, it has also been shown that a spatial working memory task shares similar neural resources in the dorsolateral prefrontal cortex with learning a visuomotor rotation (Anguera et al., 2010). In light of this previous research, we asked participants to perform a spatial paired-associate learning task. This task capitalizes on both associative memory and spa-
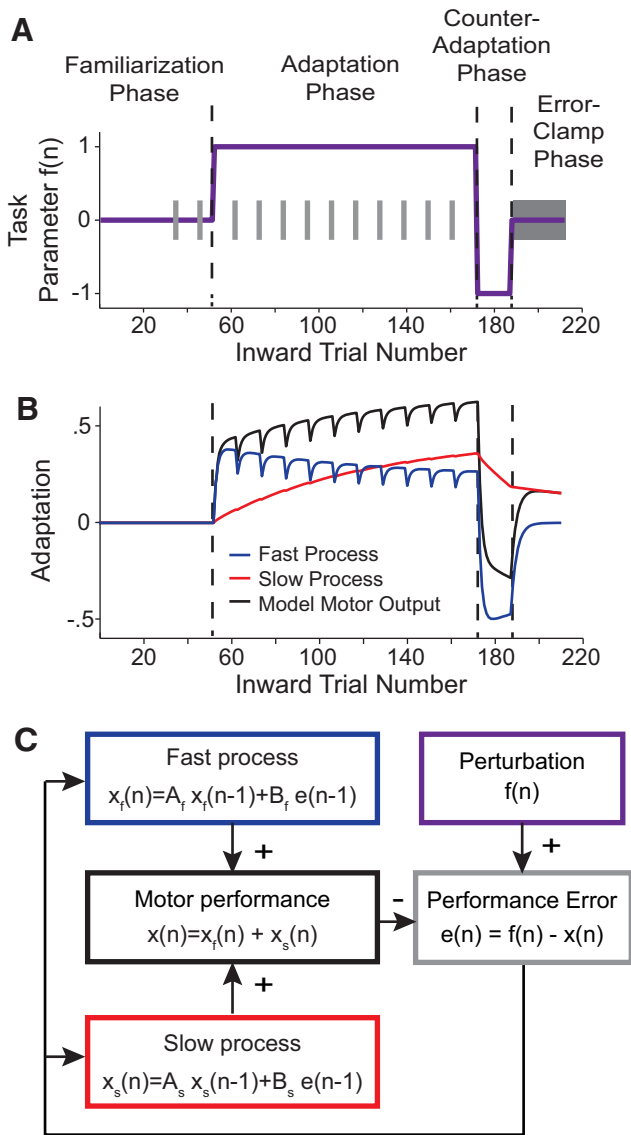
Figure 1. Experimental paradigm and two-state learning model. **A**, Schedule of force-field perturbations (purple line) applied over the four phases of the experiment. Note that the direction of the perturbations was counterbalanced across participants. At various times during the familiarization and adaptation phases and throughout the error-clamp phase, channel trials (gray bars) were used to track to progression of learning. **B**, Simulation using the two-state model showing the contributions of the fast (blue trace) and slow (red trace) learning processes to predicted motor performance (adaptation; black trace) across the experiment. **C**, In the two-state model, each process maintains a separate state (x_f and x_s) estimate, and these sum to provide an estimate of the perturbation (f) that is used as the motor command. Each state is updated based on the error from the previous trial ($f - x$) weighted by the learning rate (B) and also decays from trial to trial as specified by the retention factor (A).

tial working memory resources that may be used for motor learning and also includes explicit instructions for memorizing and recollecting the spatial locations of the visual stimuli, ensuring that the task is declarative in nature.

At the start of each trial, target regions (80 mm^2) were presented on a vertical computer screen with a black background (Fig. 2A). These regions were oriented radially 420 mm from a central home position. Initially, the target regions were filled with a white mask. During the learning phase of the trial, the mask was removed from each target region one at a time. Each mask was removed for 1000 ms, with an interstimulus interval of 1000 ms, in an order that was randomized for each memory set (see below). Removal of each mask revealed either an empty target region (unfilled white square) or one of 10 colored shapes, constructed by com-

bining squares, circles, rectangles, and triangles, that served as memory test stimuli (Fig. 2A). Participants were instructed to remember the stimulus associated with each location. In the test phase that immediately followed, participants watched the central home position as one of the stimuli that had been exposed during the learning phase was presented. Participants were required to select the spatial target location where they remembered seeing that stimulus by clicking on the location with a mouse. After their selection was made, the next stimulus was revealed at the central position, and this process continued until each stimulus that had been revealed in the learning phase was presented in the test phase. No feedback was provided about selection accuracy. The difficulty of the task increased across the session by increasing the size of the memory set. In the initial set, only one stimulus was presented at one of the locations, and the other five locations were empty. The task advanced on to the next set size if the participant correctly identified all of the memory items. If an error was made, the set size was repeated until the participant reached perfect performance or until the number of repetitions without success reached a maximum limit of 10. The set sizes ranged from one to six stimuli, and the task was continued until participants either reached perfect performance on all six set sizes or until the maximum trial repetition limit was reached on a given set.

For each participant, we determined the percentage of correct responses across all test phases and the average reaction time of all test phase responses (i.e., correct and incorrect). The former provided a robust measure of explicit memory accuracy because participants with poorer explicit memory generated a greater number of repetitions, especially on the larger set sizes.

Implicit memory task. Given previous speculations that the slow process of motor learning might rely on nondeclarative (implicit) memory resources (Keisler and Shadmehr, 2010), we opted to include an implicit memory task. However, selecting a particular task was a challenge because (1) no research to date has attempted to relate implicit memory to motor learning and (2) it is notoriously challenging to find implicit tasks that are sensitive to aging (Nyberg et al., 1996; Ward et al., 2013). In any event, we chose to include an implicit memory task that does not require intentional encoding conditions during the learning phase or intentional retrieval conditions during the test phase. Specifically, participants performed a word-identification priming task called the dot-clearing test (adapted from Hawley and Johnston, 1991). The rationale for selecting this task was that the verbal, rather than spatial, nature of the stimuli might limit the extent to which the task would rely on overlapping resources. A potential limitation of using this task is that motor learning may rely more on spatial resources. However, it is worth noting that Keisler and Shadmehr (2010) found that a verbal explicit memory task appeared to be effective in interfering with the putative fast motor learning process.

In the learning phase, 40 words were presented in the center of a vertical computer screen in 60-point white text on a black background. The words were presented one at a time for 2000 ms, with an interstimulus interval of 500 ms, and participants were asked to read each word silently but were not given explicit instructions to remember them. In the subsequent but unexpected test phase, a random selection of 30 of the learning-phase words was presented along with 30 new words in a random order. For each trial, one of the words was presented in the center of the screen, covered by a solid gray mask comprising overlapping gray dots (circles with a radius of 14 mm). The dots were removed at a rate of 90 dots/s, slowly dissolving the mask to reveal the hidden word. Participants were required to press the spacebar as soon as the word could be identified, regardless of how much of the word was visible. After pressing the spacebar, participants typed the word that they thought they identified and then automatically advanced to the next trial.

For each participant, we determined the accuracy and reaction time for every response. To provide a measure of implicit memory performance, we calculated a facilitation score for correct trials by subtracting the average reaction time for old items from the average reaction time for new items for each participant. This difference score (in milliseconds) determines the advantage of being primed with the words that were presented in the learning phase (i.e., the old words).

Analysis

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. To allow us to combine the counterbalanced subjects who experienced different force fields (CW and CCW) in the different stages of the experiment, we flipped the sign for all *x* values and *x* forces before analysis for those subjects who had experienced the CCW force field first in the adaptation phase.

