Brief Communication

Aging affects motor learning but not savings at transfer of learning

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Two important components of skill learning are the learning process itself (motor acquisition) and the ability to transfer what has been learned to new task variants (motor transfer). Many studies have documented age-related declines in the ability to learn new manual motor skills. In this study, I tested whether the degree of savings at transfer of learning is similarly affected by advancing age. Young and older adults made aiming movements with a joystick to hit targets presented on a computer screen, with real-time feedback display of their movement. They adapted to three different rotations of the feedback display in a sequential fashion, with return to the normal feedback display between each. Adaptation performance was better when it was preceded by other adaptive experiences, regardless of age.

Two important components of skill learning are the learning process itself (motor acquisition), and the ability to transfer what has been learned to new conditions and task variants (motor transfer). Motor transfer allows for adaptation of learned actions to changing task demands. Such transfer has been seen for a wide variety of motor skills (cf. McCracken and Stelmach 1977; Lee et al. 1991; Jaric et al. 1993; Zanone and Kelso 1997), including when subjects acquire new visuomotor mappings, as occurs when there is a conflict between visual and proprioceptive feedback of movement (Lazar and Van Laer 1968; Kennedy et al. 1987; Welch et al. 1993; Kagerer et al. 1997; Abeeel and Bock 2001; Seidler 2004, 2005). For example, Welch et al. (1993) had subjects alternate pointing movements made while wearing 15-diopter base left and right prism lenses. Following repeated, alternating exposures, subjects showed a savings or faster adaptation when presented with a novel 30-diopter prismatic displacement. These preceding examples provide evidence that subjects show a savings based on prior learning experiences, although it is not clear which aspect(s) of the learning process has been enhanced. It may be that, because a partially correct representation already exists, subjects are able to skip over the early stages of learning when they are faced with similar conditions in the future.

Many studies have documented declines in the ability of older adults to acquire new manual motor skills (cf. Ruch 1934; Harrington and Haaland 1992; Pratt et al. 1994; Howard and Howard 1997; McNay and Willingham 1998; Seidler-Dobrin and Stelmach 1998; Seidler 2006), but, to my knowledge, no studies have tested motor transfer in older adults. Determining whether savings in the rate of learning at transfer is preserved or impaired with age can help us to more fully understand the effects of aging on skill learning. Moreover, it can help to reveal the underlying mechanisms contributing to motor acquisition versus motor transfer in the young adult. In the current study, I tested the ability of older adults to transfer motor skills to new variations of already learned tasks. Similar to previous investigations of savings (Medina et al. 2001; Kojima et al. 2004; Smith et al. 2006), subjects underwent a washout session in between each learning experience. I wished to determine whether the degree of savings

based on prior learning history was impaired in older adults in light of the deficits that they exhibit in motor acquisition.

Nineteen older adults (OA) and 19 younger adults (YA) participated in this study (see Table 1). They were randomly assigned to either Group 1 (OA: 4 F, 6 M, one left handed, average age 73.1 yr; YA: 4 F, 6 M, one left handed, average age 24.6 yr) or Group 2 (OA: 4 F, 5 M, two left handed, average age 76.8 yr; YA: 5 F, 4 M, one left handed, average age 21.6 yr) (see below for group descriptions).

Subjects moved a joystick device with the dominant hand to move a cursor into targets presented on a computer screen under differing task requirements (cf. Seidler 2004, 2005). Subjects were instructed to move the cursor representing the joystick position from the central start location into the target as quickly as possible upon target appearance, and to hold the cursor within the target until it disappeared (3 sec following its appearance). Subjects were instructed to release their grip on the joystick handle at this point, allowing the spring-loaded device to recenter for the next trial.

Subjects adapted to three visuomotor rotations, with a return to normal display conditions in between each adaptive experience. The rotation magnitudes were 15, 30, and 45° clockwise rotations of the cursor position about the central start location (cf. Cunningham and Welch 1994). That is, in order to achieve a target in the 45° rotation condition, subjects would need to aim 45° counterclockwise of the target. Group 1 subjects acquired the visuomotor rotations in the following order: 30, 15, 45° (30–15–45 group), while Group 2 subjects acquired them in the order: 45, 15, 30° (45–15–30 group, see Table 2 for details of trial presentation), with washout trials in between each adaptive experience. This counterbalanced design allowed us to assess the amount of savings for subjects that learned the 45° or 30° rotation last in comparison to those that learned it first. Subjects were not informed in advance as to whether the upcoming block was an adaptation or control block, nor were they provided with any information about the applied rotations. They were instructed to hit the target as rapidly as possible and to attempt to minimize both reaction time and movement time.

