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RESEARCH ARTICLE

Visuomotor adaptation and proprioceptive recalibration in older adults

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Abstract Previous studies have shown that both young and older subjects adapt their reaches in response to a visuomotor distortion. It has been suggested that one's continued ability to adapt to a visuomotor distortion with advancing age is due to the preservation of implicit learning mechanisms, where implicit learning mechanisms include processes that realign sensory inputs (i.e. shift one's felt hand position to match the visual representation). The present study examined this proposal by determining if changes in sense of felt hand position (i.e. proprioceptive recalibration) follow visuomotor adaptation in older subjects. As well, we examined the influence of age on proprioceptive recalibration by comparing young and older subjects' estimates of the position at which they felt their hand was aligned with a visual reference marker before and after aiming with a misaligned cursor that was gradually rotated 30° clockwise of the actual hand location. On estimation trials, subjects moved their hand along a robot-generated constrained pathway. At the end of the movement, a reference marker appeared and subjects indicated if their hand was left or right of the marker. Results indicated that all subjects adapted their reaches at a similar rate and to the same extent across the reaching trials. More importantly, we found that both young and older subjects recalibrated proprioception, such that they felt their hand was aligned with a reference marker when it was approximately 6° more left (or counterclockwise) of the marker following reaches with a rotated cursor. The leftward shift in both young and older subjects' estimates was in the same direction and a third of the extent of adapted movement. Given that the changes in the estimate of felt hand position were only a fraction of the changes observed in the reaching movements, it is unlikely that sensory recalibration was the only source driving changes in reaches. Thus, we propose that proprioceptive recalibration combines with adapted sensorimotor mappings to produce changes in reaching movements. From the results of the present study, it is clear that changes in both sensory and motor systems are possible in older adults and could contribute to the preserved visuomotor adaptation.

Keywords Visuomotor adaptation · Sensory recalibration · Older adults · Proprioception

Introduction

The ability of the human brain to adapt to changing intrinsic (e.g. growth and aging) and extrinsic environmental conditions is essential for appropriate motor function throughout the lifespan. In light of this, many studies have examined one's ability to adapt to novel visuomotor environments with advancing age. In particular, studies have had subjects of different ages reach to targets when a

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visuomotor distortion has been introduced (Bock 2005; Bock and Girgenrath 2006; Buch et al. 2003; Heuer and Hegele 2008; McNay and Willingham 1998; Seidler 2004, 2006, 2007). For example, in the study by Buch et al. (2003), young and older subjects reached to targets in a virtual reality environment while a cursor misrepresented the location of their hand (i.e. visual and proprioceptive signals regarding hand location were misaligned). Buch et al. (2003) found that the final reach adaptation level achieved was reduced in the older subjects compared to the younger subjects when a 90° visual-proprioceptive mismatch was introduced abruptly, but was similar between the two groups when this mismatch was introduced gradually. When subjects were required to reach without a cursor following either abrupt or gradual training, all subjects reached in a similar manner, exhibiting the same degree of aftereffects.

Based on the patterns of reaching trajectories (i.e. visuomotor adaptation) achieved in young and older subjects in response to a visuomotor distortion, it has been suggested that the processes underlying visuomotor adaptation are differentially influenced by age. Specifically, it has been suggested that strategic processes, as outlined by Redding and Wallace (1996; Redding et al. 2005), deteriorate with age while spatial realignment processes are preserved. Strategic control refers to changes in reaches arising because of cognitive schemes, such as the ability to engage spatial working memory (Anguera et al. in press), as well as anticipation and feedback-based corrections. It is suggested that this type of control is engaged early during the learning process when a visuomotor distortion is introduced abruptly in order to produce rapid corrections in performance. Furthermore, these strategic control adjustments are proposed to decay with advancing age, giving rise to the changes observed between young and older subjects when a visuomotor distortion is introduced abruptly (Anguera et al. in press; Bock 2005; Bock and Girgenrath 2006). In contrast to strategic processes, spatial realignment processes are thought to be maintained with advancing age and are proposed to be responsible for reach adaptation when the visuomotor distortion is introduced gradually and aftereffect errors produced following either abrupt or gradual training (Heuer and Hegele 2008; McNay and Willingham 1998; Redding and Wallace 1996). Spatial realignment refers to the implicit remapping of sensory input and motor output that arises in response to a sensorimotor distortion. An example of such sensory realignment is proprioceptive recalibration, where proprioceptive recalibration indicates a shift in hand proprioception in the direction of the visuomotor distortion in order to eliminate the spatial discrepancy between visual and proprioceptive estimates (i.e. subjects begin to feel their hand is shifted in the direction that they see it).

While it is proposed that one's ability to adapt to novel visuomotor environments is preserved with aging due to proprioceptive recalibration, proprioceptive recalibration has not been examined in the elderly population directly. Instead, research on proprioception and aging has tended to focus on proprioceptive acuity by examining how individuals perform joint matching tasks in which they are required to (1) reproduce the perceived position of one target joint (i.e. right elbow angle) with that of the other joint (i.e. left elbow) or (2) reproduce from memory the perceived position of one joint after it has been returned to rest with either the same or opposite limb. Results from these tasks clearly demonstrate a significant deterioration in one's ability to sense the position of a body segment with advanced age, suggesting that proprioceptive acuity decreases with age (Adamo et al. 2007, 2009; Goble et al. 2009; Kaplan et al. 1985; Meeuwsen et al. 1993; Stelmach and Sirica 1986). Given that proprioceptive position sense decreases with advanced age, proprioception may be more vulnerable to recalibration in an older population compared to a younger population when visual and proprioceptive signals are misaligned. Specifically, because proprioception tends to provide more inaccurate information regarding the hand's position in space in the elderly compared to the young, these less accurate signals may be less resistant to change than the more accurate proprioceptive signals experienced by a younger population. This preserved (and possibly enhanced) proprioceptive recalibration in the elderly may then be implicated in their continued ability to adapt to a visuomotor distortion.