The lateral deviation from a straight line between the targets at the moment of peak velocity in the direction of movement was calculated to provide a measure of performance on nonchannel trials. To quantify the level of adaptation in force–channel trials, we first determined, based on the velocity of the handle along the channel, the time-varying lateral force that would have had to be generated to perfectly compensate for the force field throughout the movement, had the force field been applied. We then used least-squared regression (without an intercept) to compute the slope of the relation between this ideal force and the actual lateral force generated into the wall of the channel (Smith et al., 2006). We will refer to this slope as the adaptation index. Because participants generally under-compensate for the force field, the absolute value of the slope was almost always less than unity (in which unity would indicate perfect compensation). Note that the slope could be negative when the direction of the force field was suddenly changed because participants produced lateral forces in the wrong direction.

Model

For each participant, we fit the two-state gain independent multi-rate model described by Smith et al. (2006) to the adaptation indices obtained from inward force–channel trials. This model can account for a number of behavioral phenomena related to both reach and saccadic eye movement adaptation that are not well characterized by single-state models (Smith et al., 2006). These include savings (Kojima et al., 2004), anterograde interference (Miall et al., 2004; Sing and Smith, 2010), and spontaneous recovery (Smith et al., 2006; Ethier et al., 2008).

The multi-rate model posits that adaptation involves a fast memory process that adapts and decays quickly and a slow memory process that adapts and decays more gradually (Fig. 1 *B*, *C*). Each process maintains a state estimate (x_f and x_s for the fast and slow processes, respectively) and the sum of these states ($x = x_f + x_s$) forms an estimate of the perturbation (f) used as the motor command to compensate for the perturbation. Each state is updated based on the error from the previous trial ($f - x$) weighted by a learning rate (B) and also decays from trial to trial as specified by a retention factor (A), which is inversely related to the rate of decay. On error-clamp trials, the error is set to 0. For each participant, predictions were made by simulating the entire experiment using the series $f(n)$ and optimizing the four parameters (A_f, B_f, A_s, B_s) so as to minimize the sum of squared errors between the predicted and measured adaptation indices on clamp trials (using MATLAB fminsearch). Note that, by setting the perturbations (f) associated with the adaptation and counter-adaptation force fields to +1 and −1, respectively, the motor output from the model (x) corresponds to the adaptation index.

An example of a simulation is shown in Figure 1*B*, which correspond to the perturbation schedule depicted in Figure 1*A*. This illustrates how
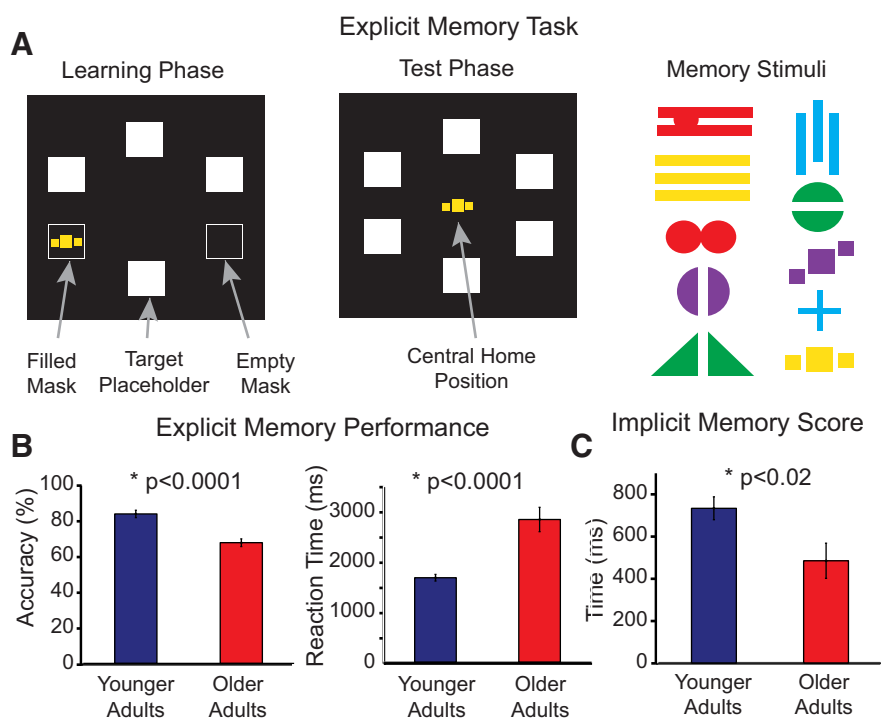
Explicit Memory Task

A
Learning Phase
Filled Mask   Target Placeholder   Empty Mask

Test Phase
Central Home Position

Memory Stimuli

B Explicit Memory Performance
* p<0.0001

Accuracy (%) — Younger Adults / Older Adults

* p<0.0001

Reaction Time (ms) — Younger Adults / Older Adults

C Implicit Memory Score
* p<0.02

Time (ms) — Younger Adults / Older Adults

Figure 2. *A*, Illustration of the spatial paired-associate learning (explicit memory) task. During the learning phase (left), the masks at the target locations are removed one at a time revealing either an empty box or a box containing one of the memory stimuli (right). During the test phase (middle), these memory stimuli are presented one at a time at the central home position, and the participant selects the target location they remember being associated with the stimulus. *B*, *C*, Average accuracy and reaction time in the explicit memory task (*B*), and average facilitation scores on the word priming, dot-clearing (implicit memory) task (*C*) for younger and older adults. Vertical lines represent ±1 SE.

the fast (blue) and slow (red) memory processes combine (black) to capture several features of adaptation. First, the model predicts rapid and transient decreases in adaptation immediately after single force–channel trials. Similar behavioral effects have been observed previously after rest breaks during adaptation (Thoroughman and Shadmehr, 2000; Tong et al., 2002; Hadipour-Niktarash et al., 2007). This effect is primarily attributable the putative fast process that decays rapidly when the kinematic error is set to 0. Second, the model also predicts the spontaneous recovery, or rebound, observed during the error-clamp phase (Smith et al., 2006; Keisler and Shadmehr, 2010). According to the model, the rebound occurs because the state of the fast process rapidly decays to 0 during the error-clamp phase, revealing the state of the slow process that decays slowly during the brief counter-adaptation phase and the error-clamp phase and thus remains partially adapted to the initial perturbation (+1). Although alternative models have been proposed to account for sensorimotor learning (Zarahn et al., 2008; Lee and Schweighofer, 2009), as we will show below, the two-state model provides a parsimonious account of the motor adaptation observed in our participants.

Results

Explicit and implicit memory performance

The paired-associate learning task was administered to provide a measure of explicit memory abilities. A comparison of performance on this test between younger and older adults is summarized in Figure 2*B*. Older adults were less accurate ($p < 0.001$) and slower to respond ($p < 0.001$) than younger adults. Consistent with other observations in the cognitive aging literature (Craik, 2000; Hoyer and Verhaeghen, 2006), this finding shows that older adults exhibited a decline in explicit memory relative to younger adults.