I calculated two performance variables using the initial ballistic movement (cf. Meyer et al. 1988) toward the target: the direction error (DE) at the peak of the tangential velocity profile and the initial endpoint error (IEE). The algorithm we used to calculate the end of the initial ballistic movement searches for a

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Article published online in January 2007. Article and publication date are at <http://www.learnmem.org/cgi/doi/10.1101/lm.394707>.

Table 1. Subject group demographics

Group	Mean age (years)	Mean hours of exercise per week	Mean years of education	Mean number of medications ^a	MMSE ^b
OA	74.9	4.9	16.2	1.3	28.9
YA	23.2	4.1	15.0	0.2	N/A

^aSignificant group difference $t_{1,36} = 4.4$, $P < 0.001$.^bMini-mental state exam score.

period of acceleration following a period of deceleration or a change in the sign of velocity. Thus, this initial movement has “ended” when there is either a change in movement direction or an additional propulsive action is made. I also computed a final endpoint error, which was the distance from the target after subjects made any corrective actions (at the point of movement offset), and the overall movement time. These variables are not presented, but the results were similar to those obtained with DE and IEE. I used mixed model analyses of variance designs to examine acquisition and generalization. Since I assessed performance using two different measures, I utilized an adjusted P threshold of 0.025.

Figure 1 shows example spatial trajectories for a representative young and older adult making movements to the left target. The plots on the left depict performance for subjects during the first few trials of exposure to the 45° rotation. The plots on the right depict performance for subjects during the first few trials of exposure to the 45° rotation following prior experience with the 30° and 15° conditions. The benefits of prior experience are evidenced by the straighter trajectories in this case.

Significant block, trial, and block $\times$ trial effects were interpreted as support that subjects were acquiring the adaptation. Any significant age differences in these effects indicated that the two age groups adapted at different rates. Main effects or interactions involving order were interpreted as evidence of savings based on previous experience with adaptation. The age differences in initial adaptation to the 30° and 45° rotations have been previously reported (Seidler 2006). In general, the OA showed less learning and poorer performance during adaptation than the YA. Error measures for initial adaptation and transfer are shown in Figures 2 and 3 (top, 30° adaptation and transfer, bottom, 45° adaptation and transfer).

An important initial assessment to make is whether the groups were equated in terms of baseline (normal feedback) per-

formance. The two age groups did not differ in terms of the direction error at baseline for either rotation condition, but older adults exhibited significantly larger initial endpoint error than the young adults for the 30° rotation (Figs. 2, 3, age main effect for IEE 30°, $F_{(1,33)} = 6.3$, $P = 0.01$). Initially, baseline performance also differed for the 30–15–45 and the 45–15–30 groups for the two error variables (DE 30°: order $\times$ block $\times$ trial interaction, $F_{(23,782)} = 3.6$, $P < 0.01$; DE 45°: order $\times$ block $\times$ trial interaction $F_{(23,782)} = 3.1$, $P < 0.01$; IEE 30°: order $\times$ block $\times$ trial interaction, $F_{(23,759)} = 1.98$, $P < 0.01$; IEE 45°: order $\times$ block $\times$ trial interaction $F_{(23,759)} = 2.7$, $P < 0.01$). This indicates that there were some lingering effects of the prior adaptive experience at the first baseline block. This group difference no longer existed at the second baseline block.

It was also important to determine whether the washout trials in between each adaptive experience were successful in restoring performance to baseline measures. This was achieved by comparing performance from the second pre-test block (Block 2 of Table 2) with block 2 of the subsequent two washout periods (Blocks 7 and 12 of Table 2). Specifically, I tested whether the mean of the last three trials from each of these blocks differed significantly from each other for each of the four subject groups. These values did not differ for any of the groups for either DE or IEE, indicating that each adaptive experience was initiated from the same level.

