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Proprioceptive Acuity is Enhanced During Arm Movements Compared to When the Arm is Stationary: A Study of Young and Older Adults

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Abstract—Proprioception in old age is thought to be poorer due to degeneration of the central (CNS) and peripheral nervous systems (PNS). We tested whether community-dwelling older adults (65–83 years) make larger proprioceptive errors than young adults (18–22 years) using a natural reaching task. Subjects moved the right arm to touch the index fingertip to the stationary or moving left index fingertip. The range of locations of the target index fingertip was large, sampling the natural workspace of the human arm. The target arm was moved actively by the subject or passively by the experimenter and reaching arm movements towards the target were made under visual guidance, or with vision blocked (proprioceptive guidance). Subjects did not know the direction or speed of upcoming target hand motion in the passive conditions. Mean 3D distance errors between the right and left index finger tips were small in both groups and only slightly larger when vision was blocked than when allowed, but averaged 2–5 mm larger in older than in younger adults in moving ($p = 0.002$) and stationary ($p = 0.07$) conditions, respectively. Variable errors were small and similar in the two groups ($p > 0.35$). Importantly, clearly larger errors were observed for reaching to the stationary than to the moving index fingertip in both groups, demonstrating that dynamic proprioceptive information during movement permits more accurate localization of the endpoint of the moving arm. This novel finding demonstrates the importance of dynamic proprioceptive information in movement guidance and bimanual coordination. © 2021 Published by Elsevier Ltd on behalf of IBRO.

Key words: proprioception, kinesthesia, pointing movements, motor control in elders.

INTRODUCTION

The sense of position, movement, and orientation of our articulated body parts is known as proprioception. It is necessary to control goal-directed movements (Sainburg et al., 1995; Capaday and Cooke, 1981, 1983). For example, to successfully bring the index fingertip to the tip of the nose without vision, the motor system must have a precise estimate of location of the index fingertip relative to the nose, a task that is easily performed by neurologically normal individuals. Localization errors of a few mm would result in missing the tip of the nose. Possible declines of proprioceptive acuity with aging may partially explain motor performance deficits observed in older adults, such as slower motor learning (e.g., Cole and Shields, 2019), slower movements (Welford, 1988) and greater movement variability (e.g., (Cooke et al., 1989; Darling et al., 1989).

Degenerative changes in the PNS and CNS of older adults could contribute to a possible decline in proprioceptive acuity. There is evidence of degenerative changes in neurons and neuronal function in all divisions and levels of the nervous system (Walker et al., 1988; Romanovsky et al., 2015; Morales et al., 1987) along with MRI evidence of degenerative changes in gray and white matter in elders (Agosta et al., 2007; Callaghan et al., 2014; Gong et al., 2014) that may impair transmission and processing of proprioceptive inputs. There is a greater loss of large myelinated axons compared with other fiber types in peripheral nerves (e.g., Swallow, 1966), suggesting reduced input from muscle spindle Ia and cutaneous afferents thought to be essential for proprioception (e.g., McCloskey, 1978; Capaday and Cooke, 1981; Collins et al., 2005; Kuling et al., 2016). Muscle spindle sensitivity may also decrease due to changes in their mechanical properties (Kim et al., 2007) along with loss of intrafusal fibers, possibly leading to denervation (Swash and Fox, 1972). Compounding these effects, there is a loss of cutaneous and joint mechanoreceptors with aging (Bolton et al., 1966; Shaffer and Harrison, 2007) (Morisawa, 1998; Aydoğ et al., 2006) which may also reduce proprioceptive acuity. Consistent with these findings is that velocity discrimination thresholds for detecting passive motion (Wright et al., 2011) and perceptual illusions of hand motion induced by muscle tendon vibration and tactile stimulation were about twice higher in 65–75 years old adults than in 20–30 year old adults (Landelle et al., 2018). These find-

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ings suggest that older adults have functionally impaired proprioceptive acuity of hand movements, but there was no direct test of such an impairment in that study.

Despite such neural degeneration, older adults may be able to compensate for reduced sensory information transmission and processing due to the sheer redundancy of receptors and neural processing networks. For example, stereognosis, the ability to perceive and recognize the shape of 3D objects with touch alone, is unimpaired in older adults, even though they have far fewer sensory receptors in the glabrous skin of the digits than young adults (Norman et al., 2011). Previous work has suggested that older adults co-contract muscles more than younger adults while performing proprioceptive matching tasks. There may thus be more alpha-gamma coactivation, leading to an increase of muscle spindle sensitivity in both agonists and antagonist muscles to partially compensate for age-related changes of spindle mechanical properties and reduced motor innervation (Madhavan and Shields, 2005).

Whether in fact proprioceptive acuity declines with age and its functional consequences thus remain to be elucidated. Some previous studies investigating proprioception in the upper limb have reported small decreases in proprioceptive accuracy (Stelmach and Sirica, 1986; Adamo et al., 2007, 2009; Goble et al., 2012; Schaap et al., 2015) while other studies have suggested that proprioception is minimally impacted, if at all, (Lovelace and Aikens, 1990; Boisgontier and Nougier, 2013; Herter et al., 2014). The implications of this previous work for movements in the real world are limited by the artificial nature of the tasks used, such as joint angle matching paradigms (e.g., Adamo et al., 2007, 2009; Goble et al., 2012), one-dimensional sliders (e.g., Stelmach and Sirica, 1986), movements restricted to a plane (e.g., Lovelace and Aikens, 1990), and spatial memory requirements (e.g., Schaap et al., 2015) with a focus on perception rather than on how proprioception is used to control movements. With the possible exception of the ipsilateral condition in the study by Schaap et al. (2015), the tasks used in these experiments are not representative of the movements we make daily in our 3-dimensional (3D) gravitational environment and thus, may not be functionally relevant. Indeed, Schapp and colleagues showed that that both young and older adults performed with similar errors averaging about 3 cm when reproducing hand locations with the same hand (ipsilateral condition). Older adults exhibited larger errors than young adults only when reproducing the mirrored location of one hand with the other hand (contralateral condition), a rather complex task unlike common daily tasks. Other studies have also reported that poorer proprioceptive accuracy in older adults is only observed in more complex tasks (e.g., Adamo et al., 2007). Moreover, despite larger errors by older adults in proprioceptive perceptual tasks, proprioceptively guided upper limb movements to external targets are similarly accurate in older and young adults (Helsen et al., 2016; Kitchen and Miall, 2019). We recently introduced a novel task that involves moving one arm toward the other to appose the left and right index fingertips (Capaday et al., 2013; Darling et al., 2018). With such natural and unconstrained 3-D movements very small errors in finger apposition were observed when the movements were proprioceptively guided. Indeed, the errors during proprioceptive guidance were only slightly larger than when vision was allowed (Darling et al., 2018) and were far lower than would be predicted from the results of studies of, for example, shoulder or elbow joint angle matching tasks (van Beers et al., 1998).

In this study we measured proprioceptive acuity in stationary and moving target conditions, as in our previous investigations in a natural task similar to everyday movements (Capaday et al., 2013; Darling et al., 2018). Participants moved their hands in multiple directions without restraint or support against gravity and were asked to locate self-determined or passively imposed locations of the left index fingertip by touching it with the right index fingertip. We hypothesized that older adults would be similarly accurate to young adults when locating the stationary or moving target index fingertip despite degeneration of the CNS and PNS because the natural task tests how proprioception is used to coordinate movements of one hand to touch a functionally important location on the other hand.