The word priming task was administered to provide a measure of implicit memory performance. To quantify performance on this task, a facilitation score was calculated by subtracting the
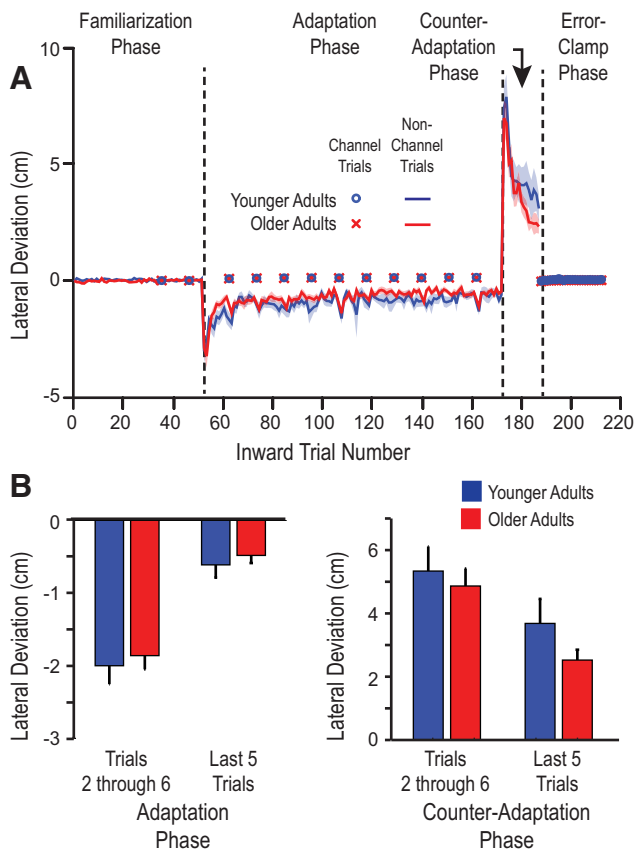
Figure 3. *A*, Averages, for younger (blue) and older (red) adults, of the lateral deviation of the hand path at peak velocity throughout the experiment. The height of the shaded regions denote ±1 SE. The ○ and × symbols represent channel trials for younger and older adults, respectively. *B*, Comparisons between younger and older adults in the mean lateral deviations for trials 2–6 and the last five trials of the adaptation and counter-adaptation phases, respectively.

Figure 4. The average adaptation index for all channel trials in younger (blue trace) and older (red trace) adults across all phases of the experiment. The height of the shaded regions represents ±1 SE. The blue and red circles represent the comparison of the adaptation index on each trial from 0 for younger and older adults, respectively. The black circles denote the comparison between younger and older adults for each trial. Filled circles indicate that the comparison was significant ($p < 0.05$).

averaged reaction time for old items from the average reaction time for new items. The facilitation effect was significantly larger in the younger adults compared with the older adults ($p < 0.02$), indicating a small but reliable difference in implicit memory between the age groups (Fig. 2*C*).

Kinematics for the motor learning task

Figure 3*A* presents group averages for the lateral deviation from a straight movement between the targets at peak velocity for all inward trials. To assess performance and learning in both the adaptation and counter-adaptation phases, we computed, for each participant, the mean lateral deviation over trials 2–6 and the last five trials of the adaptation and counter-adaptation phases, respectively (Fig. 3*B*). For the adaptation phase, a group × stage (early vs late) ANOVA revealed a main effect of stage ($p < 0.001$) but no main effect of group ($p = 0.51$) and no interaction ($p = 0.98$). Similarly, for the deadaptation phase, there was a main effect of stage ($p < 0.001$) but no main effect of group ($p = 0.62$) and no interaction ($p = 0.89$). Thus, both groups exhibited similar performance and similar and significant learning in both phases. The average ± SD lateral deviation across all force–channel trials was 0.53 ± 0.16 mm for younger adults and 0.35 ± 0.19 mm for older adults. Thus, the channel was effective in maintaining a relatively straight hand path between the targets, minimizing the kinematic errors for both age groups.
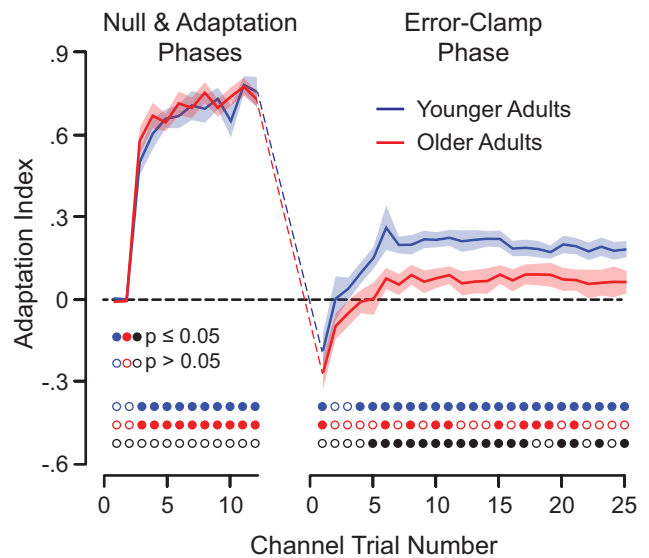
Feedback was provided to participants throughout the experiment about the speed of their movement in an effort to equate the velocity of the movements between the age groups. To compare velocities across groups and phases, we focused on the error-clamp trials. The average ± SE peak velocity in the familiarization, adaptation, and error-clamp phases were −0.44 ± 0.04, −0.52 ± 0.07, and −0.48 ± 0.05 m/s for the younger adults and −0.45 ± 0.04, −0.49 ± 0.07, and −0.47 ± 0.06 m/s for the older adults. An ANOVA comparing the peak velocity of younger and older adults during the familiarization, adaptation, and error-clamp phases of the experiment revealed a main effect of phase ($p < 0.001$). Pairwise comparisons revealed that participants were slightly but significantly slower during the familiarization phase than the adaptation ($p < 0.001$) and error-clamp ($p < 0.01$) phases. However, there was no significant difference between younger and older adults ($p = 0.50$) and no interaction between age group and phase ($p = 0.13$). These results indicate that the feedback was effective in equating the velocity produced by younger and older adults and that the two age groups responded similarly across phases.

Adaptation revealed by channel trials

The level of adaptation in channel trials was quantified using an adaptation index that relates the actual force exerted into the side of the force channel to the ideal force that would be required for perfect compensation (see Materials and Methods). Figure 4 shows the average adaptation index as a function of all channel trials for the younger and older adults. The blue and red circles indicate, for each channel trial, whether the adaptation index was different from 0 (circles filled if $p < 0.05$) for the younger and older adults, respectively. The black circles indicate whether the adaptation index differed between the groups (circles filled if $p < 0.05$). During the adaptation phase, both groups adapted to the perturbation, as indicated by the increase in the adaptation index, and did so equally well. That is, there was no significant difference between groups for any of the channel trials during this phase.

The adaptation index at the start of the error-clamp phase was initially negative, in the direction of the forces produced in the counter-adaptation phase. The adaptation index for the first trial of the error-clamp phase did not differ between the groups, indicating that the younger and older adults not only adapted equally well and quickly to the initial perturbation but also adapted equally well to the opposite perturbation delivered during the counter-adaptation phase. The adaptation index for the second and third error-clamp trials did not differ from 0 for either age group, indicating that the state of the fast system quickly returned to 0 once the perturbation was turned off. These trials also did not differ between the groups. For the younger adults, a rebound in the adaptation index in the direction of the initial adaptation phase was evident by the fourth trial, by which time the adaptation index was significantly >0 and remained so for the rest of the error-clamp trials. For the older adults, the rebound was not evident until the sixth error-clamp trial, and the adaptation index remained significantly >0 for a number of error-clamp trials (8, 10, 11, 15, 17, 18, 19, and 21), until the end of the error-clamp phase, at which time it was not significantly different from 0 (trials 22–25). In addition, by the fifth error-clamp trial, the adaptation index was significantly greater for younger compared with older adults and remained so throughout the rest of the error-clamp trials, with a few exceptions (trials 18, 19, 22, and 24).