In the current study, we examined if proprioception is recalibrated in the elderly and compared the magnitude of proprioceptive recalibration in the elderly to a younger population. Specifically, we examined proprioceptive recalibration in young and older adults following visuomotor adaptation to a cursor that was rotated 30° clockwise (CW) with respect to the hand. The cursor rotation was introduced gradually as we wanted young and older subjects to adapt to the visuomotor distortion to a similar extent, engaging potential recalibration processes as much as possible. Following adaptation to this visuomotor distortion, subjects completed a proprioceptive estimation task. This estimation task consisted of subjects making perceptual decisions regarding the position of their hand relative to a reference marker (Cressman and Henriques 2009, 2010; Jones et al. 2010). This task differs from previous paradigms examining sensory recalibration, which have typically required subjects to perform reaching movements [e.g. subjects reach to a proprioceptive target (i.e. their left finger) with their adapted (right) hand (Simani et al. 2007; van Beers et al. 2002)]. While subjects' reaches to a proprioceptive target are typically altered in these previous studies following visuomotor adaptation, it is not possible to conclude that these changes in reaches arise due to changes in felt hand position of the adapted or opposite (non-adapted) hand. Instead, changes in proprioceptive reaches may arise because the motor commands or sensorimotor mappings underlying the reaching movement have been adapted. In our task, we assessed changes in felt hand position following exposure to a visual-proprioceptive conflict in a task in which there was no goal-directed reaching component. In particular, subjects moved their hands out along a constrained pathway. Once the hand was at the end of the path, a visual reference marker appeared and subjects indicated if their hand was to the left or to the right of the marker.

In a previous study, we have shown that the magnitude of errors achieved in this perceptual task do not differ from those completed during proprioceptively guided reaches (Jones et al. 2010). As well, using this paradigm, and hence eliminating any influence of potential motor recalibration, we have shown that proprioceptive recalibration arises in younger subjects following exposure to a visuomotor distortion (Cressman and Henriques 2009, 2010). Subjects change their felt hand position such that it is perceived to be shifted in the same direction as visuomotor adaptation. Based on these previous findings, we have suggested that reach adaptation is due in part to changes in visually driven proprioceptive recalibration. If the visuomotor adaptation observed in older subjects is due to proprioceptive recalibration as suggested, we would expect to see shifts in the positions at which older subjects feel their hands are aligned with a reference marker following visuomotor adaptation. As well, the current study will also allow us to compare potential levels of proprioceptive recalibration between young and older adults to see if proprioception is more vulnerable to recalibration in the elderly compared to the young.

Methods

Subjects

Nine healthy older subjects between the ages of 61 and 80 (6 women and three men; mean age = 66.3, SD 6.0 years) and ten healthy young subjects between the ages of 18 and 36 (6 women and 4 men; mean age = 27.3, SD 5.1 years) were recruited to participate in the experiment described below. Before starting the testing procedures, all subjects were pre-screened verbally for self-reported right handedness, and history of visual, neurological, and/or motor dysfunction. As well, all older subjects completed the Mini-Mental State Examination test (MMSE) (mean score: 29.0 out of 30, SD 1.3). All subjects gave informed consent and the study was conducted in accordance with the ethical guidelines set by the York Human Participants Review Subcommittee.

General experimental setup

A side view of the setup is illustrated in Fig. 1a and is the same as that used in Cressman and Henriques (2009, 2010). Subjects were seated at the table so that they could comfortably see and reach to all target positions. Subjects were then instructed to grasp the vertical handle of a two-joint robot manipulandum (Interactive Motion Technologies) with their right hand such that their thumb was positioned on a top marker (1.4 cm in diameter). Visual stimuli were projected from a monitor (model: Samsung 510 N, refresh rate: 72 Hz) installed 17 cm above the robot and viewed by subjects as a reflected image. The reflective surface was opaque and positioned in order that images displayed on the monitor appeared to lie in the same horizontal plane as the robot handle. The room lights were dimmed and subjects' view of their right hand was blocked by the reflective

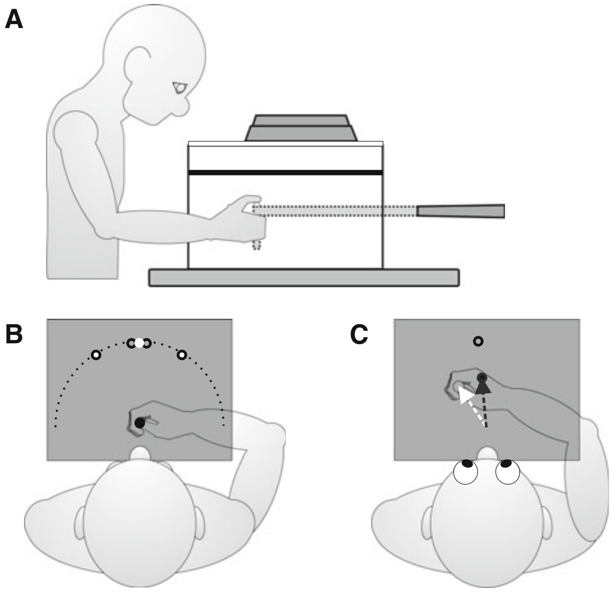

Fig. 1 Experimental setup and design. **a** Side view of the experimental setup. **b** and **c** Top view of experimental surface. **b** Reach targets (*open black circles*) and reference markers (*filled white circles*) for the proprioceptive estimation task were located along a circular arc, 10 cm from the home position (*filled black circle*). Reach targets were positioned 5° and 30° left and right of center and the reference markers were located 30° left and right of center and at center. Note that the black dotted line is provided as a reference to indicate the locations of the targets and reference markers and illustrate potential positions that the hand could have been moved to during the proprioceptive estimate trials. **c** Visuomotor distortion introduced in the reach training task when subjects reached with a misaligned cursor. The black cursor (representing the hand) was rotated 30° clockwise with respect to the actual hand location

surface and a black cloth draped between the experiment setup and subjects' right shoulders.