All subjects showed decreasing errors with practice (DE 30°: Fig. 2, top, trial main effect $F_{(23,782)} = 7.6$, $P < 0.001$; block main effect $F_{(2,68)} = 8.2$, $P = 0.001$; DE 45°: block main effect $F_{(2,64)} = 25.1$, $P < 0.01$; trial main effect $F_{(23,736)} = 6.4$, $P < 0.01$; block $\times$ trial $F_{(46,1472)} = 5.2$, $P < 0.01$; IEE 30°: Fig. 3, top, block $\times$ trial interaction $F_{(46,1518)} = 1.6$, $P < 0.01$; trial main effect $F_{(23,759)} = 4.4$, $P < 0.01$; block main effect $F_{(2,66)} = 55.0$, $P < 0.01$;

Table 2. Trial presentation for each block (rotations 1, 2, and 3 were 30°, 15°, and 45° for one group of subjects, and 45°, 15°, and 30° for the other group)

Block number	Rotation	# of Trials
1	None (baseline display)	24
2	None (baseline display)	24
3	Rotation 1	28
4	Rotation 1	28
5	Rotation 1	28
6	None (baseline display)	28
7	None (baseline display)	28
8	Rotation 2	28
9	Rotation 2	28
10	Rotation 2	28
11	None (baseline display)	28
12	None (baseline display)	28
13	Rotation 3	28
14	Rotation 3	28
15	Rotation 3	28
16	None (baseline display)	28
17	None (baseline display)	28

Figure 1. Spatial trajectories are presented for movements made to the left under the 45° rotation condition (top row, young adults; bottom row, older adults). The target appears in the location of the filled circle, but, due to the imposed rotation, subjects must move to the location of the open circle (not visible to the subjects) in order to achieve the target. Trials on the left are from movements made during the first few trials of exposure to the 45° rotation, while those on the right are from the first few trials of exposure to the 45° rotation following experience with the 30° and 15° conditions.

Figure 2. Group mean values for direction error (DE) during motor acquisition and generalization are presented for the young and older adults. The *top* plots show initial adaptation and transfer for the 30° rotation; 45° rotation data are presented in the *bottom* plots. The first data point for each block reflects performance on the first trial, and subsequent data points are the mean over three trials. BL and A refer to baseline (normal feedback) and adaptation (rotated feedback) blocks. Motor generalization can be observed as better performance for subjects that had prior adaptive experience (triangles) than naive subjects (diamonds), reflected as significant test order effects. The amount of savings at transfer did not differ between the two age groups (lack of age $\times$ order interactions).

IEE 45°: block main effect $F_{(2,66)} = 48.2$, $P < 0.01$; trial main effect $F_{(23,759)} = 6.8$, $P < 0.01$; block $\times$ trial $F_{(46,1518)} = 2.4$, $P < 0.01$). The amount of original learning that took place for each age group was also quantified, as this could potentially influence the amount of subsequent savings that subjects would show. The maximum possible amount of learning was estimated as the difference in performance from the mean of the last three pre-test trials (Block 2 of Table 2) and the mean of the first three adaptation trials (Block 3 of Table 2). The amount of learning that occurred was then estimated as the performance level at the end of adaptation (mean of the last three trials of Block 5) as a percentage of the maximum possible amount of learning. Thus, a value of 100% would mean that learning was “complete” (i.e., performance returned to baseline levels), and a value of 0% would mean that no learning had taken place (i.e., performance for the last adaptation trials was no different from the initial

adaptation trials). The mean values were 24% and 52% for the older and the young adults adapting to the 45° rotation, respectively, and 19% and 46% for the older and the young adults adapting to the 30° rotation. While there was a main effect of age for this variable ($F_{(1,34)} = 6.4$, $P = 0.01$), there was neither a main effect nor an interaction for rotation magnitude.

Both age groups showed an equivalent amount of transfer to the 30° condition, with the 45–15–30 subjects performing better than the 30–15–45 subjects (DE, Fig. 2, top; order $\times$ block $\times$ trial effect across the adaptation blocks, $F_{(46,1564)} = 5.3$, $P < 0.001$, trial $\times$ order $F_{(23,782)} = 4.5$, $P < 0.001$, no age main effect or age $\times$ order interactions; IEE, Fig. 3, top, order main effect $F_{(1,33)} = 36.8$, $P < 0.01$, age main effect $F_{(1,33)} = 15.1$, $P < 0.01$, no age $\times$ order interactions).