According to the two-state model, the rapid rebound in the adaptation index during the error-clamp phase arises because the state of the fast process rapidly returned to 0 as a result of the removal of kinematic errors, revealing the state of the slow process that is still partially adapted to the perturbation encountered during the adaptation phase. Our results show that older adults exhibited a rebound effect that was slower to develop, smaller in magnitude, and less stable compared with younger adults. Within the context of the model, a possible explanation for this finding is that the state of the slow process changes more slowly in younger adults, because of a greater retention factor, a smaller learning rate, or both.

Model

A two-state, multi-rate model (Fig. 1C) was used to assess the contributions of the fast and slow processes to motor learning. Figure 5 shows model fits to the data for representative younger and older adults. As illustrated in this figure, the model successfully captures the improvement in the adaptation index during the adaptation phase and the rebound, or spontaneous recovery, in the adaptation index during the error-clamp phase. Figure 6A
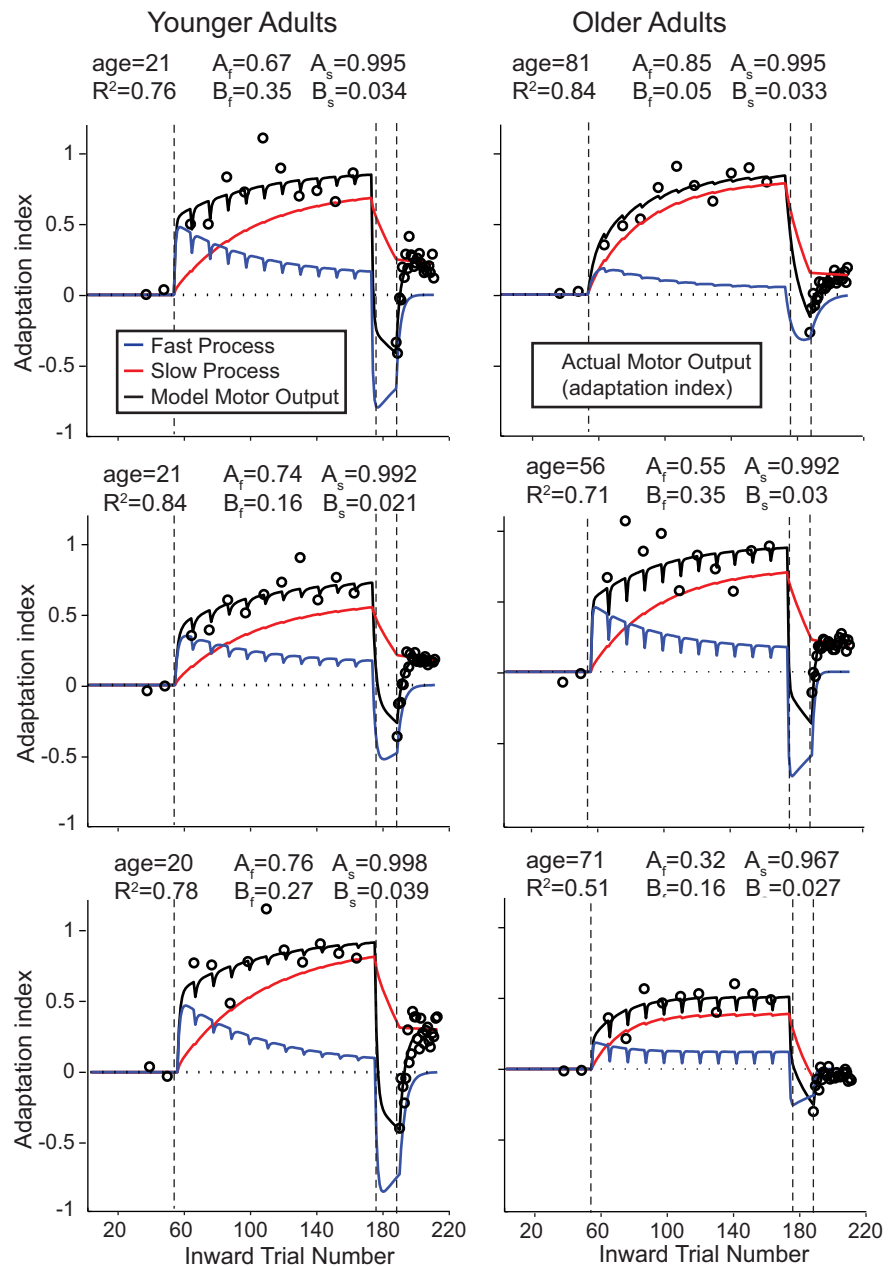

Figure 5. The two-state model fit to the individual data of representative younger and older adults. For each individual, the empirical data (adaptation index scores) are plotted for each channel trial as black circles. The motor output predicted by the model (black traces) and the states of the fast (blue traces) and slow (red traces) motor learning processes are shown as a function of trial. The retention factors (A_f, A_s) and learning rates (B_f, B_s) of the fast and slow processes are displayed for each participant, along with the R^2 value comparing the two-state model with a one-state model.

shows, for both the younger and older adults, the average ± SE of the individual participant fits of the two-state model.

To test whether the two-state model provides a better fit than a one-state model (with a single learning rate and single retention factor), we also fit a one-state model to each participant. For each age group, we performed an F test comparing the two-state model, fit separately to all participants so that the model included 84 parameters (i.e., the 4 learning parameters × 21 participants), and the one-state model, which included 42 parameters (i.e., 2 learning parameters × 21 participants). The two-state model was significantly better than the one-state model for both the younger ($F_{(42,693)} = 42.8$; $p < 0.001$) and older ($F_{(42,693)} = 55.5$; $p < 0.001$) adults. We also compared the two-state and one-state models for
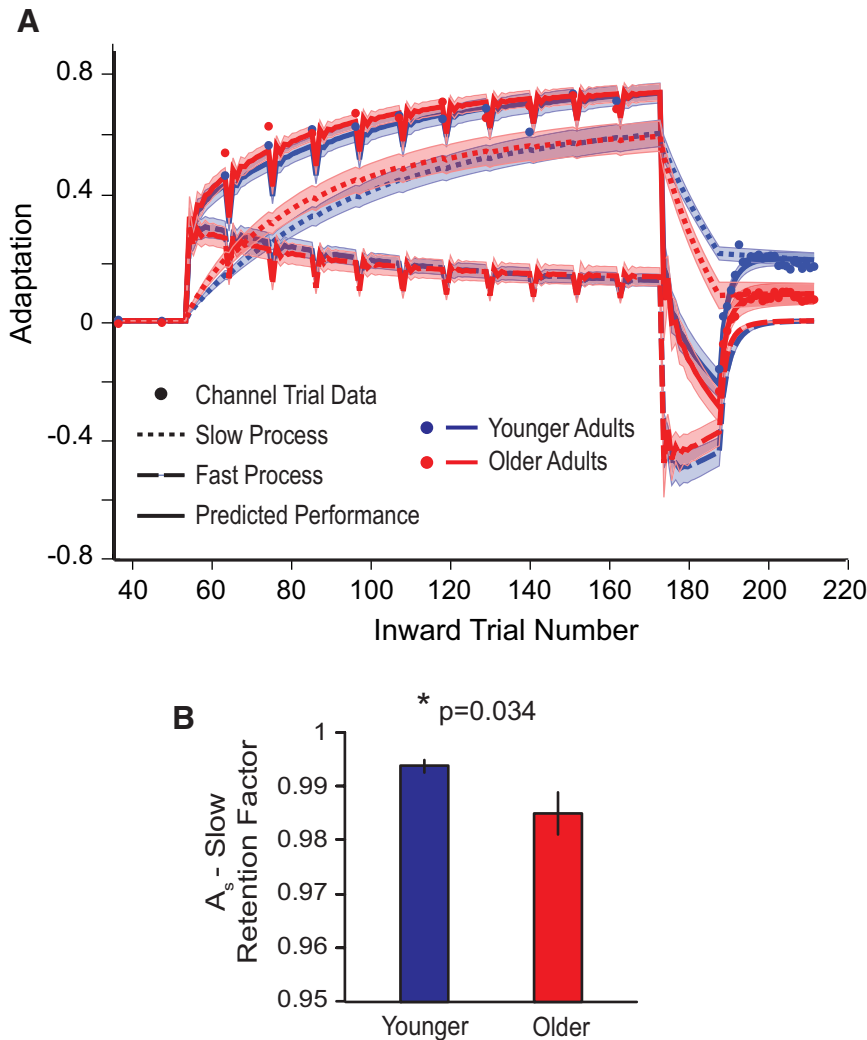
A