EXPERIMENTAL PROCEDURES

Participants

Thirteen older, community dwelling, adults (5 males) age 65–83 (73 ± 5.1 SD) years of age, and 14 younger adults (5 males) age 18–22 years of age (20 ± 1.4 SD) participated in this study. Data from 9 subjects was included from a previous report (Darling et al., 2018). Participants self-identified as right-handed, in good health, no cardiac pacemaker (contraindication for our motion capture system), no history of neurological disease, or arthritis in either upper limb. All participants gave written informed consent, and the experiment was approved by the University of Iowa Institutional Review Board.

Experimental set-up, tasks, and conditions

We compared the performance of older and younger adults in a moving target task (M), as well as a stationary (S), or non-moving target task. The task required subjects to appose the index fingertip of the reaching right hand to the target left hand index fingertip. The target was either moved actively by the subject (A), or passively (P) by the experimenter. Each of these tasks could be done with either vision (V) allowed or blocked (NV). There are therefore eight possible tasks. We studied five: VA_M, NVA_M, NVPM, NVA_S, NVP_S, because our purpose was to measure proprioceptive acuity on its own (Fig. 1A). Reducing the number of tasks also alleviated the burden of protracted sessions for the elderly subjects. Note that the subscript in each task acronyms (M or S) refers to the target, either moving (M) or stationary (S). As will be explained below, the VA_M task served as a measure of best

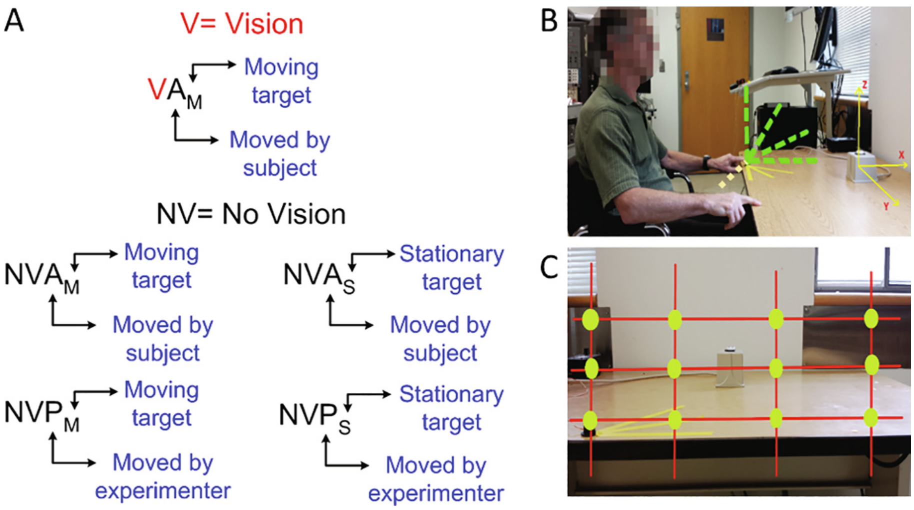

Fig. 1. Experimental conditions and setup. The five experimental conditions for testing proprioception of moving and stationary targets are shown in **(A)**. A photograph of a subject positioned in front of the table overlaid with the vertical (green dashed lines) and horizontal (yellow tape on the table and yellow dashed line) angular directions for motion of the target hand is shown in **(B)** along with the location of the transmitter for the Trakstar system and the directions of the X, Y and Z axes. The approximate locations for 12 stationary targets within a grid in the frontal plane (i.e., 4 horizontal levels: outer left, inner left, inner right, outer right horizontal positions and three vertical levels at each horizontal level: just above the table, sternum, and shoulder level heights) from the subject's viewpoint are shown in **(C)**. The subject was seated such that the mid-sagittal plane would pass through the transmitter (cube-shaped object on the table) of the Trakstar system. Note the position of the release switch, which upon release triggers a randomly delayed auditory cue for movement onset of the reaching arm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

performance. A detailed description of each of the tasks studied follows.

The moving target tasks were done using methods previously described (Darling et al., 2018). Participants started with the target index fingertip depressing a button, and the index fingertip of the reaching arm on a tactile marker that subjects could locate without vision (Fig. 1B). Participants were instructed to move the target index fingertip in a specified direction at a comfortable speed. When participants moved the target index finger off the button, they heard a beep (1 KHz, 200 ms duration) shortly afterwards (at random delays of 50–300 ms). The subjects were instructed to reach the moving target at a comfortable speed in a single, continuous, smooth movement and not attempt to correct after either contacting the target or missing it. Participants were given practice trials to ensure they understood the task, did not start both hands moving at the same time, continued to move the target until the fingertips made contact, or attempt to use the target arm as a reaching arm (i.e., stop the reaching index fingertip and then move the target index fingertip to touch it). Twenty-six total trials were performed in each condition involving 13 discrete movements repeated twice for each combination of horizontal and vertical directions (horizontal angles −30, 0, 30, 60 degrees; elevation angles 0, 30, 60, 90 degrees – Fig. 1B) giving 13 movement directions (i.e., 4 horizontal angles × 3 elevation angles plus 90° elevation, which is a pure vertical movement direction). Three of the horizontal plane directions (0, 30, 60 degrees) were marked on the table surface (Fig. 1B) and subjects were given practice trials with vision allowed to be sure they understood all the different directions. The horizontal plane direction towards the subject's chest (−30°) was estimated as were vertical plane directions associated with each of the 4 horizontal plane directions. Subjects practiced moving the target index fingertip in all these directions with vision allowed and given the associated direction instruction (e.g. H30V60 for a movement at 30° in the horizontal plane and 60o in the vertical plane). After subjects demonstrated they understood the target movement directions the experiment began and movements were recorded. If a participant began to move their left and right arms simultaneously or moved the target hand in the wrong movement direction, the trial was discarded and repeated. Trials were also discarded and repeated if the cables obstructed hand movement.

Participants completed the moving target (M) tasks under 3 conditions. (1) VA_M – vision was allowed (V), both arms were moved actively (A) by the subject, (2) NVA_M – the subject was blindfolded (NV), both arms were moved actively by the subject and (3) NVP_M – the subject was blindfolded, the target arm was moved by the experimenter and the subject voluntarily moved the reaching arm. In this condition, the experimenter supported the elbow with one hand, and the wrist with the other hand while moving the arm and attempted to match the participants voluntary moving speed from the active condition. During active conditions, participants were verbally given the direction to move. During passive conditions they were not told the direction of the imposed movements. Thus, they had to predict the location of the target index tip based on kinesthetically sensed motion of the target arm.

In the stationary target (S) tasks, the subject's target arm was placed in a location and held in place for about 1 s. They were then given a "Go" command and started to move their right index fingertip to touch their left index fingertip. Similar to the moving target task, participants were to only make one smooth comfortable speed movement, and not to attempt to correct for any errors. Participants were instructed to visualize a vertical grid immediately above the table with 12 target positions (4 horizontal levels: outer left, inner left, inner right, outer right horizontal positions and three vertical levels at each horizontal level: just above the table, sternum, and shoulder level vertical positions (Fig. 1C). One trial was performed for each target position. The stationary target task was performed under two conditions. (1) NVA_S – the target index fingertip was positioned by the subject and (2) NVP_S – the target index fingertip was positioned and held in place by the experimenter. If resistance to the movement was felt by the experimenter, the trial was stopped and repeated. The VA_M task was always performed first, followed by the NVA_M and NVP_M tasks in random order. The stationary target tasks, NVA_S and NVP_S were always completed after the moving target tasks, in random order. Target locations and directions were randomized.