Stimulus display/hand movement

At the start of each trial, the robot manipulandum was positioned below the home position, ~25 cm directly in front of the subject's midline (filled black circle in Fig. 1b). This position was indicated visually by a filled black circle, 1 cm in diameter. Visual stimuli were displayed 10 cm from the home position, 5 and 30° left (counter clockwise, CCW) and right (clockwise, CW) of center and directly in front of the home position (0°). The open black circle displayed in Fig. 1b indicate target positions (5 and 30° left and right of center) to which subjects actively reached in the reach trials discussed below. Subjects estimated the location of their hands relative to the visual reference markers displayed at 30° left and right of center and center (filled white circles in Fig. 1b). Having the targets and reference markers in these positions (i.e. at the specified angles 10 cm from the home position) ensured that all subjects were able to reach comfortably to the required positions and complete the tasks outlined below in a timely manner.

Procedure

Subjects were tested on 2 days. On each day of testing subjects completed four tasks, which consisted of reach trials and/or proprioceptive estimates. The first testing day produced baseline measures, in which we assessed reaching performance and proprioceptive estimates of hand position after subjects reached with a veridical (i.e. aligned) cursor during the reach training task described below (Fig. 2). On the second day of testing we assessed reaching performance (i.e. visuomotor adaptation) and sense of felt hand position after subjects reached with a misaligned cursor during the reach training task.

Reach training task

Similar to the study by Cressman and Henriques (2009), subjects began by completing a Reach Training Task (1st box in Fig. 2). A reach trial began with subjects grasping the robot manipulandum with a comfortable, but firm grip. At the start of each trial, the robot was positioned at the home position. After maintaining the hand at the home position for 300 ms, a reach target appeared. Subjects were instructed to move as quickly and accurately as possible to the target while gripping the handle of the free-moving robot manipulandum. The position of the unseen hand was represented by a cursor (1-cm filled black circle, shown in Fig. 1c) that appeared after the robot handle had moved 4 cm outwards from the home position. By having the cursor appear only after subjects had moved 4 cm from the home position, we ensured that subjects achieved peak velocity before vision of the hand became available.

In order to complete the reach, subjects had to move the center of the cursor within 0.5 cm of the target's center. At that point, both the target and cursor were removed and the robot was locked to a grooved path. This grooved path guided subjects back to the home position by a direct linear route in the absence of visual feedback. If subjects attempted to move outside of the established path, a resistance force (proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous damping of 5 N/(mm/s)) was generated perpendicular to the grooved wall (Henriques and Soechting 2003).

The order of the reach trials was pseudo-randomized such that subjects reached once to 3 of the reach targets, specifically the two peripheral targets and one of the pair of

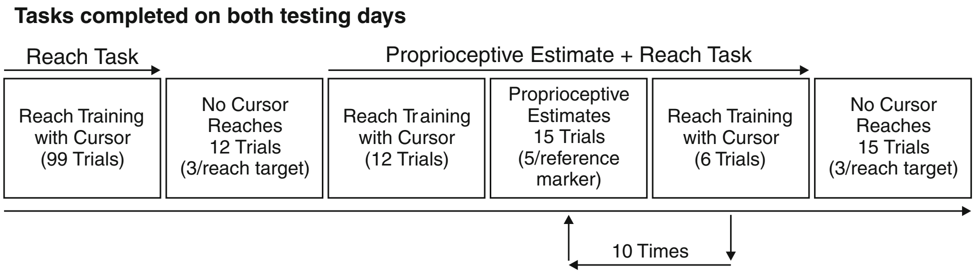

Fig. 2 Schematic showing the order in which the different tasks were completed within a testing session. On the first day of testing, subjects reached with an aligned cursor on all reach training trials. On the second day of testing, the cursor was gradually rotated clockwise with respect to the actual hand location over the first 41 trials in the first reach training task (*Box 1*). On all subsequent reach training trials on this second day, the cursor was rotated 30° clockwise with respect to the actual hand location. After completing the first 99 visually guided reach training trials, subjects next reached to each of the 4 reach targets three times without a cursor in order to assess visuomotor adaptation (No cursor reaches, *Box 2*). Subjects then completed an additional 12 reaches to the reach targets with the cursor present (*Box 3*). This was followed by 10 sets of 15 proprioceptive estimates (*Box 4*) and 6 visually guided reaches (*Box 5*). Finally, subjects completed an additional 15 no cursor reaches (3 to each target and reference marker) to end the testing session

peri-central (5°) targets, before any target was repeated. Subjects completed 99 reach trials.

No cursor reaching task: to assess reaching performance

After completing the Reach Training Task, subjects immediately completed 12 aiming movements, 3 reaches to each of the 4 reach targets, without the cursor (2nd box in Fig. 2). These trials were included to establish that subjects had adapted their reaches in response to the misaligned cursor on the second testing day (i.e. exhibited aftereffects). On these trials, subjects were instructed to aim to a target and to remain at their end position. Once this end position had been maintained for 500 ms, the visual target disappeared and the trial was considered complete. Subjects were guided back to the home position by a linear grooved path. The position of the robot manipulandum was recorded throughout all reaching trials at a sampling rate of 50 Hz and a spatial accuracy of 0.1 mm.

Proprioceptive Estimate + Reach Task

In this task, proprioceptive estimates and reach trials (boxes 3–5 in Fig. 2) were systematically interleaved. Subjects began by completing an additional 12 reaching trials with an aligned cursor (box 3). These reaches were then immediately followed by interleaving sets of 15 proprioceptive estimate trials (box 4) and 6 reaching trials (box 5). The test sequence of 15 proprioceptive estimates followed by 6 reaches was completed 10 times, for a total of 222 trials (150 proprioceptive estimate trials (50 at each target) + 72 reach trials).