B

Figure 6. *A*, Average fits for younger (blue) and older (red) adults of the two-state model based on individual fits. The dots represent the average adaptation indices on channel trials for the younger (blue) and older (red) adults. The predicted motor output and the states of the fast and slow learning processes are denoted by solid, dashed, and dotted lines, respectively. The height of the shaded region represents ±1 SE. *B*, Average slow retention factor for younger and older adults. The vertical lines represent ±1 SE.

allowing correlations between the parameters to play a role). Note that, in stepwise discriminant analysis—like stepwise regression analysis—independent variables are entered into the model in order of significance, provided they meet the entry criteria (set to $p < 0.05$), and are removed from the model if they meet the removal criteria (set to $p > 0.10$). The only variable entered into the discriminant model was A_s, the slow retention factor ($p = 0.034$). That is, with this variable included in the discriminant model, no other variable improved the discrimination between age groups and thus the final discriminant model only has a single variable. The slow retention factor was smaller for the older adults (mean ± SD, 0.985 ± 0.017) than the younger adults (0.994 ± 0.005; Fig. 6*B*). The means ± SDs for B_s, A_f, and B_f were 0.025 ± 0.012, 0.521 ± 0.280, and 0.268 ± 0.224 for the younger adults and 0.037 ± 0.025, 0.498 ± 0.247, and 0.311 ± 0.305 for the older adults. For completeness, we performed separate t tests, comparing younger and older adults, for each of these four parameters. The test for the slow retention factor (A_s) was significant ($p = 0.034$), and there was a trend ($p = 0.074$) toward an age difference in the slow learning rate (B_s). As noted above, adding B_s to the discriminant model with A_s already entered did not improve the discrimination.

Within the older group, we performed a stepwise linear regression analysis to determine whether chronological age could be predicted from the four learning parameters and all possible interactions between these parameters. No variables were entered into the regression model ($p > 0.05$ for all 15 variables). These observations suggest that the smaller rebound effect in the older compared with younger adults (Fig. 4) is the result of alterations in the slow learning process and, in particular, the slow retention factor and that chronological age may not be the determining factor of age-related differences in motor learning.

Association between cognitive performance and motor learning parameters

Given that recent evidence has linked the fast process and explicit memory resources (Keisler and Shadmehr, 2010) and the fact that explicit memory is known to decline substantially in aging, a main aim of the current project was to assess whether the fast process of motor learning is correlated with explicit memory performance in older adults. On the paired-associate learning task, a significant difference was observed between younger and older adults, and although younger adults generally all performed at a high level, a subset of older adults performed reasonably well but others did not. This variance in the older group is consistent with observations that individuals differ greatly in the extent and rate

each individual participant and found that the two-state model was significantly better ($p < 0.05$) for 20 of 21 younger adults and 18 of 21 older adults. The mean R^2 values comparing the two-state model with the one-state model (i.e., the proportion of variance unaccounted for by the one-state model that is accounted for by the two-state model) were 0.70 (ranging from 0.11 to 0.92) and 0.62 (ranging from 0.03 to 0.96) for the younger and older adults, respectively, and the corresponding median R^2 values were 0.78 and 0.71. Thus, the two-state, multi-rate model was remarkably successful at fitting the data of both younger and older adults on the group and individual levels.

To examine age differences in the model parameters, we performed a stepwise discriminant analysis with age group as the dependent variable and the four model parameters plus all possible interactions among these parameters (i.e., the six two-parameter interactions, the four three-parameter interactions, and the one four-parameter interaction) as potential independent variables. By including these interaction terms, we could not only test whether single parameters could predict age group but also whether combinations of parameters could do so (thereby
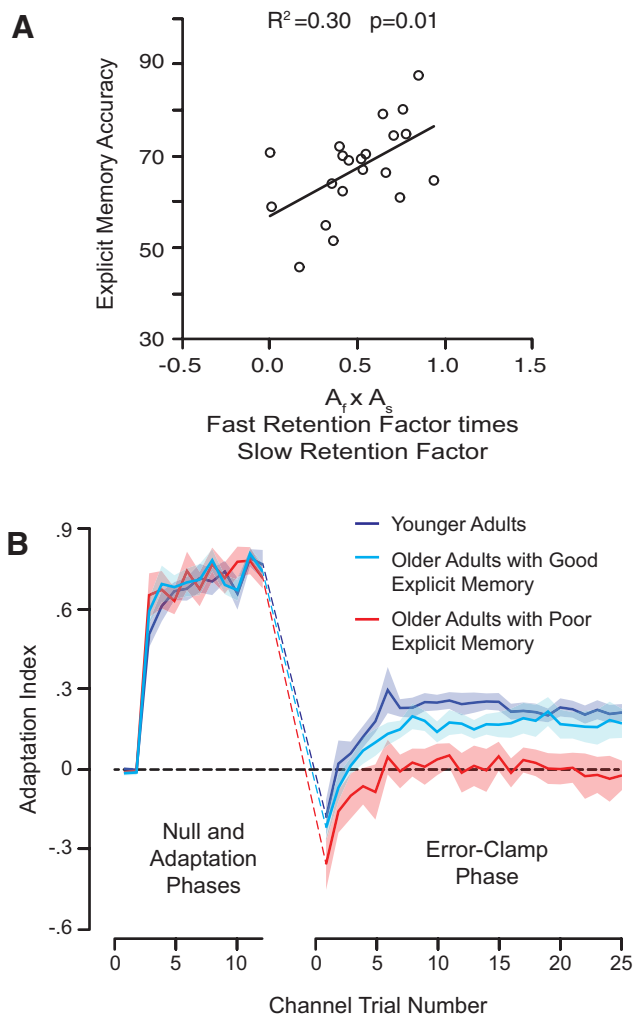
A

B

Figure 7. *A*, Correlation between explicit memory performance and the interaction between the fast and slow retention factors for the older adults. *B*, The average adaptation index for all channel trials in younger adults (blue trace) and older adults above (light blue trace) and below (red trace) the median explicit memory accuracy. The height of the shaded regions represents ±1 SE.

of cognitive declines in later adulthood (Wilson et al., 2002; Nyberg et al., 2012).