Data acquisition

Index fingertip positions were collected using small cylindrical (1.5×7.7 mm) magnetic sensors (Ascension Technologies TrakSTAR model 130, Burlington, VT, USA). We recorded kinematic data at 240 Hz using a custom MATLAB program. Position sensors were attached to the fingernails of each index finger with double sided tape and secured with surgical tape. The cable of each motion sensor was taped to the dorsum of the hand such that the cable did not interfere with natural wrist and index movements. We placed the Trakstar transmitter in the center of the table beyond the range of motion used by participants during the experiment.

Data reduction and analysis

Kinematic data were analyzed using Datapac 2k2 (Run Technologies, Mission Viejo, CA, USA), a custom visual basic (VBA) script in MS Excel, and a custom SAS 9.4 script. Statistical tests were performed with SAS 9.4, and Statistica 5.1. Three-dimensional (3D) position data were filtered with a lowpass butterworth filter (15 hz rolloff frequency). Movement onset and terminations of the index fingers were determined using a velocity threshold of 2.3 cm/s and verified by visual inspection. The start and end times of movements were adjusted visually if the marked onset did not appear to represent the true start of the movement (e.g., if the subject made a very small initial movement of the right index, then slowed and started again when the beep sounded) or end of a movement (e.g., if the movements were rather slow). Movement end points, duration and peak tangential velocity were measured. Directional errors (X-forward/backward, Y-right/left and Z-up/down) were computed as the distance between the voluntary and target index tips at the end of the right-hand movement. A 3D distance error was computed using the vector magnitude of the directional errors. Mean distance errors were computed as the average of distance errors for all trials in a single condition. Variable distance errors were computed as the S.D. of distance errors for all trials in a single condition. It should be noted that the distance between the motion sensors cannot be zero, because the two sensors cannot occupy the same spatial location. Indeed, distance between the sensors when the index-fingertips are apposed depends on orientation of the fingers (Darling et al., 2018). We therefore used the average errors in the VA_M condition as a measure of baseline performance for all other conditions because subjects cannot be expected to perform better than that without vision. We did not include a VA_S condition because we found in our previous work that mean and variable distance errors in the VA_M condition (Darling et al., 2018) and in a condition similar to a VA_S condition (Capaday et al., 2013) were comparable and very small.

Trials in the moving target tasks were discarded if the subject appeared to grope for the left index tip, (i.e., multiple velocity peaks at the end of the right arm movement), if the left hand nearly finished moving before the right hand started or if the movement was very erratic, making it impossible to clearly identify movement onset and end. Overall, only six trials were eliminated by these criteria (0.22% of all trials). Trials in the stationary target tasks were eliminated if the participant did not hold the target arm moderately still. This resulted in elimination of only two trials from one subject. Trials with a distance error of more than 3 standard deviations from the mean of the distance errors within each condition for individual subjects were flagged and individually inspected. Flagged trials were eliminated, unless there were multiple trials with similar errors, or if the variable error was very small (i.e., 0.5 cm or less). Overall, only twenty trials (0.73% of all trials) were eliminated by this criterion.

Mean and variable distance errors were compared between groups among the moving target tasks using separate 2×3 (group - young/old $\times$ condition – VA_M, NVA_M, NVP_M) repeated measures analysis of variance (rmANOVA) and in the stationary conditions errors were compared using 2×2 (group – young/old $\times$ condition – NVA_S, NVP_S) rmANOVA. Huynh-Feldt adjustments were applied to significant repeated measures factors with 3 or more levels with probability values reported as p_{corr}. Significant main effects and interactions were further investigated using Tukey's post-hoc tests. Effect sizes are reported as partial η_p^2 for ANOVA effects or Cohen's d for comparisons of mean and variable errors of specific conditions (e.g., NVA_M vs. NVP_M). We also tested whether errors in each subject were lower in active than in passive conditions using independent t-tests comparing errors in NVA_M to NVP_M and NVA_S to NVP_S. To determine whether target movement speed differences among conditions may account for differences in errors in the moving target tasks we also tested whether there were differences in mean and variability (SD) of peak target index tip speeds using separate 2×3 (group $\times$ condition) rmANOVA.

We also tested for an association between peak target index fingertip speed and distance error and between peak reaching index fingertip speed and distance error using Pearson's product-moment correlation coefficient. These correlation analyses were performed in each subject because each subject moved the target and reaching arms at their own comfortable speeds in VA_M and NVA_M and the experimenter moved the target at similar speeds in NVP_M. We did not apply a Bonferroni-type or similar correction to *p*-values of the correlation coefficients because we were aiming to robustly assess whether there was evidence of significant positive correlations in most subjects and conditions. We expected that each subject operates on an individual speed-accuracy tradeoff due to subjective biases towards higher accuracy or higher speed. It has been reported that speed-accuracy tradeoffs vary with age and appear to vary across the sexes (York and Biederman, 1990; Bianco et al., 2020). To test whether the experimenter moved the target arm at similar velocities in the passive conditions to the subject-selected speeds in the active conditions we compared peak target speed and target movement duration between NVA_M and NVP_M using 2 (condition) × 2 (age group) rmANOVA.

We also examined whether the range of motion tested differed in the two age groups by computing the range of target positions tested as target workspace volume of spheres with radii equal to the range of tested final target positions in X, Y and Z directions. Specifically, we compared these volumes using a 2 × 5 (group × 5 conditions) rmANOVA with Huynh-Feldt adjustments and Tukey's post-hoc tests as appropriate.

RESULTS

Moving target tasks

Both younger and older subjects were accurate in the moving target tasks. Average distance errors in the moving conditions without vision were small (average 1.5–2 cm) and not much larger than the average distance errors observed when vision was allowed (average 1.2–1.3 cm). Errors were similar whether the subject actively moved the target arm, or it was passively moved.

Movement characteristics

We observed different voluntary movement kinematics for the two age groups. Older adults often exhibited multiple peaks in tangential velocity profiles whereas younger subjects usually had only a single tangential velocity peak (e.g., Figs. 2,3). Older adults had more difficulty starting the reaching arm movement after target arm movement began during the NVA_M task, therefore needing more practice trials until they were able to initiate movement of the reaching hand after target hand motion began. Older adults more frequently changed motion of the target arm when they initiated movement with the voluntary arm. They would either slow movement of the target arm during the initiation of the reaching arm movement (e.g., Fig. 3A), and/or they would initiate movement with both arms and then attempt to stop the reaching arm until cued to start by the tone (e.g., Fig. 3B). Both older and younger subjects were able to predict future location of the moving target as the reaching index fingertip usually moved directly toward the location where the target fingertip would eventually stop moving (e.g., Fig. 4).