In the proprioceptive estimate trials, subjects grasped the handle of the robot manipulandum at the visible home position for 500 ms. After 500 ms, the home position was removed and subjects actively pushed the robot outwards along a constrained path to a location somewhere along the dotted line shown in Fig. 1b. Once the hand reached its final position, one of the three reference markers appeared and subjects made a two-alternative forced choice (2-AFC) judgment about the position of their hand relative to the reference marker. Specifically, subjects were instructed that the reference markers were positioned along a circular arc and that their responses were to be based on the felt position of their hand along this arc with respect to the reference marker (i.e. left (CCW) or right (CW) of the reference marker). As well, subjects were instructed that there were no time constraints during the task.

Hand positioning The position of the hand with respect to each reference marker was adjusted over trials using an adaptive staircase algorithm (Kesten 1958; Treutwein 1995). For each reference marker, there were two staircases, one starting 20° to the left (CCW) of the reference marker and one starting 20° to the right (CW). The two staircases were adjusted independently and randomly interleaved as outlined in Cressman and Henriques (2009, 2010).

No cursor reaching task: to assess reaching performance

Subjects completed 15 final no cursor reaches (box 6 in Fig. 2) immediately after completing the Proprioceptive Estimate + Reach Task in order to ensure that they were still reaching in a similar manner as before the proprioceptive estimate trials. These reaches were carried out like the previous 12 no cursor reach trials (2nd box in Fig. 2) but all 5 reach targets and reference marker positions were now presented.

This ended the first day of testing. On the second day of testing, subjects completed the same tasks as outlined above. However, this time we introduced a visuomotor distortion during all the cursor reach training trials (1st, 3rd and 5th boxes in Fig. 2). Specifically, the cursor representing the hand position was gradually rotated 30° CW with respect to the hand over the first 41 trials in increments of 0.75° in the first set of reach training trials (1st box), and then maintained a 30° CW rotation for all cursor reaching trials thereafter (Fig. 1c).

Data analyses

The goal of this study was to determine if age influences the extent to which one recalibrates proprioception. However, before examining proprioceptive recalibration, we first wanted to ensure that all subjects adapted to the visuomotor distortion introduced, as well as examine subjects' ability to localize their hand relative to the reference markers under baseline conditions.

Reaching performance

To examine if age influenced subjects' reaching movements, we calculated angular deviations of the hand for all reach trials completed in the reach training task (with cursor present) and in the no cursor reaching trials. Hand deviations were defined as the angular difference between a reference vector joining the center home position and the target and the vector joining the center home position and the position of the reaching hand at peak velocity (PV). On average, PV was achieved approximately 550 ms into the movement (mean time of PV in the young subjects = 581 ms (SD 126), mean time of PV in the older subjects = 525 ms (SD 160)), after the hand had moved only 3.75 cm from the home position (mean hand movement distance at PV in the young subjects = 3.97 cm (SD 0.58), mean hand movement distance at PV in the older subjects = 3.52 cm (SD 0.50)). Given that visual feedback of the hand was not available until the hand had moved 4 cm outwards from the home position, by examining hand deviations at PV we were able to determine initial movement planning errors before subjects had the opportunity to use visual feedback of the hand to correct trajectory errors.

Hand deviations completed during the reach training trials were averaged over three consecutive trials such that 33 blocks of three reaches were completed by each subject, as shown in Fig. 3a. In order to determine if subjects reached in a similar manner when reaching with an aligned cursor over all blocks of trials, average hand deviations over blocks of trials were analyzed in a 2 Group (Young vs. Older) × 33 Trial Blocks analyses of variance with repeated measures on the last factor (RM-ANOVA). We also examined differences in reach variability between the two groups of subjects by performing an independent *t* test on the standard deviation of subjects' hand deviations across all reaching trials.

To examine if age influenced the rate at which subjects adapted their reaches in response to the visuomotor distortion, average hand deviations over blocks of trials when subjects reached with a rotated cursor were analyzed with a 2 Group × 33 Trial Blocks RM-ANOVA. For both the young and older subjects, we then used paired sample *t*-tests to compare hand deviations for each of the first 32 blocks of reaching with a misaligned cursor to the average hand deviations achieved in the last learning block to determine at which block hand deviations began to saturate. Differences in reach variability between the two groups of subjects were also examined using an independent *t*-test on the standard deviation of subjects' reaching movements. In order to determine each subject's standard deviation for reaches completed when the cursor was misaligned from the hand, we found the standard deviation of the cursor position at PV across reaching trials (difference between a reference vector joining the center home position and the target and the vector joining the center home position and the position of the cursor at PV).

The extent of visuomotor adaptation was examined by looking at the angular deviations of the hand in the first set of no cursor reaches, as we found no difference in reaches completed before and after the Proprioceptive Estimate + Reach Task for either the young ($t(9) < 1$) or older subjects ($t(8) < 1$). Hand deviations were averaged across all 12 trials for each subject and the average deviations for trials completed after reaching with an aligned cursor were then subtracted from average deviations after reaching with a rotated cursor (Fig. 3b). These difference scores were then compared between groups using an independent *t*-test. Finally, the standard deviation of hand deviations completed during the no cursor reaching trials after training with both an aligned and misaligned cursor were analyzed to determine if age influenced the variability of reaches completed without a cursor using independent *t*-tests.