To examine the relation between declines in explicit memory and age differences in motor learning, we performed separate stepwise linear regressions for the younger and older adults, with performance on the paired-associate learning task as the dependent variable and the four model parameters and all possible interactions among these parameters (i.e., the six two-parameter interactions, the four three-parameter interactions, and the one four-parameter interaction) as the independent variables. For the older adults, the only independent variable entered into the regression model was $A_f \times A_s$, the interaction between the retention factor of the fast process and the retention factor of the slow process ($R^2 = 0.35$; $p = 0.005$; Fig. 7A). When considered alone, both of these learning parameters increased with explicit memory performance, although whereas A_f was significantly correlated explicit memory performance ($r = 0.583$; $p = 0.006$), A_s was not ($r = 0.372$; $p = 0.096$). Note that, when considered alone, neither B_f ($r = 0.40$; $p = 0.72$) nor B_s ($r = 0.18$; $p = 0.43$) was significant. This interaction indicates that the slope of the relation between each independent variable and explicit memory performance in-

creases as the other independent variable increases. Thus, greater retention in the fast learning process is linked to better explicit memory performance, and this relation is moderated by the slow retention factor. Unsurprisingly, given the high performance and relatively low variability in the explicit memory task in the younger adults, when the same stepwise linear regression analysis was performed with the young adults, no variables were entered into the regression model ($p > 0.05$ for all 15 variables).

For descriptive purposes, we show the averaged adaptation index as a function of all force–channel trials for older adults above and below the median accuracy score for the explicit memory test compared with younger adults (Fig. 7B). It is evident that older adults with good explicit memory produced a greater rebound than older adults with poor explicit memory, although this rebound was not as pronounced as in the young adults. The greater rebound observed in older adults with good, compared with poor, explicit memory can be linked to the marginally greater slow retention factor (A_s) observed in the good older adults, as suggested by the marginally significant positive relation between A_s and explicit memory performance (see above).

These analyses provide clear support for the idea that explicit memory resources are related to the fast process, and particularly to the fast retention factor, and demonstrate that the extent to which the fast retention factor is diminished in older adults depends on individual differences in explicit memory resources.

We also performed, for both the younger and older adults, stepwise linear regression analyses with performance on the implicit memory task as the dependent variable and the four model parameters and all possible interactions among these parameters as independent variables. Given our finding that the slow process was affected by aging and previous suggestions that the slow learning process may be supported by implicit or nondeclarative memory mechanisms (Keisler and Shadmehr, 2010), one might expect the parameters of the slow process to be correlated with implicit memory performance. However, no independent variables were entered into the regression model ($p > 0.05$) for either age group.

Finally, to explore whether other types of cognitive processes, such as executive functioning, are related to motor learning, we conducted, for both younger and older adults, stepwise linear regression analyses with performance on each neuropsychological test as dependent variables and the four motor learning parameters and all possible interactions among these parameters as independent variables. For the older adults, no variables were entered into the regression model for any of the neuropsychological tests ($p > 0.05$). For younger adults, no variables were entered into the regression models for either the Stroop task or the trail-making test. However, for the letter–number sequencing test, only the $A_f \times B_f \times B_s$ interaction was entered into the model ($R^2 = 0.44$; $p = 0.045$), indicating that a linear combination of the fast retention factor, fast learning rate, and the slow learning rate predicted letter–number sequencing scores in the younger adults. Generally, these observations highlight the specificity of the cognitive resources used in the motor learning task, demonstrating that motor learning relies in part on explicit working memory resources.

Discussion

The aim of this study was to investigate the status, in older adults, of the fast and slow memory processes that characterize sensorimotor adaptation in younger adults (Smith et al., 2006; Kording et al., 2007). We found that the two-state, multi-rate learning model (Smith et al., 2006) not only captured the adaptation in

younger adults, as expected, but also characterized adaptation in older adults. Our first key finding was that, although younger and older adults adapted equally well, the retention factor of the slow process was diminished in the older compared with younger adults. Our second key finding was that, within the older adults, explicit memory performance was associated with interaction of the retention factors of both the fast and slow processes and that both retention factors tended to be smaller for individuals with poor explicit memory. These findings suggest that age-related declines in motor learning are associated with impaired retention associated with the slow process and that additional declines in the retention factors of both processes depend on individual differences in explicit memory resources.

Recent empirical evidence suggests that explicit memory systems support the fast learning process associated with the multi-rate model (Keisler and Shadmehr, 2010). This result is consistent with the finding that early stages of adaptation to a visuomotor rotation, which should be strongly influenced by the fast process, appear to rely on spatial working memory resources (Anguera et al., 2010; Fernández-Ruiz et al., 2011). Given that explicit memory resources decline with aging (Craik, 2000; Hoyer and Verhaeghen, 2006), one might predict that early stages of motor learning are slowed in the elderly. Consistent with this prediction, visuomotor adaptation experiments have reported steeper learning curves during early adaptation for younger, compared with older, adults (Fernández-Ruiz et al., 2000; Seidler, 2006; Anguera et al., 2011). In the current study, which examined force-field adaptation rather than visuomotor adaptation, older adults of comparable age (70 years of age compared with 64–75 years of age in the three studies cited) did not exhibit age differences in performance during early adaptation, or counter-adaptation. This observation is consistent with another recent comparison of force-field adaptation in younger and older adults (Huang and Ahmed, 2014). This discrepancy could be attributable to task-related differences in error processing and the computational and neural mechanisms involved (Kalaska et al., 1990; Diedrichsen et al., 2005).

Applying the multi-rate model allows a more nuanced assessment of age differences in learning. As expected, the older adults exhibited reduced explicit memory performance on a spatial paired-associate learning task compared with younger adults. However, there was no difference, on average, between age groups in the fast learning rate or fast retention factor, suggesting that the fast process is not diminished with age. Although age per se did not significantly affect the parameters of the fast process, within the older adults, accuracy on the explicit memory task was positively correlated with the retention factor of the fast process, and this relationship was moderated by the retention factor of the slow process. That is, older adults with good explicit memory performance tended to have a larger fast retention factor, in addition to a larger slow retention factor. These findings are consistent with reports that older adults perform poorly on motor skill learning tasks that require strategic learning, associated with working memory resources (McNay and Willingham, 1998), and support the proposal that the fast process is related to declarative memory processes (Keisler and Shadmehr, 2010). Our finding adds to this literature by demonstrating that individual differences in the decline of explicit memory, rather than age per se, is a determining factor for a disrupted fast process for motor learning in later adulthood.

We found that aging altered the slow process because older adults exhibited a diminished slow retention factor compared with younger adults. Within the older adults, those individuals with poor explicit memory exhibited a smaller fast retention factor but also tended to have exaggerated impairments in the slow retention factor. However, neither the slow retention factor nor the slow learning rate, considered in isolation, correlated with explicit memory performance, consistent with the suggestion that the slow process relies on implicit or nondeclarative memory systems (Keisler and Shadmehr, 2010). The challenge with this interpretation is that implicit memory is thought to be less vulnerable to aging than declarative memory (Craik, 2000; Hoyer and Verhaeghen, 2006). Our results were broadly consistent with this view. Although we observed an age-related decline in performance on our implicit learning task, which focused on implicit priming, this effect was clearly weaker than the effect of our explicit memory task. Moreover, within the older adults, implicit memory performance was not correlated with any of the four learning parameters. However, a number of studies have challenged the idea that implicit memory systems are globally spared by aging (La Voie and Light, 1994; Ward et al., 2013). Motor tasks considered to involve implicit memory, including mirror drawing (Rodrigue et al., 2005), higher-order sequence learning (Howard et al., 2004), and sequential serial reaction time tasks (Salthouse et al., 1999), have demonstrated age-related impairments. Thus, it is possible that implicit memory processes other than those assessed in our priming task may underlie the slow process. Of course, it is also possible that the slow process engages explicit memory processes other than those assessed by the explicit memory tasks used in the current study and by Keisler and Shadmehr (2010). Thus, an important direction for future research will be to explore alternative implicit memory tasks to determine the nature of shared resources between nondeclarative memory systems and the slow process of motor learning. Additionally, given that our explicit memory task relies on numerous underlying memory processes (i.e., explicit memory, associative learning, and working memory), it will be important to further explore the precise declarative memory processes that are associated with the fast process of motor learning and with declines in the fast process with age-related cognitive impairments.