Target and reaching arm kinematics were similar for the two age groups in the NVA_M and NVP_M conditions. Peak target hand speeds were similar for the two age groups ($F_{1,25}$ = 1.56, p = 0.22) and conditions ($F_{1,25}$ = 0.06, p = 0.80) with no interaction effect (Table 1; $F_{1,25}$ = 1.82, p = 0.19). Target arm movement durations also did not differ between age groups ($F_{1,25}$ = 1.20, p = 0.29) or conditions ($F_{1,25}$ = 1.00, p = 0.32) with no interaction effect ($F_{1,25}$ < 0.01, p = 0.93). Peak reaching hand speeds of older subjects were lower on average (Table 2) but did not differ between age groups ($F_{1,25}$ = 0.44, p = 0.51) or conditions ($F_{1,25}$ = 3.14, p = 0.09) and with no interaction effect ($F_{1,25}$ = 1.26, p = 0.27). Reaching hand durations of older subjects were longer on average (Table 2) but did not differ between age groups ($F_{1,25}$ = 1.00, p = 0.33). However, reaching hand durations were shorter in the passive condition than in the active condition in both age groups (Table 1, $F_{1,25}$ = 12.45, p = 0.002) with no interaction effect ($F_{1,25}$ = 0.73, p = 0.40).

Errors

Younger and older subjects were accurate in placing the reaching index fingertip onto the target index fingertip (Figs. 5 and 6), with most errors being less than 2 cm or less than 1 cm larger than in the VA_M condition. Group mean distance errors averaged only 0.19 cm greater in

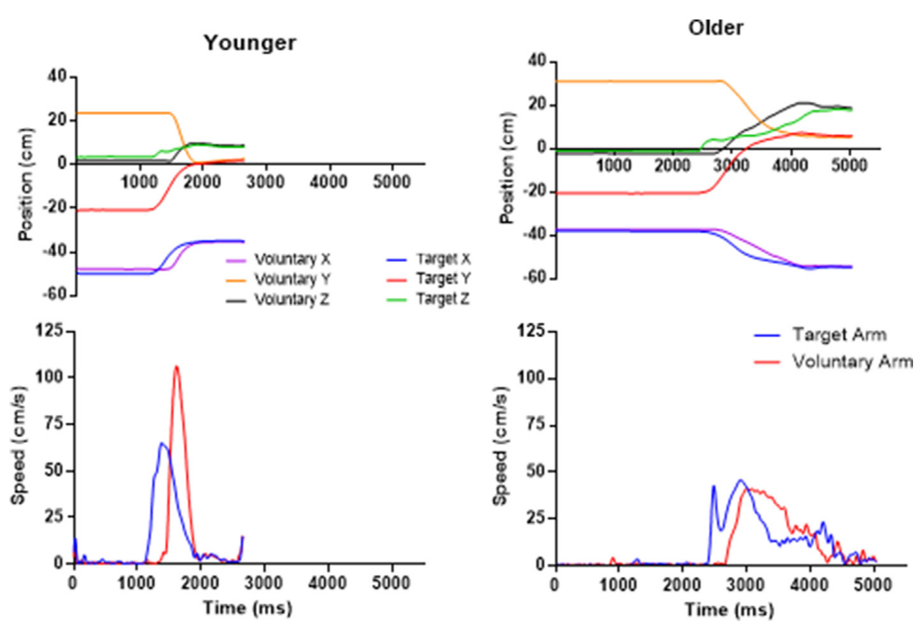

Fig. 2. Examples of kinematics of target and reaching index fingertip movements. Three-dimensional position of the index fingertips and tangential index fingertip speed versus time for representative younger (left side) and older (right side) subjects. The top row shows X, Y, and Z positions of the target and reaching index fingertips and the bottom row shows the tangential speeds of the target and reaching index fingertips throughout the movements in the NVA_M condition. (For a colour version of this figure the reader is referred to the web version of this article.)

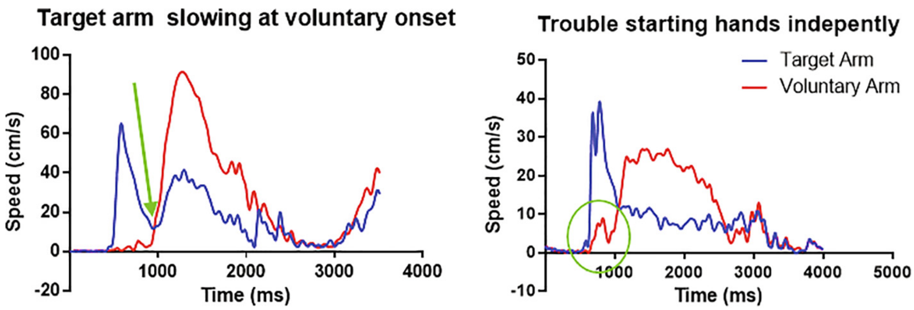

Fig. 3. Difficulties in controlling target hand movement by some older subjects the NVA_M condition. Tangential speeds versus time of the target (blue) and reaching (red) index fingertips of older subjects are shown in **(A)** and **(B)**. In **(A)** the green arrow shows slowing of target hand movement when reaching hand movement begins. In **(B)** the green circle shows simultaneous onset of target and reaching hand movements. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

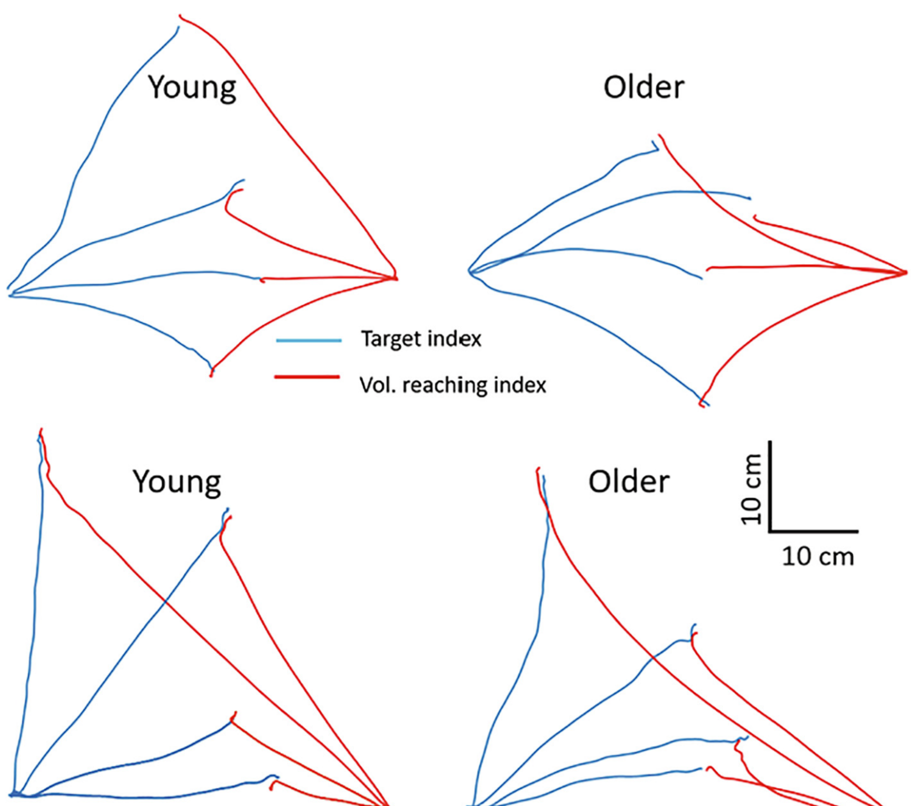

Fig. 4. Movement paths of the target and reaching index fingertips motions in the NVP_M condition in one young and one older subject. Target motion is shown in blue and reaching motion is shown in red. The top row shows paths in the horizontal plane in 4 directions (H–30, H0, H30, H60). The bottom row shows paths in the frontal plane in 4 directions (V0, V30, V60, V90). Note that movement of the voluntary (right) index fingertip is relatively straight toward its final position. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