Prior adaptive experience also resulted in faster changes in DE when subjects transferred to the 45° condition (Fig. 2 bottom, order $\times$ block $\times$ trial interaction $F_{(46,1472)} = 4.6$, $P < 0.01$, order $\times$ trial interaction $F_{(23,736)} = 4.8$, $P < 0.01$). Although this benefit appears to be larger for the young adults than the older adults, the appropriate supporting statistic did not quite achieve significance (age $\times$ order interaction $F_{(1,32)} = 4.5$, $P = 0.04$). Both of the age groups showed an equivalent amount of transfer to the 45° condition when performance was assessed using IEE, with 30–15–45 subjects performing better than 45–15–30 subjects (Fig. 3 bottom, order $\times$ block $\times$ trial interaction $F_{(46,1518)} = 1.8$, $P < 0.01$, order main effect $F_{(1,33)} = 9.5$, $P < 0.01$), despite higher errors for the older adults (age main effect, $F_{(1,33)} = 9.0$, $P < 0.01$). Similarly to DE, the interaction statistic that would indicate greater transfer for the young than the older adults just missed significance (age $\times$ order $\times$ block $F_{(2,66)} = 3.5$, $P = 0.04$).

I also analyzed the after effects of the sensorimotor adaptation by evaluating performance when subjects returned to the normal visual display. Subjects with prior adaptive experience were able to readapt to the baseline display more quickly, regardless of age (DE 30°: order $\times$ block $\times$ trial interaction $F_{(23,782)} = 2.8$, $P < 0.001$; IEE 30°: block $\times$ order interaction, $F_{(1,33)} = 6.8$, $P = 0.01$, absence of age $\times$ order interactions; IEE 45°: order $\times$ block $\times$ trial interaction, $F_{(23,759)} = 2.6$, $P < 0.01$).

To help represent the magnitude of savings at transfer, I computed a savings score in which I present performance at transfer as a fraction of original performance for each of the error measures. Specifically, savings scores were computed by dividing the mean performance for the first block at generalization (Block 13 of Table 2) by the mean performance for the first block at adaptation (Block 3 of Table 2) to yield the data points under column “A1” of Table 3. Note that this measure was computed

Figure 3. Group mean values for initial endpoint error (IEE) during motor acquisition and generalization are presented for the young and older adults. The *top* plots show initial adaptation and transfer for the 30° rotation; 45° rotation data are presented in the *bottom* plots. The first data point for each block reflects performance on the first trial, and subsequent data points are the mean over three trials. BL and A refer to baseline (normal feedback) and adaptation (rotated feedback) blocks. Motor generalization can be observed as better performance for subjects that had prior adaptive experience (triangles) than naive subjects (diamonds), reflected as significant test order effects. The amount of savings at transfer did not differ between the two age groups (lack of age $\times$ order interactions).

using group averages rather than individual data because different subject groups performed under the 30° and 45° rotations at initial learning and at transfer. A savings score <1.0 indicates that transfer was positive; scores >1.0 indicate negative transfer. These data are presented in Table 3. As can be seen in the table, and supported by the statistics reported above, savings scores for the older adults are within the range of those attained by the younger adults.

Thus, despite age-related declines in motor acquisition (cf. Ruch 1934; Harrington and Haaland 1992; Pratt et al. 1994; Howard and Howard 1997; McNay and Willingham 1998; Seidler-Dobrin and Stelmach 1998; Seidler 2006), the current data demonstrate that older adults show a normal amount of savings from prior adaptive experience. These results suggest that the underlying processes contributing to motor acquisition and transfer are distinct, and furthermore, that these processes are differentially affected by age. Such results argue against global theories of performance changes with age, which suggest that one (or more) global underlying construct, such as processing

speed (cf. Salthouse 2000), contributes to reduced performance in older adults. Rather, it seems that there are specific age-related changes that overlap with the underlying components of motor acquisition but not motor transfer.