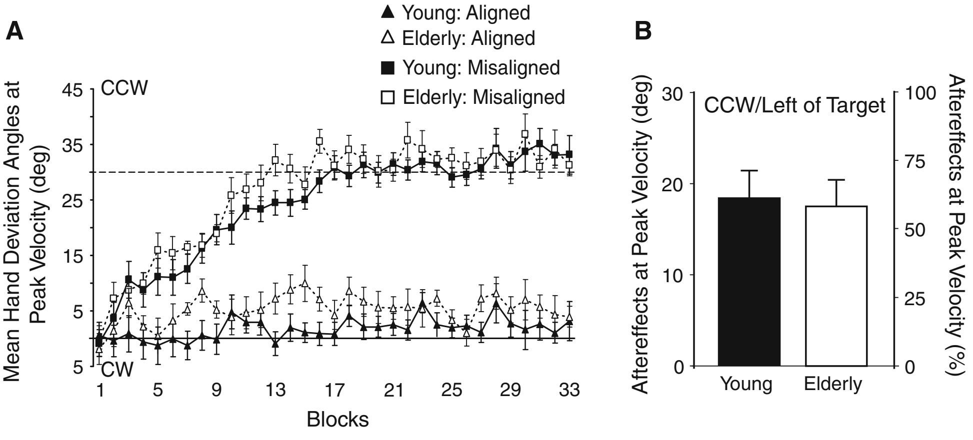

Fig. 3 Visuomotor adaptation during the **a** reach training trials and **b** aftereffect trials. In **a**, we show the mean angular deviation of the hand at peak velocity. Hand deviations were averaged over blocks of three trials for each subject and then averaged across all subjects while subjects reached with an aligned (*triangles*) or misaligned cursor (*squares*). In **b**, we show mean hand deviations on aftereffect trials averaged across subjects and targets. Results are shown in degrees and as a percentage of the distortion introduced during reach training trials. Aftereffects are presented taking performance on reaches completed after reaching with an aligned cursor as baseline, such that hand deviations achieved on the no cursor reaching trials after reaching with an aligned cursor were subtracted from corresponding hand deviations achieved after reaching with a misaligned cursor. The *filled* (*black*) symbols show performance by the young subjects, while the *open* (*white*) symbols show aftereffects achieved by the older subjects. *Error bars* reflect standard error of the mean

Proprioceptive estimates of hand position

In order to examine the influence of age on possible changes in proprioceptive estimates of hand position, we determined the locations at which subjects felt their hands were aligned with the reference markers. This location was determined by fitting a logistic function to each subject's responses for each reference marker in each testing session and calculating the bias (the point of 50% probability). In addition to calculating bias, we also determined subjects' absolute bias errors with respect to each reference marker (i.e. the absolute difference between a reference marker position and a subject's biased position) and the uncertainty (or precision) of subjects' estimates of hand position at each reference marker (i.e. the difference between the values at which the response probability was 25 and 75%). Biases and absolute bias values achieved on the first (baseline) day of testing were submitted to a 2 Group × 3 target (30° left, 30° right and 0°) RM-ANOVA to determine if age influenced one's ability to localize his or her hand relative to a visual reference marker. In order to determine the influence of age on proprioceptive recalibration, bias values and uncertainty results were analyzed using a 2 Group × 2 Visual Feedback during reach training (Aligned vs. Misaligned cursor) × 3 target (30° left, 30° right and 0°) RM-ANOVA. For all results, differences with a probability of less than .05 were considered to be significant. As well, for P values between 0.05 and 0.1, we indicate effect size (Cohen's d).

Results

Reaching performance

We first examined subjects' reaching trajectories. Figure 3a displays mean angular deviations of the hand over blocks of reaching trials for the 99 reaches completed during the reach training tasks. Hand deviations for the young subjects are shown as filled symbols (black triangles = aligned cursor during reach training and black squares = misaligned cursor during reach training) and hand deviations for the older subjects are open symbols (white triangles = aligned cursor during reach training and white squares = misaligned cursor during reach training). If we focus on the trials completed with an aligned cursor, we see that, for the most part, both groups of subjects reached such that their hand travelled along a fairly linear route to the target across all trials (i.e. hand deviations were minimal). In accordance with this observations, RM-ANOVA revealed no differences between the two groups with respect to hand deviations (though there was a trend toward significance, $F(1, 17) = 3.902$, $P = 0.065$, $d = 0.52$), a non-significant effect for Trial Block ($F(32, 544 = 1.703$, $P = 0.108$) and a non-significant Trial Block x Group interaction ($F(32, 544) < 1$). In addition, the variability between hand deviations across trials was similar between the two groups of subjects ($t(17) = 1.662$, $P = 0.115$). However, on the no cursor reach trials following reach training, hand deviation values were more variable in the older subjects' than the younger subjects (mean variability in the young subjects = 6.5° (SD 3.2), mean variability in the elderly = 11.6° (SD 3.2); $t(17) = 3.451$, $P = 0.003$).

In terms of the trials in which the cursor was rotated with respect to the hand, we see from Fig. 3 that both groups of subjects began to reach so that their hand was left of the target. Moreover, from the figure it appears that for all subjects, deviations of the hand from the target vector gradually increased in magnitude over the first 10–13 blocks of trials as the magnitude of the distortion was increased. RM-ANOVA revealed no differences between the two groups with respect to hand deviations achieved across the blocks of learning trials (Group: $F(1, 17) = 2.523$, $P = 0.131$, Trial Block × Group: $F(32, 544) = 1.077$, $P = 0.357$). However, hand deviations did increase over blocks of trials as expected with the increased distortion in order to guide the rotated cursor to the target in a more direct path ($F(32, 544) = 45.261$, $P < 0.001$). Paired sample t-tests revealed that hand deviations saturated for the young subjects by Block 13 (with Bonferroni correction, $P < 0.0015$). After this subjects reached with similar trajectories throughout the rest of the training trials. For the older subjects, there was no difference in hand deviations from block 10 and on, indicating a slightly earlier saturation in reaching performance when compared to the young subjects. With respect to reach variability, both groups of subjects reached with similar levels of variability on trials in which the cursor was present ($t(17) < 1$).

The differences in hand deviations on aftereffect trials after reaching with a misaligned cursor compared to an aligned cursor are shown in Fig. 3b. On average, all subjects reached 18.0° more left of the target following reach training with a misaligned cursor. Analysis revealed no differences between the two age groups with respect to the extent of visuomotor adaptation achieved ($t(17) < 1$). Similar to the reach variability observed after training with an aligned cursor, reaching variability after training with a misaligned cursor was higher in the older subjects compared to the younger subjects (mean variability in the younger subjects = 7.8° (SD 4.0), mean variability in the elderly = 10.9° (SD 4.5)). However, this difference in variability failed to reach significance ($t(17) = 1.604$, $P = 0.127$).