older adults than younger adults across the three moving target conditions (Fig. 6A; $F_{1,25} = 5.88$, $p = 0.02$, $\eta_p^2 = 0.19$) and were similar within each condition for the two age groups (Fig. 6A; group × condition interaction: $F_{2,50} = 0.57$, $p = 0.57$). Errors in the NVA_M condition averaged only 0.38 cm higher than in VA_M and errors in NVP_M were only 0.16 cm higher than in NVA_M (Fig. 6A, $F_{2,50} = 49.56$, $p_{corr} < 0.001$, $\eta_p^2 = 0.66$; $p = 0.012$ for post hoc test comparing NVA_M to NVP_M, $d = 0.56$). Variable errors were also similar for the two age groups (Fig. 6B, $F_{1,25} = 0.90$, $p = 0.35$) within each condition (Fig. 6B, group × condition interaction: $F_{2,50} = 0.757$, $p = 0.475$), but were slightly larger in NVP_M (0.72 cm) and NVA_M (0.58 cm) than in VA_M ($F_{2,50} = 28.67$, $p_{corr} < 0.001$, $\eta_p^2 = 0.53$; $p < 0.05$ for all post hoc tests; $d = 0.58$ for comparison of variable errors of NVA_M and NVP_M). Importantly, both mean and variable errors in the NVP_M condition averaged less than 2 mm greater than in the NVA_M condition.

An important additional finding was that distance errors on individual trials did not increase with speed of target or reaching arm movement. Distance errors on individual trials were only weakly correlated with peak target index fingertip speed [mean $r = 0.05$; $p > 0.05$ for 75 of 81 (3 conditions × 27 subjects) correlation coefficients among the 27 subjects]. Similar weak correlations of errors with reaching index fingertip speed were observed (mean $r = 0.07$, $p > 0.05$ for 68 of 81 correlation coefficients). Notably, only 9 of the 13 statistically significant correlation coefficients were positive and only 3 of those were in older subjects.

3D directional (X, Y, Z) errors between the index fingertips did not show evidence of consistent overshooting of the target index fingertip (e.g., Fig. 5). Mean directional errors averaged less than 1 cm with the reaching (right) index fingertip positioned on average slightly to the right and above the target (left) index fingertip in all conditions. Variable errors averaged less than 1.2 cm in all 3 axes and were only slightly larger in older subjects.

Stationary target tasks

Movement characteristics. Reaching arm peak speeds were similar in older and younger subjects in both active and passive stationary target conditions but movement durations were shorter in young subjects.

Table 1. Mean durations and peak tangential speeds of target hand movements in the moving target conditions

Group	Peak Speed (cm/s)		Duration (s)	
	NVA_M mean(range)	NVP_M mean(range)	NVA_M mean(range)	NVP_M mean(range)
Older	46.9(23.1–80.5)	50.2(31.5–77.0)	1.94(1.19–3.38)	1.88(1.46–2.47)
Young	45.7(29.5–85.9)	40.8(31.2–51.1)	1.78(1.22–2.38)	1.73(1.38–2.43)

Table 2. Mean durations and peak tangential speeds of reaching hand movements in the moving target conditions

Group	Peak Speed (cm/s)		Duration (s)	
	NVA_M mean(range)	NVP_M mean(range)	NVA_M mean(range)	NVP_M mean(range)
Older	59.9(25.1–98.8)	68.7(34.0–115.8)	1.60(1.07–2.58)	1.35(1.04–2.00)
Young	69.6(31.2–141.7)	71.5(34.3–125.0)	1.36(0.87–2.07)	1.27(0.97–2.06)

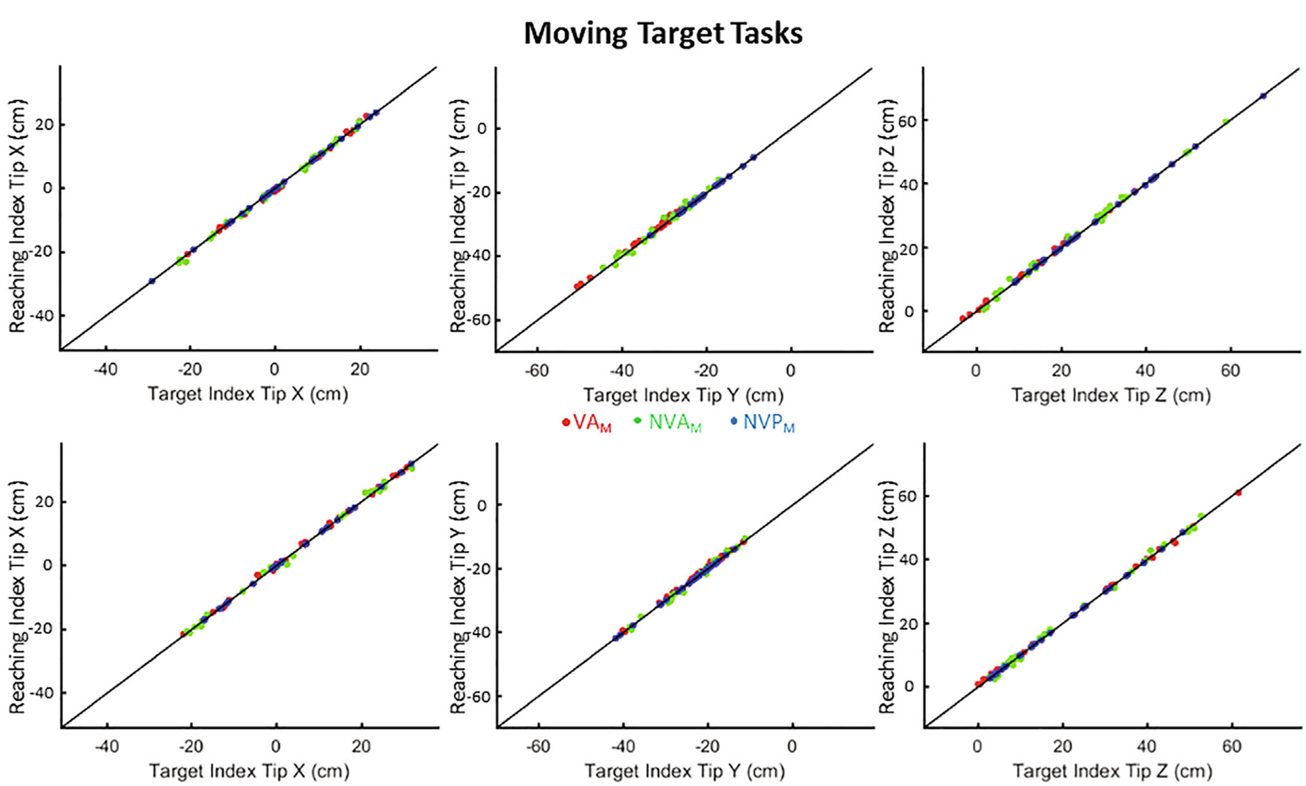

Fig. 5. Scatterplots of final positions of the reaching vs. the target index fingertips in an older subject and a young subject in the moving target tasks. The top row of graphs show final locations of the target and reaching index fingertips from an older subject and the bottom row from a young subject. The plotted line is the line of identity. Each plotted point is data from a single trial in the VA_M, NVA_M or NVP_M condition. Note that all plotted points are very close to the line of identity in all experimental conditions. (For a colour version of this figure the reader is referred to the web version of this article.)