Our finding that the slow retention factor is diminished in aging adds to existing reports in the cognitive aging literature of increased forgetting rates in the elderly (Munro Cullum et al., 1990; Davis et al., 2003) and of disproportionate age effects on forgetting, compared with learning, of verbal information (Zimprich and Kurtz, 2013). The sensitivity of the multi-rate model to delineate age differences in learning rates and retention factors may prove to be a useful tool for assessing the nature of age-related differences in other types of memory. To our knowledge, state–space models—with distinct learning and decay rates—have not been applied to other types of cognitive tasks.

Research shows that the cerebellum plays an important role in sensorimotor adaptation, and patients with cerebellar lesions perform poorly on both visuomotor rotation and force-field adaptation tasks (Martin et al., 1996; Maschke et al., 2004; Smith and Shadmehr, 2005; Tseng et al., 2007; Rabe et al., 2009; Criscimagna-Hemminger et al., 2010; Gibo et al., 2013). Functional imaging studies have consistently observed cerebellar activity when participants adapt to such perturbations (Diedrichsen et al., 2005; Smith and Shadmehr, 2005). The cerebellar cortex appears to support learning akin to the fast process, whereas the cerebellar nuclei may support learning akin to the slow process (Medina et al., 2001), suggesting that dissociable cerebellar regions support the fast and slow learning processes. Areas within the cerebral cortex may also play distinct roles in the fast and slow learning processes. For example, early stages of learning, when

the fast process is dominant, have been associated with the prefrontal and inferior parietal cortex, whereas late learning is associated with the middle temporal gyrus (Anguera et al., 2010).

Diminished adaptive processes for motor learning in aging is consistent with the selective and differential atrophy of the prefrontal cortices and the cerebellum (Raz et al., 2000, 2010; Kennedy and Raz, 2005). Moreover, it has been suggested that disruptions of frontocerebellar circuitry may underlie functional declines commonly observed in the elderly (Sullivan and Pfefferbaum, 2006). Atrophy in the cerebellum may underlie the age-related reduction in the retention factor of the slow process. Conversely, given that overlapping prefrontal regions support both early stages of motor learning (Anguera et al., 2010) and performance on spatial paired-associate learning tasks (Owen et al., 1996), it is possible that the correlation between the fast retention factor and explicit memory performance in the older adults is related to individual differences in prefrontal cortex function. One possibility is that a subset of older adults was better able to recruit prefrontal resources to minimize impairments in the fast process for motor learning. This interpretation is consistent with theories of cognitive aging that propose compensatory recruitment of neural mechanisms, beyond those used by younger adults, to support task performance (e.g., the cognitive reserve hypothesis; Stern, 2009). Alternatively, individual differences in the fast process for motor learning may reflect underlying differences in prefrontal atrophy (Raz et al., 2010), consistent with the concept of brain maintenance by which individual differences in the manifestation of brain pathology can explain why some older individuals experience cognitive decline but others do not (Nyberg et al., 2012). Given the role of both prefrontal cortex and the cerebellum in sensorimotor adaptation and our observation that the slow retention factor moderated the relation between the fast retention factor and explicit memory performance in older adults, we speculate that disruptions in frontocerebellar circuitry may underlie age differences in sensorimotor learning reported here and previously (Fernández-Ruiz et al., 2000; Seidler, 2006; Anguera et al., 2011).

References

Anguera JA, Reuter-Lorenz PA, Willingham DT, Seidler RD (2010) Contributions of spatial working memory to visuomotor learning. J Cogn Neurosci 22:1917–1930. CrossRef Medline
Anguera JA, Reuter-Lorenz PA, Willingham DT, Seidler RD (2011) Failure to engage spatial working memory contributes to age-related declines in visuomotor learning. J Cogn Neurosci 23:11–25. CrossRef Medline
Craik FIM (2000) Age-related changes in human memory. In: Cognitive aging: a primer (Park D, Schwarz N, eds), pp 75–92. New York: Psychology.
Criscimagna-Hemminger SE, Bastian AJ, Shadmehr R (2010) Size of error affects cerebellar contributions to motor learning. J Neurophysiol 103:2275–2284. CrossRef Medline
Davis HP, Small SA, Stern Y, Mayeux R, Feldstein SN, Keller FR (2003) Acquisition, recall, and forgetting of verbal information in long-term memory by young, middle-aged, and elderly individuals. Cortex 39:1063–1091. CrossRef Medline
Diedrichsen J, Hashambhoy Y, Rane T, Shadmehr R (2005) Neural correlates of reach errors. J Neurosci 25:9919–9931. CrossRef Medline
Ethier V, Zee DS, Shadmehr R (2008) Spontaneous recovery of motor memory during saccade adaptation. J Neurophysiol 99:2577–2583. CrossRef Medline
Fernández-Ruiz J, Hall C, Vergara P, Díaz R (2000) Prism adaptation in normal aging: slower adaptation rate and larger aftereffect. Brain Res Cogn Brain Res 9:223–226. CrossRef Medline
Fernández-Ruiz J, Wong W, Armstrong IT, Flanagan JR (2011) Relation between reaction time and reach errors during visuomotor adaptation. Behav Brain Res 219:8–14. CrossRef Medline
Gibo TL, Criscimagna-Hemminger SE, Okamura AM, Bastian AJ (2013) Cerebellar motor learning: are environment dynamics more important than error size? J Neurophysiol 110:322–333. CrossRef Medline
Hadipour-Niktarash A, Lee CK, Desmond JE, Shadmehr R (2007) Impairment of retention but not acquisition of a visuomotor skill through time-dependent disruption of primary motor cortex. J Neurosci 27:13413–13419. CrossRef Medline
Hawley KJ, Johnston WA (1991) Long-term perceptual memory for briefly exposed words as a function of awareness and attention. J Exp Psychol Hum Percept Perform 17:807–815. CrossRef Medline
Howard DV, Howard JH Jr, Japikse K, DiYanni C, Thompson A, Somberg R (2004) Implicit sequence learning: effects of level of structure, adult age, and extended practice. Psychol Aging 19:79–92. CrossRef Medline
Hoyer WJ, Verhaeghen P (2006) Memory aging. In: Handbook of the psychology of aging (Birren JE, Schaie KW, eds), pp 209–232. San Diego: Elsevier Academic.
Huang HJ, Ahmed AA (2014) Older adults learn less, but still reduce metabolic cost, during motor adaptation. J Neurophysiol 111:135–144. CrossRef Medline
Ingram JN, Howard IS, Flanagan JR, Wolpert DM (2010) Multiple grasp-specific representations of tool dynamics mediate skillful manipulation. Curr Biol 20:618–623. CrossRef Medline
Ingram JN, Howard IS, Flanagan JR, Wolpert DM (2011) A single-rate context-dependent learning process underlies rapid adaptation to familiar object dynamics. PLoS Comput Biol 7:e1002196. CrossRef Medline
Kalaska JF, Cohen DA, Prud'Homme M, Hyde ML (1990) Parietal area 5 neuronal activity encodes movement kinematics, not movement dynamics. Exp Brain Res 80:351–364. Medline
Keisler A, Shadmehr R (2010) A shared resource between declarative memory and motor memory. J Neurosci 30:14817–14823. CrossRef Medline
Kennedy KM, Raz N (2005) Age, sex and regional brain volumes predict perceptual-motor skill acquisition. Cortex 41:560–569. CrossRef Medline
Kojima Y, Iwamoto Y, Yoshida K (2004) Memory of learning facilitates saccadic adaptation in the monkey. J Neurosci 24:7531–7539. CrossRef Medline
Kording KP, Tenenbaum JB, Shadmehr R (2007) The dynamics of memory as a consequence of optimal adaptation to a changing body. Nat Neurosci 10:779–786. CrossRef Medline
La Voie D, Light LL (1994) Adult age differences in repetition priming: a meta-analysis. Psychol Aging 9:539–553. CrossRef Medline
Lee JY, Schweighofer N (2009) Dual adaptation supports a parallel architecture of motor memory. J Neurosci 29:10396–10404. CrossRef Medline
Martin TA, Keating JG, Goodkin HP, Bastian AJ, Thach WT (1996) Throwing while looking through prisms I. Focal olivocerebellar lesions impair adaptation. Brain 119:1183–1198. CrossRef Medline
Maschke M, Gomez CM, Ebner TJ, Konczak J (2004) Hereditary cerebellar ataxia progressively impairs force adaptation during goal-directed arm movements. J Neurophysiol 91:230–238. CrossRef Medline
McNay EC, Willingham DB (1998) Deficit in learning of a motor skill requiring strategy, but not of perceptuomotor recalibration, with aging. Learn Mem 4:411–420. CrossRef Medline
Medina JF, Garcia KS, Mauk MD (2001) A mechanism for savings in the cerebellum. J Neurosci 21:4081–4089. Medline
Miall RC, Jenkinson N, Kulkarni K (2004) Adaptation to rotated visual feedback: a re-examination of motor interference. Exp Brain Res 154:201–210. CrossRef Medline
Munro Cullum C, Butters N, Tröster AI, Salmon DP (1990) Normal aging and forgetting rates on the Wechsler memory scale-revised. Arch Clin Neuropsychol 5:23–30. CrossRef Medline
Nyberg L, Bäckman L, Erngrund K, Olofsson U, Nilsson LG (1996) Age differences in episodic memory, semantic memory, and priming: Relationships to demographic, intellectual, and biological factors. J Gerontol B Psychol Sci Soc Sci 51:P234–P240. Medline
Nyberg L, Lövdén M, Riklund K, Lindenberger U, Bäckman L (2012) Memory aging and brain maintenance. Trends Cogn Sci 16:292–305. CrossRef Medline
Owen AM, Evans AC, Petrides M (1996) Evidence for a two-stage model of spatial working memory processing within the lateral frontal cortex: a positron emission tomography study. Cereb Cortex 6:31–38. CrossRef Medline
Rabe K, Livne O, Gizewski ER, Aurich V, Beck A, Timmann D, Donchin O (2009) Adaptation to visuomotor rotation and force field perturbation is