Proprioceptive recalibration

Bias

Figure 4a displays mean proprioceptive biases at each of the three reference marker locations for both the young (filled symbols: black triangles = estimates after reaching with an aligned cursor and black squares = estimates after reaching with a rotated cursor) and older subjects (open symbols: white triangles = estimates after reaching with an aligned cursor and white squares = estimates after reaching with a rotated cursor). For both groups of subjects we see that, on average, estimates of unseen hand location were slightly biased to the left after reaching with an aligned cursor (triangles). The mean bias collapsed across all reference markers was 2.7° left of the reference marker. Analyses revealed that both young and older subjects had similar levels of bias ($F(1, 17) < 1$) and that biases were independent of reference marker location ($F(2, 34) < 1$). Similar results were attained when absolute bias values were analyzed. In particular, analyses revealed that absolute biases were similar in magnitude across both groups of subjects ($F(1, 17) < 1$; mean absolute bias error = 7.9° (SD = 6.5)) and independent of reference marker location ($F(2, 34) = 2.807$, $P = 0.074$, $d = 0.62$).

In addition to finding that subjects had similar levels of proprioceptive acuity regardless of age under baseline conditions, we found that both groups of subjects recalibrated proprioception. Specifically, after learning to reach with the misaligned cursor, both groups felt their hand was at a reference marker when it was shifted significantly to the left of the aligned estimates (on average 6.1° more left as shown in Fig. 4b, $F(1, 17) = 13.688$, $P = 0.002$). This leftward shift in proprioceptive estimates was of a similar magnitude across all reference marker locations ($F(2, 34) < 1$) for both groups of subjects ($F(2, 34) < 1$).

Visuomotor adaptation versus proprioceptive recalibration

In Fig. 5, we plot changes in proprioceptive estimates after training with a misaligned cursor compared to an aligned cursor in relation to the level of visuomotor adaptation achieved for young (filled squares) and older subjects (white squares) as a percentage of the 30° distortion introduced. On average, subjects recalibrated proprioception by 20% and adapted their reaches by 60% of the visual distortion introduced. Moreover, from Fig. 5, we see that (1) almost all subjects adapted their reaches and recalibrated proprioception to some extent, (2) in all but one instance proprioceptive recalibration was less than visuomotor adaptation and (3) the magnitude of proprioceptive recalibration was similar regardless of the level of visuomotor adaptation obtained. In accordance with this last observation, analysis did not reveal any significant correlations between the magnitude of proprioceptive recalibration and the extent of visuomotor adaptation achieved by either the young or older subjects ($P > 0.5$).

Uncertainty range

Figure 6 depicts the magnitude of the uncertainty ranges for both the young (black bars) and older subjects (white

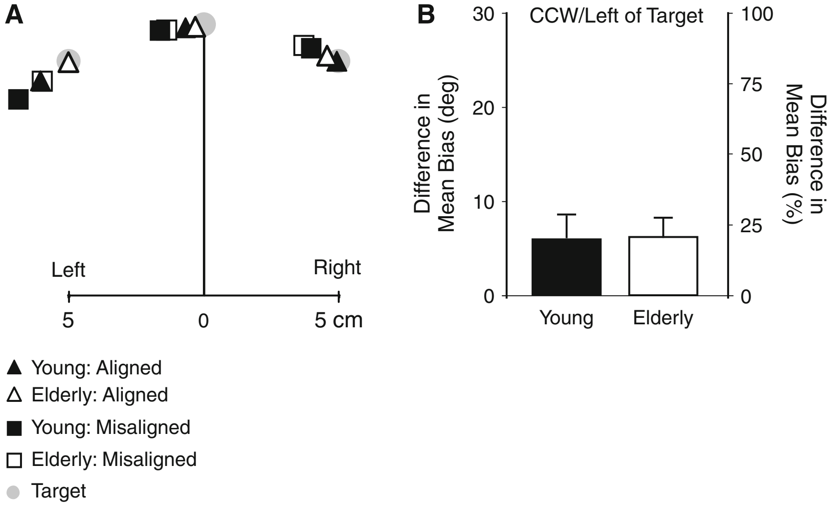

Fig. 4 **a** Mean 2-D biases on the proprioceptive estimation task after subjects reached with an aligned (*triangles*) or misaligned (*squares*) cursor during the reach training task. The *filled* (*black*) symbols show performance by the young subjects, while the *open* (*white*) symbols depict biases of the older subjects. Reference markers are represented as *filled gray circles*. In **b**, we show mean changes in bias after subjects reached with a misaligned compared to aligned cursor. Changes in bias were averaged across subjects and reference markers for both the young (*black bar*) and older subjects (*white bar*). Results are shown in degrees and as a percentage of the distortion introduced during reach training trials. *Error bars* reflect standard error of the mean

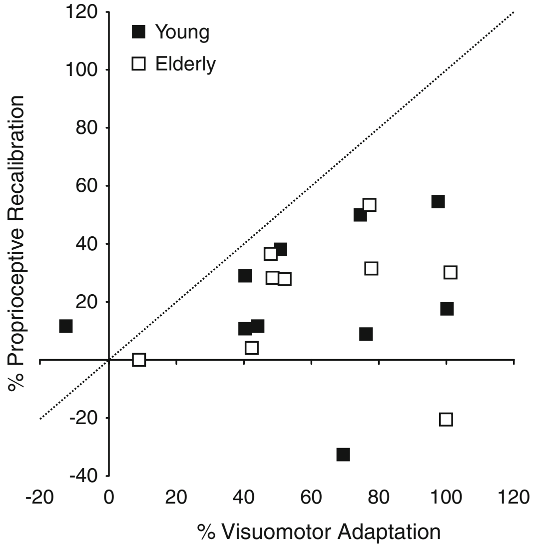

Fig. 5 The changes in proprioceptive estimates are plotted as a function of changes in reach aftereffects for each subject after exposure to a misaligned cursor compared to an aligned cursor (young subject group: *black squares*, older subject group: *white squares*). The *dashed line* is a unit slope and thus indicates equivalent levels of proprioceptive recalibration and visuomotor adaptation