Peak speeds averaged about 75 cm/s in both groups (Table 3) and did not differ between groups ($F_{1,25} < 0.01$, $p = 0.99$) or conditions ($F_{1,25} = 0.05$, $p = 0.83$) and there was no interaction effect ($F_{1,25} = 0.13$, $p = 0.72$). However, durations of reaching arm movements were longer on average in older subjects in both active and passive conditions (Table 3, group main effect: $F_{1,25} = 8.88$, $p = 0.006$, condition main effect: $F_{1,25} = 0.007$, $p = 0.93$) with no interaction effect ($F_{1,25} = 0.62$, $p = 0.44$).

Errors

Overall, participants were also accurate at performing the stationary target task with mostly small errors on

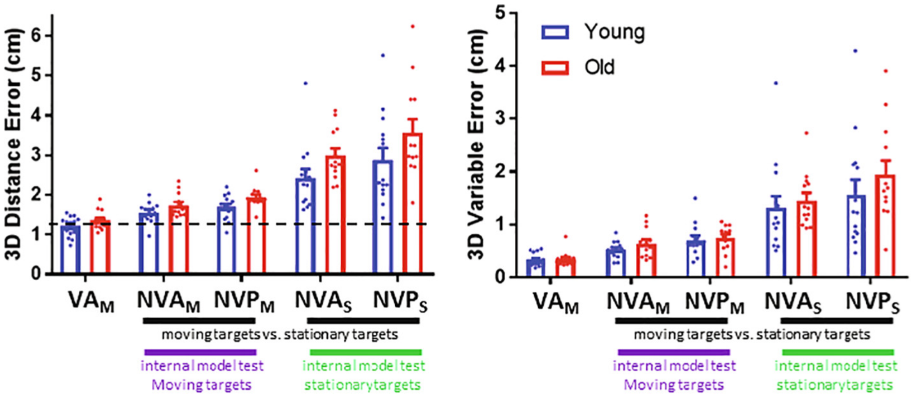

Fig. 6. Mean and variable distance errors in the five experimental conditions. Each bar shows the average of the mean **(A)** or variable **(B)** distance errors for 14 young subjects or 13 older subjects. Each plotted point is the mean or variable distance error for a single subject in a single condition. Error bars are 1 S.E. The horizontal dashed black line in **(A)** represent the mean across all subjects of the mean distance errors observed in the vision allowed, active movement to moving target condition (VA$_M$). The black bars beneath the graphs show which data compare errors in moving target conditions to errors in the stationary target conditions. The purple (moving target conditions) and green (stationary target conditions) bars show which data were used to test the internal model hypothesis that errors in active conditions would be lower than in passive conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

individual trials (Fig. 7). Older and younger subjects typically made a single smooth movement to the target. Subjects in both age groups occasionally failed to contact the target index tip resulting in larger errors than in the moving target conditions (e.g., Fig. 7). Group mean distance errors averaged only 0.5 cm larger in the NVP$_S$ condition than in the NVA$_S$ condition (Fig. 6A, $F_{1,25} = 7.56$, $p = 0.01$, $\eta_p^2 = 0.23$) and tended to be larger in older adults ($F_{1,25} = 3.53$, $p = 0.12$). Variable errors were also similar in the two age groups (Fig. 6B; $F_{1,25} = 0.25$, $p = 0.62$) but were slightly larger in NVP$_S$ compared with NVA$_S$ ($F_{1,25} = 0.7.98$, $p < 0.01$, $\eta_p^2 = 0.24$).

Similar to the moving target tasks, distance errors on individual trials in the stationary target tasks did not increase with speed of reaching hand movement. Distance errors were weakly correlated with peak reaching index fingertip movement speed (mean $r = -0.03$, $p > 0.05$ for 49 of 54 (2 conditions × 27 subjects) correlation coefficients). Notably, all 5 statistically significant correlation coefficients were negative indicating that faster movements were associated with lower errors.

Mean directional errors averaged less than 1.5 cm and did not show evidence of overshooting the target (left) index fingertip (e.g., Fig. 7). The right index fingertip was usually positioned slightly to the right (younger) and slightly (less than 0.5 cm) to the left (older) and above the target index fingertip. Variable errors averaged less than 2.2 cm along all 3 axes and were only slightly larger in older subjects.

Comparison of moving target and stationary target errors

Although errors were small in all conditions, the mean distance and variable errors in the moving target tasks without vision were clearly smaller than those in the stationary target tasks. Group mean distance errors without vision averaged 1.23 cm less in the moving target than in the stationary target tasks ($F_{1,25} = 57.78$, $p < 0.001$). Variable errors for moving targets averaged about half of those for stationary targets (0.93 cm smaller, $F_{1,25} = 38.56$, $p < 0.001$).

Comparison of target workspace volumes

There were no overall age group differences in target workspace volumes but some conditions had lower volumes than others. Workspace volumes averaged about 0.25 m^3 in the moving target conditions and were larger than in the stationary target conditions (average volume of about 0.1 m^3; $F_{4,100} = 23.94$, $p < 0.001$) but with no age-related differences overall ($F_{1,25} = 1.01$, $p = 0.33$). Older subjects did have statistically lower target workspace volumes in the VA$_M$ and NVA$_M$ conditions (group × condition interaction: $F_{1,25} = 4.89$, $p = 0.01$, $p < 0.05$ on post-hoc tests). Importantly, however, older subjects had nearly equal average volumes in NVP$_M$ of about 0.28 m$_3$ and larger volumes on average in NVP$_S$ (0.1 m^3 vs. 0.07 m^3 in young subjects).

DISCUSSION

Overall performance

All subjects moved the right index fingertip to touch the left index fingertip target accurately in both moving

Table 3. Mean durations and peak reaching hand speeds in the stationary target conditions

Group	Peak Speed (cm/s)		Duration (s)	
	NVA$_S$ mean(range)	NVP$_S$ mean(range)	NVA$_S$ mean(range)	NVP$_S$ mean(range)
Older	75.7(31.5–126.0)	75.4(28.4–123.2)	1.56(1.08–2.45)	1.59(0.96–2.60)
Young	75.0(36.8–111.5)	76.4(43.9–112.3)	1.17(0.85–2.15)	1.13(0.80–1.62)