Recent work has contributed greatly to our understanding of the processes contributing to sensorimotor adaptation. Early in learning, adaptation is associated with brain activation in prefrontal, parietal, and motor cortices, as well as the basal ganglia and cerebellum (cf. Inoue et al. 1997; Contreras-Vidal and Kerick 2004; Seidler et al. 2006). Late adaptation is associated with a reduced subset of brain activation encompassing motor and parietal cortex and the cerebellum. This shift in underlying neural substrates is paralleled by changes in the cognitive and sensorimotor processes contributing to skill acquisition. Studies using dual tasks during skill learning have shown that secondary tasks that place demands on cognitive processes such as spatial attention and working memory interfere with the early stages of learning, while those placing demands on motor preparation interfere with the later stages of learning (Eversheim and Bock 2001; Puttemans et al. 2005). Age-related declines in a variety of spatial cognitive processes (Klitz 1978; Goldstein and Shelly 1981; Park et al. 2001) may contribute to the difficulties that older adults have with motor acquisition.

In contrast, the underlying components of motor savings have not been well studied for adaptation tasks (although, see Kojima et al. 2004; Smith et al. 2006). Presumably, subjects need to retrieve motor memories and elaborate upon them during transfer of learning. It may be that the cognitive processes associated with motor acquisition are no longer required at motor transfer. This

interpretation is somewhat speculative, but is supported by reduced involvement of the prefrontal cortices during late learning and consolidation of learning, with a shift to motor cortical and subcortical regions (Shadmehr and Holcomb 1997; Nezafat et al. 2001; Doyon and Benali 2005). It remains to be seen whether the reduced cognitive component for motor transfer allows older adults to exhibit normal savings. Recent data have documented normal retention of motor skills in older adults (Smith et al. 2005).

It should be noted that, although there were no significant age differences in the amount of savings in the current study in terms of error measures, there were trends for the young adults to show better transfer than the older adults to the 45° rotation. Furthermore, the young adults showed better transfer than the older adults to the 45° rotation in terms of movement time, while the older adults showed better transfer than the young to the 30° condition for movement time. I have recently shown that young adults show better transfer when acquiring rotations in the order 30°, 15°, and 45° if performance is assessed using direction error

Table 3. Savings scores

Transfer to 30°	A1	A2	A3
OA, DE	0.82	0.69	0.71
YA, DE	0.86	0.96	1.05
OA, IEE	0.80	0.81	0.88
YA, IEE	0.80	0.81	0.83
Transfer to 45°			
OA, DE	1.05	0.93	0.98
YA, DE	0.66	0.61	0.64
OA, IEE	0.96	0.92	0.82
YA, IEE	0.71	0.68	0.78

A1, A2, and A3 refer to the first, second, and third blocks of practice with either the 30° or the 45° rotation.

and initial endpoint error (Seidler 2005). In contrast, if performance is assessed using final endpoint error, young adults show better transfer when acquiring rotations in the order 45°, 15°, and 30°. In fact, in the latter case, transfer is 100% when analyzed using final endpoint error. These data suggest that multiple fundamentally distinct processes lead to savings. The trend for age-related differences in transfer magnitude for the two orders of adaptation hints that aging may differentially affect these components of transfer.

In summary, I found that, although older adults have deficits in motor acquisition, they exhibit normal savings based on prior learning history. These data suggest that motor acquisition and transfer are distinct processes, differentially affected by age. I suggest that this newly documented age-related dissociation between acquisition and transfer may be fundamentally important to clarifying the mechanisms and course of age-related motor declines. Moreover, this dissociation may provide new insights into acquisition and transfer processes and their neural underpinnings in young adults.

Acknowledgments

I thank D. Willingham for insightful comments on an earlier draft of this manuscript. I thank the following undergraduate students for their assistance with data acquisition and analysis: M. Zafar, E. Andreae, C. Chase, K. Gustafson, and K. Keen. This work was supported by NIH AG20883, NIH AG024106, and the UM Claude D. Pepper OAIC Research Career Development and Human Subjects Cores (NIH AG08808).

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Received August 2, 2006; accepted in revised form October 20, 2006.

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Learn. Mem. 2007, **14**: originally published online January 3, 2007
Access the most recent version at doi:[10.1101/lm.394707](https://doi.org/10.1101/lm.394707)

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