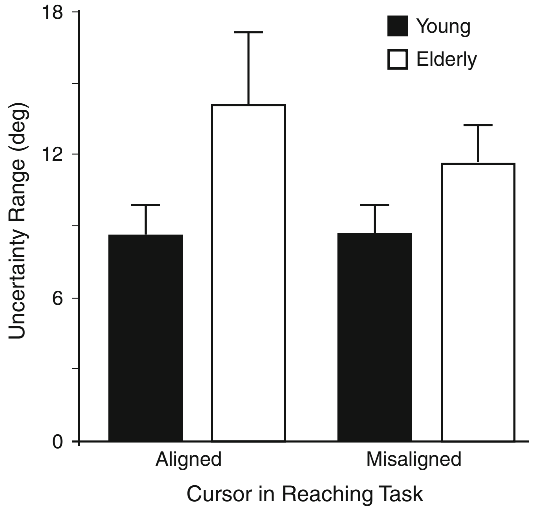

Fig. 6 Magnitude of the uncertainty ranges in the Proprioceptive Estimation tasks averaged across reference markers and subjects following reach training with an aligned (*right bars*) or misaligned cursor (*left bars*) for younger (*black bars*) and older subjects (*white bars*). *Error bars* reflect standard error of the mean

bars) following reaches with an aligned (right bars) and misaligned cursor (left bars). Subjects' levels of precision in estimating the location of their unseen hands were comparable after reach training with an aligned and misaligned cursor ($F(1, 17) < 1$) at all reference markers ($F(2, 34) = 2.281$, $P = 0.118$). However, results revealed a significant difference between the groups ($F(1, 17) = 4.283$, $P = 0.05$), such that estimates by the young subjects were more precise than estimates by the older subjects (young: 8.6° (SD 3.4) vs. older: 12.9° (SD 5.5)). Taken together, the proprioceptive estimation data indicate that while the estimates by the older subjects were slightly less precise than the young subjects' estimates, subjects recalibrated proprioception after reaching with a misaligned cursor without changing the precision of their estimates.

Discussion

In the current study, we examined if proprioception is recalibrated in the elderly after they learn to reach with misaligned visual feedback of the hand. In addition, we compared the magnitude of proprioceptive recalibration in the elderly to a younger population in order to determine if age influences the extent to which proprioception is recalibrated. Results revealed that both groups of subjects shifted the position at which they felt their hand was aligned with a reference marker after learning to reach with a cursor that was rotated 30° CW with respect to the hand. Moreover, subjects in both age groups shifted their sense of felt hand position on average 6.1° leftwards after reaching with the visuomotor distortion. This leftward shift was in the same direction that subjects adapted their reaches and was approximately 20% of the visuomotor distortion introduced. These results indicate that proprioception can be recalibrated throughout the lifespan and that the extent of potential proprioceptive recalibration is independent of age, when a visuomotor distortion is introduced gradually and similar levels of visuomotor adaptation are achieved.

Proprioceptive acuity

Previous studies examining the sense of limb position across the lifespan have typically required subjects to perform joint matching tasks in which they match a remembered target joint angle in the absence of vision with the previously displaced limb (ipsilateral remembered matching) or match a concurrently held limb position with the contralateral limb (contralateral concurrent matching). In most cases, absolute matching errors are reported and results indicate a significant deterioration in one's ability to report the position of their limb with advanced age (Adamo et al. 2007, 2009; Goble et al. 2009; Kaplan et al. 1985; Meeuwsen et al. 1993; Stelmach and Sirica 1986). In the present study, we assessed proprioceptive position sense in a visual to proprioceptive matching task in which subjects indicated the felt position of their hand (left or right) relative to a visual marker. In contrast to previous reports, we found that all subjects reported the position of their limb with similar levels of accuracy. Specifically, proprioceptive biases (constant errors) were similar across the two groups, as were their estimates of hand position when absolute errors were analyzed. In accordance with our results, Ferrell et al. (1992) have also reported similar constant errors across young and older adults when they had to match a visual silhouette of a finger with their felt finger position. However, Ferrell et al. (1992) did find that absolute errors were larger for older subjects.

The differences between the proprioceptive results attained in the present study compared to previous work may be due in part to the type of measurement analyzed. The similar constant error scores across subjects indicate that one's proprioceptive acuity may not deteriorate with age (Ferrell et al. 1992; Meeuwsen et al. 1993), while the previously reported differences in absolute errors reflect differences in the consistency of performance across age groups—older subjects are more variable in localizing their limb when using proprioceptive information. This claim of increased variability with aging is supported by the differences in uncertainty ranges found in the present study. Specifically, older subjects had uncertainty ranges that were on average 4.3° larger than (or equal to 1.5 times) the younger subjects.

In addition to the variables analyzed, task demands could also account for the differences in findings between our results and previous studies. In contrast to previous tasks, our subjects indicated the position of their hand as opposed to a joint angle. Recent work by Fuentes and Bastian (2010) suggests that estimates regarding the endpoint position of the limb (fingertip position) are more precise compared to joint angle (elbow angle) estimates. Fuentes and Bastian explain this finding by suggesting that the central nervous system optimizes estimates of limb endpoint positions rather than joint angles due to the greater behavioral need to estimate hand position. Specifically, the CNS directly calculates hand position information from peripheral proprioceptive signals, whereas joint angle estimates are extracted from limb endpoint position information. Given this suggested optimization, perhaps endpoint position information does not deteriorate or does not deteriorate as quickly with age as angle position information, thus giving rise to the similar performance by young and older subjects in the present study. Future work is required in order to determine exactly how proprioceptive acuity for endpoint positions versus joint angles changes with age.