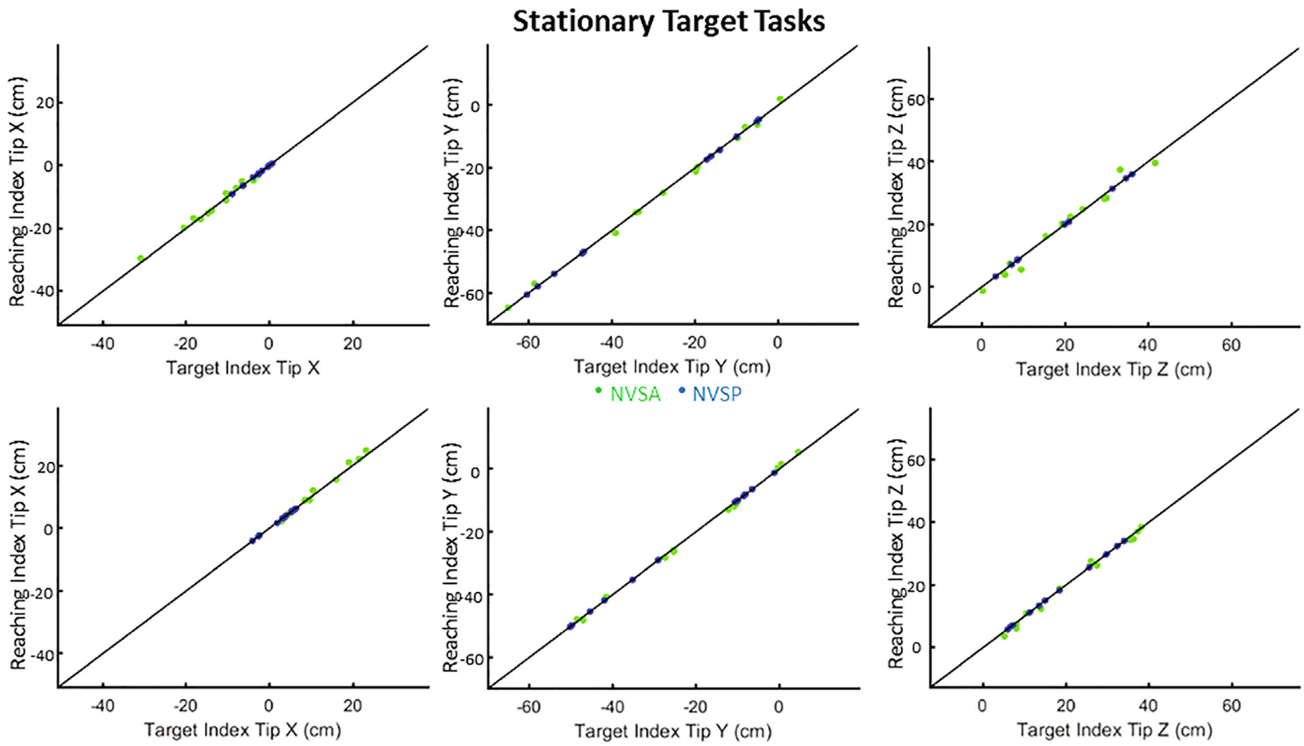

Fig. 7. Scatterplots of final positions of the reaching vs. the target index fingertip in an older subject and a young subject in the stationary target tasks. The top row of graphs show final locations of the target and reaching index fingertips from an older subject and the bottom row from a young subject. The plotted line is the line of identity. Each plotted point is data from a single trial in the NVA_S or NVP_S condition. Note that all plotted points are very close to the line of identity in all experimental conditions. (For a colour version of this figure the reader is referred to the web version of this article.)

target and stationary target conditions and when the target arm was moved voluntarily by the subject or passively by the experimenter. Mean distance errors for both age groups in experimental conditions without vision averaged about 2.2 cm, only about 0.4 cm more than when vision was allowed. A novel and surprising result was the finding of lower errors in moving target than in stationary target conditions. This demonstrates that dynamic afferent inflow during movement improves proprioceptive localization. A major theory of sensorimotor neuroscience is that processing efference copy of cortical motor commands through an internal forward model to predict limb location and motion is an important contributor to proprioception because sensory input is noisy and subject to large errors (Wolpert et al., 1995). However, confirming our previous work, there were minimal differences in mean and variable distance errors between active (i.e., NVA_M, NVA_S) and passive (i.e, NVP_M, NVP_S) conditions, indicating that availability of motor commands via efference copy does not improve proprioceptive acuity as hypothesized by internal model theories (Capaday et al., 2013; Darling et al., 2018). The better performance in the moving target conditions may be due to increased afferent inflow, particularly the velocity sensitive component of spindle afferent discharge (Matthews, 1972).

Overall, the results suggest that regardless of age, availability of visual information, active/passive movement of the target hand, or whether it is stationary or moving, younger and older adults exhibit very good to excellent proprioceptive acuity as clearly shown in Figs. 5–7. Despite reports of degeneration of the CNS and PNS with age as discussed in the Introduction, proprioceptive errors were on average no more than 2 mm greater in older adults than in young adults in the moving target conditions. Thus, such degeneration apparently has little effects on proprioception even in a bimanual task that one might expect to be affected due to thinning of the corpus callosum with age and its possible effects on inter-hemispheric communication (e.g., (Sullivan et al., 2002). Importantly, there were no differences of target index finger speed between the two groups, in either active or passive conditions. Thus, the comparable performance of older vs. younger subjects cannot be attributed to older adults having slower target index finger speeds.

It is possible that the range of target positions differed between young and older subjects such that a smaller range of positions was tested in older subjects, which could make the task easier. For example, the plots of movement paths in Fig. 4 suggest the possibility of a smaller range of movement endpoints in the older subject than in the young subject. However, the scatterplots in Figs. 5 and 7 for all targets in the moving and stationary target conditions show a wide range of target positions in both the young and older subjects. Moreover, target workspace volumes were similar in young and older subjects in the NVP_M condition and larger for older subjects in NVP_S. Thus, there was no evidence that the low errors by older subjects were due to testing a smaller range of target positions.

Sensory mechanisms

There are no sensory receptors known to directly sense finger tip location in 3D space. Yet this study and our previous studies (Capaday et al., 2013; Darling et al., 2018), show that humans are very proficient at locating their fingertips based on purely proprioceptive information. Fingertip position must be computed from the proprioceptors signaling joint angles, or muscle lengths, proximal to the fingertip. Given the previously reported angular errors at each of these joints in perceptual tasks (Darling, 1991; Darling and Gilchrist, 1991; Darling and Miller, 1995; Adamo et al., 2007, 2009; Gritsenko et al., 2007; Fuentes and Bastian, 2010; Ingemanson et al., 2016) and the lengths of the arm and forearm, we would expect to see much larger errors in locating the fingertips. It was estimated that shoulder and elbow angles would have to be known to the CNS with a precision of 0.6°–1.1° to explain the accuracy of proprioceptive finger tip localization (van Beers et al., 1998). However, previous studies of perception of shoulder and elbow angles in constrained conditions (i.e., planar, single joint, etc.) report much poorer proprioceptive acuity with absolute or RMS errors averaging 5–19° at the shoulder (e.g., Hung and Darling, 2012) and 1.5–6° at the elbow (e.g., Adamo et al., 2007). Under less constrained 3D conditions absolute errors (estimated from mean constant and variable errors) average about 12°–18° at the shoulder for different angles (Darling and Miller, 1995) and about 12° for the elbow (Darling, 1991) in perceptual tasks. Our task requiring subjects to appose the index fingertips in 3D is unconstrained and is similar to how proprioception is normally used in controlling the natural movements of everyday (e.g., passing a small object between the hands without looking). Contrived laboratory tasks involving constrained movements, perception, memory, etc. clearly do not measure true proprioceptive acuity in natural conditions. Proprioception is normally used to automatically guide movements, as was understood long ago by Sherrington (Sherrington, 1900).