correlated to different brain areas in patients with cerebellar degeneration. J Neurophysiol 101:1961–1971. CrossRef Medline

Raz N, Williamson A, Gunning-Dixon F, Head D, Acker JD (2000) Neuroanatomical and cognitive correlates of adult age differences in acquisition of a perceptual-motor skill. Microsc Res Tech 51:85–93. CrossRef Medline

Raz N, Ghisletta P, Rodrigue KM, Kennedy KM, Lindenberger U (2010) Trajectories of brain aging in middle-aged and older adults: regional and individual differences. Neuroimage 51:501–511. CrossRef Medline

Reitan RM (1958) Trail making test: manual for administration, scoring and interpretation. Indianapolis: Indiana University Medical Center.

Rodrigue KM, Kennedy KM, Raz N (2005) Aging and longitudinal change in perceptual-motor skill acquisition in healthy adults. J Gerontol B Psychol Sci Soc Sci 60:P174–P181. CrossRef Medline

Salthouse TA, McGuthry KE, Hambrick DZ (1999) A framework for analyzing and interpreting differential aging patterns: application to three measures of implicit learning. Aging Neuropsychol Cogn 6:1–18. CrossRef

Scheidt RA, Reinkensmeyer DJ, Conditt MA, Rymer WZ, Mussa-Ivaldi FA (2000) Persistence of motor adaptation during constrained, multi-joint, arm movements. J Neurophysiol 84:853–862. Medline

Seidler RD (2006) Differential effects of age on sequence learning and sensorimotor adaptation. Brain Res Bull 70:337–346. CrossRef Medline

Shadmehr R, Smith MA, Krakauer JW (2010) Error correction, sensory prediction, and adaptation in motor control. Annu Rev Neurosci 33:89–108. CrossRef Medline

Sing GC, Smith MA (2010) Reduction in learning rates associated with anterograde interference results from interactions between different timescales in motor adaptation. PLoS Comput Biol 6:e1000893. CrossRef Medline

Smith MA, Shadmehr R (2005) Intact ability to learn internal models of arm dynamics in Huntington's disease but not cerebellar degeneration. J Neurophysiol 93:2809–2821. CrossRef Medline

Smith MA, Ghazizadeh A, Shadmehr R (2006) Interacting adaptive processes with different timescales underlie short-term motor learning. PLoS Biol 4:e179. CrossRef Medline

Spreen O, Strauss E (2001) A compendium of neuropsychological tests: administration, norms, and commentary, pp 213–218. New York: Oxford UP.

Stern Y (2009) Cognitive reserve. Neuropsychologia 47:2015–2028. CrossRef Medline

Sullivan EV, Pfefferbaum A (2006) Diffusion tensor imaging and aging. Neurosci Biobehav Rev 30:749–761. CrossRef Medline

Taylor JA, Ivry RB (2011) Flexible cognitive strategies during motor learning. PLoS Comput Biol 7:e1001096. CrossRef Medline

Thoroughman K, Shadmehr R (2000) Learning of action through adaptive combination of motor primitives. Nature 407:742–747. CrossRef Medline

Tong C, Wolpert DM, Flanagan JR (2002) Kinematics and dynamics are not represented independently in motor working memory: evidence from an interference study. J Neurosci 22:1108–1113. Medline

Tseng YW, Diedrichsen J, Krakauer JW, Shadmehr R, Bastian AJ (2007) Sensory prediction errors drive cerebellum-dependent adaptation of reaching. J Neurophysiol 98:54–62. CrossRef Medline

Ward EV, Berry CJ, Shanks DR (2013) Age effects on explicit and implicit memory. Front Psychol 4:639. CrossRef Medline

Wechsler D (1997) WAIS-III administration and scoring manual. San Antonio, TX: Pearson.

Wilson RS, Beckett LA, Barnes LL, Schneider JA, Bach J, Evans DA, Bennett DA (2002) Individual differences in rates of change in cognitive abilities of older persons. Psychol Aging 17:179–193. CrossRef Medline

Wolpert DM, Diedrichsen J, Flanagan JR (2011) Principles of sensorimotor learning. Nat Rev Neurosci 12:739–751. CrossRef Medline

Zarahn E, Weston GD, Liang J, Mazzoni P, Krakauer JW (2008) Explaining savings for visuomotor adaptation: linear time-invariant state-space models are not sufficient. J Neurophysiol 100:2537–2548. CrossRef Medline

Zimprich D, Kurtz T (2013) Individual differences and predictors of forgetting in old age: the role of processing speed and working memory. Neuropsychol Dev Cogn B Aging Neuropsychol Cogn 20:195–219. CrossRef Medline