As well as differences in task matching requirements between this study and previous research (i.e. endpoint position vs. joint angle), previous joint matching tasks have required subjects to remember a proprioceptive position and/or transfer information across hemispheres. Given that both memory and the integrity of the corpus callosum have been shown to decrease with age (Ota et al. 2006; Reuter-Lorenz and Sylvester 2005; Salat et al. 2005), previously reported differences in proprioceptive acuity across age groups may not reflect decrements in proprioceptive processing per se. Instead, the difficulty of older subjects in localizing their limbs in joint matching tasks may be due to changes in proprioceptive memory processing or one's ability to transfer information across the corpus callosum (i.e. changes in central processing). The present study and work by Ferrell et al. (1992) used a visual to proprioceptive matching task that measured proprioceptive acuity without requiring proprioceptive memory or information to cross hemispheres. Thus, we feel that the current task provides an accurate assessment of one's ability to localize the endpoint position of the limb across the lifespan under conditions in which central, task-related factors are reduced. Given that our results reveal that, on average, one's ability to localize his or her limb (i.e. endpoint) does not change with age but one becomes less sensitive to shifts in hand position, this would suggest that increased variability may arise in older individuals due to changes in the periphery (e.g. changes to the proprioceptors (for a review see Shaffer and Harrison 2007)). However, at this time, this is merely a proposal and future research is required in order to determine the locus of this increased variability in limb position sense in older individuals (i.e. peripheral versus central nervous system changes). For now, our results suggest that caution should be taken when assessing performance (i.e. constant errors should be analyzed instead of or in addition to absolute errors).

Proprioceptive recalibration

Given the increase in response variability in limb localization, potentially reflecting a reduced signal to noise ratio in older individuals (Goble et al. 2009; Krampe 2002; Welford 1981), we might expect older subjects to recalibrate proprioception to a greater extent than younger individuals after reaching with a cursor that was misaligned from their hand. For example, older subjects would pay attention or weigh the visual representation of their hand more than the proprioceptive position, given the error associated with the proprioceptive signal. This increased reliance on vision would cause subjects to feel their hand was shifted in the direction that they saw it (Simani et al. 2007; van Beers et al. 2002). While older individuals did recalibrate proprioception in the expected direction (i.e. they began to feel their hand was shifted in the direction of the cursor), there was no difference in the magnitude of proprioceptive recalibration between the two groups of subjects. Both older and young subjects shifted the position that they felt that their hand was aligned with a visual reference approximately 6° leftwards (or CCW) after reaching with a cursor that was rotated CW with respect to the hand. This 6° corresponds to a shift in proprioception that is approximately a fifth (20%) of the magnitude of the visuomotor distortion introduced, or approximately a third of the magnitude of the reach aftereffects observed.

The magnitude of proprioceptive recalibration observed in both groups of subjects in the present study is similar to levels we have reported previously when young subjects were required to report the position of their hand with respect to both a visual and a proprioceptive reference (body midline) after reaching with a rotated cursor (Cressman and Henriques 2009) or merely being exposed to a sensory mismatch in the absence of movement-related error signals (Cressman and Henriques 2010). Furthermore, recent work by Ostry et al. (2010) has also reported average changes in felt hand position equivalent to 33% of reach adaptation after subjects learned to reach in a velocity dependent force field, when the extent of reach adaptation was defined as the average perpendicular displacement from a straight line connecting movement start and end of movement. Taken together, the consistency in proprioceptive recalibration across different reaching tasks (i.e. visuomotor distortion vs. velocity dependent force field), exposure conditions (active reaching movements vs. passive limb displacement) and age suggest that there may be an upper limit to how much proprioception can be recalibrated. At the moment, it is unclear if this upper limit is in relation to the magnitude of visuomotor distortion introduced, or if there is a maximum value. In attempt to address this issue, current research in our laboratory is examining the extent of proprioceptive recalibration achieved when subjects are exposed to different levels of visuomotor distortion. In addition to shedding light on proprioceptive recalibration, these results will provide further insight into the relationship between proprioceptive recalibration and visuomotor adaptation.

The link between proprioceptive recalibration and visuomotor adaptation

Given that we were interested in examining differences in proprioceptive recalibration processes between young and older subjects after visuomotor adaptation, we introduced our visuomotor distortion gradually in attempt to have all subjects adapt to the visuomotor distortion as much as possible. In accordance with previous research (Buch et al. 2003; Heuer and Hegele 2008), we found comparable levels of visuomotor adaptation between young and older subjects. Specifically, both groups of subjects adapted their reaches at a similar rate and to the same extent across all reaching trials.

It has been implied that one's continued ability to adapt to a visuomotor distortion with advancing age is due to the preservation of implicit learning mechanisms, where implicit learning mechanisms consist of recalibration processes that realign sensory input (i.e. shift one's felt hand position to match the visual representation) (Redding et al. 2005) and update sensorimotor mappings (i.e. adapt an internal model based on the differences between predicted and actual sensory feedback, Miall and Wolpert 1996; Wolpert et al. 1995; Wolpert 1997). Based on this proposal, one would expect a link between the ability of subjects to recalibrate proprioception and visuomotor adaptation. As discussed previously, we found that all subjects recalibrated proprioception and adapted their movements following reaches completed with misaligned visual feedback of the hand. However, there was no direct link between the two measures. Specifically, we found that subjects with greater levels of proprioceptive recalibration did not show increased levels of visuomotor adaptation or vice versa. These results agree with our previous findings (Cressman and Henriques 2009) and reveal that the extent that subjects adapt their reaches is independent of proprioceptive recalibration across the lifespan.

Thus, it is unclear how the observed changes in sense of felt hand position are related to changes in reaches. Given that the changes in the estimate of felt hand position were only a fraction of the changes observed in the reaching movements, it is unlikely that sensory recalibration is the only source driving changes in reaches. Based on recent work in our laboratory (Cressman and Henriques 2010), we suggest that proprioceptive recalibration combines with the adaptation of sensorimotor mappings to produce changes in reaching movements. From the results of the present study, it is clear that changes in both sensory and motor systems are preserved with age and could contribute to the preserved visuomotor adaptation. It remains to be determined if deficits in visuomotor adaptation experienced in older individuals (i.e. deficits in performance when a visuomotor distortion is introduced abruptly) are associated with decreases in proprioceptive recalibration. Answers to this question may provide insight into the link between changes in felt hand position and changes in reaches.

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