Moving target task performance

The slightly larger mean distance errors of older (1.84 cm) compared to younger (1.62 cm) adults in the moving target tasks, along with the similar small variable errors of both age groups (0.69 and 0.61 cm in older and younger adults, respectively) suggests that our proprioceptive sense is well maintained in late adulthood. The small observed differences are unlikely to affect the performance of most unimanual (e.g., reaching for an object without vision of the hand) or bimanual (e.g., buttoning a shirt without vision) motor tasks, except possibly for those requiring the finest precision. It is noteworthy that the worst performing younger subject (18 years) only slightly outperformed the oldest (83 years) subject by 0.55 cm on mean distance error with nearly identical variable errors (0.08 cm difference) in the NVA_M and NVP_M conditions.

It is doubtful that an internal model using efference copies of motor commands in the active conditions contributes to improving the prediction of target arm motion as distance errors of younger and older subjects averaged only slightly larger (by 0.16 cm) in the NVP_M condition than in the NVA_M condition. Although this very small group difference in error magnitude was statistically significant, it unlikely to be physiologically significant considering that 0.16 cm is an order of magnitude smaller than the index fingertip width, which averages slightly less than 1.5 cm (Maleki-Ghahfarokhi et al., 2019).

Stationary target task performance

Mean distance errors in the stationary target tasks did not differ between groups, although older adults' mean distance errors averaged 0.61 cm higher than in younger adults ($p = 0.07$). Since the average width of the index fingertip is about 1.5 cm, the 0.61 cm larger mean errors in older adults represents less than half the width of the index. Of note, our oldest subject, at age 83, outperformed the worst performing young subject on mean distance error in the stationary target tasks by 2.47 cm, and by 2.89 cm in mean variable error. In summary, our findings show that that stationary position sense is also well maintained in late adulthood, in agreement with the conclusions of Lovelace and Aikens (1990).

We observed slightly larger mean and variable distance errors (by 0.5 and 0.39 cm respectively) in the passive (NVP_S) condition than in the active (NVA_S) condition ($p < 0.001$ and $p = 0.011$ respectively for mean and variable errors). Although these findings may appear to contradict our previous report (Capaday et al., 2013), this is likely a statistical ''artifact'' of studying a larger number of subjects (27 vs. 11), thus being of little, if any, functional significance. As discussed above, 0.5 cm is about one third the width of the index fingertip. This small effect, in, may be attributed to additional sensory information from muscle spindle and Golgi tendon organ afferent activity in muscles actively resisting gravitational torques.

Movement strategies and characteristics during task performance

The greater difficulty of older adults in delaying the start of the reaching arm movement may reflect age-related differences in inter-hemispheric inhibition. The corpus callosum, the main bundle of axons connecting the hemispheres of the brain, thins with aging (Sullivan et al., 2002). A growing body of evidence suggests that the strength of inter-hemispheric inhibition, which is conveyed largely through the corpus callosum, is reduced in older adults (reviewed by Fling et al., 2011). Furthermore, studies using fMRI have reported that older adults exhibit less lateralized processing than younger adults during a simple thumb to fingers apposition task (Naccarato et al., 2006). It has also been shown that older adults have more difficulty suppressing muscle activation contralateral to the willed muscle activation, this was true for isometric as well as anisometric contractions of the first dorsal interosseus (Shinohara et al., 2003). This could explain why older adults had more difficulty delaying the onset of reaching arm movements, despite the delayed auditory cue for the onset of voluntary arm movement. Additionally, the moving target task in active conditions (VA_M, NVA_M) may be considered a dual-task paradigm as voluntarily moving the target and reaching limb independently are separate tasks whereas during passive movement of the target limb (NVP_M) the subjects can focus on voluntary movement of one limb. It is well documented that older adults have more difficulty performing dual tasks than younger adults (see (Verhaeghen et al., 2003) for a meta-analysis of such studies).

Older and younger adults had similar peak speeds of target arm movements, but older adults moved the reaching arm 24% slower (293.4 ms longer mean duration across all conditions) than young adults. This may be interpreted as a possible compensatory strategy to increase the amount of time available to process sensory inputs to improve the prediction of the target index fingertip path in the moving target tasks and minimize errors in the stationary target tasks. It is well established that older adults move more slowly during targeted reaching and fine motor movements than younger adults (Smith et al., 1999). Thus, the longer duration arm movements probably reflect a general compensatory strategy of older adults targeted movements. The lack of high positive correlations of errors with peak speed of the reaching arm movements in young and older subjects is probably due to the instruction to move at comfortable speed, rather than as fast as possible which would likely result in observing a speed-accuracy trade-off.

Implications for the internal model hypothesis

The similar small errors we observed in active and passive conditions do not support the notion that internal models are necessary for accurate limb localization. Consistent with our previous work (Capaday et al., 2013; Darling et al., 2018), errors were similar in active and passive conditions and we did not observe overshoot biases in the active conditions without vision (e.g., Figs. 5, 7), thereby contradicting predictions of the internal forward model hypothesis (Wolpert et al., 1995). Others have also failed to observe such overshoot biases (e.g., (Gritsenko et al., 2007; Fuentes and Bastian, 2010; Cordo et al., 2011) and a recent study reported undershoot biases and larger errors in active than in passive elbow movements (Gurari et al., 2018).

Performance in moving target vs. stationary target conditions

The greater mean distance errors (by 1.23 cm on average) and variable errors (by 0.93 cm on average) in the stationary target conditions (NVA_S, NVP_S) compared to the moving target conditions (NVA_M, NVP_M) show that localization of a moving limb is better than that of a stationary limb. This could be due to greater velocity dependent activity of Ia afferents from lengthening muscles during motion (Capaday and Cooke, 1981, 1983), increasing the information available to the CNS for predicting limb location. This improved accuracy while moving would be useful when performing bimanual tasks such as tying a shoe, buttoning a shirt, or playing a piano without vision. More generally, it demonstrates the importance of dynamic proprioceptive information for the guidance of movements.

We found that, in the elderly as compared to the young, proprioceptive localization of the stationary or moving index fingertip by unconstrained movements in 3D space is slightly diminished by less than 2 mm (moving targets) and 5 mm (static targets) in mean errors, with no increase in variable errors. These differences in distance measures are much less than the width of a fingernail. This slight reduction in proprioceptive acuity is thus unlikely to be functionally significant in relation to performing most manual activities of daily living. Thus, the slower and more clumsy finer movements of the hand and digits by elderly individuals (Smith et al., 1999; Cole et al., 2010), may be due to other types of neuromuscular degeneration. There were two important secondary findings, first, we observed that proprioceptive localization of a moving limb's endpoint is better than that of a stationary limb, suggesting that dynamic and presumably greater afferent inflow during motion enhances proprioception. Second, we confirmed previous work demonstrating that internal models do not contribute to proprioception (Capaday et al., 2013; Darling et al., 2018). This rightly called 'sixth sense' appears to operate by central processing of afferent inflow, independently of motor outflow (efference copy). Given the well-known deterioration of other senses (vision, hearing, cutaneous) with age it is remarkable that our 'sixth-sense' is far more resilient, perhaps due to redundant inputs from muscle, joint and cutaneous receptors and their central processing.

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