Exp Brain Res (2015) 233:631–639
DOI 10.1007/s00221-014-4142-3

RESEARCH ARTICLE

Proprioceptively guided reaching movements in 3D space: effects of age, task complexity and handedness

T. S. Schaap · T. I. Gonzales · T. W. J. Janssen · S. H. Brown

Received: 22 July 2014 / Accepted: 4 November 2014 / Published online: 15 November 2014

Abstract Aging is associated with impaired upper limb proprioceptive acuity, as reflected by decreased position matching accuracy with increasing task complexity and movement extent. Most studies have primarily used single-joint or planar paradigms to examine age-related changes in proprioception. It is unclear whether these changes can be generalized to more complex multi-joint movements, where additional sensory feedback may affect performance. Since age-related declines in cognitive function may impair the ability to integrate multiple sources of sensory feedback, deficits in position matching ability in older adults may persist when tasks are performed in three-dimensional space. The accuracy with which young and older participants reproduced remembered reference hand positions was assessed under different experimental conditions. Participants matched target locations located directly to the front or 45° to the side relative to the midline using the preferred and non-preferred arms. Either the same (i.e., ipsilateral matching) or the opposite (i.e., contralateral matching) arm was used to reproduce the target location. No differences in matching accuracy were found between young and older participants when matching ipsilaterally. When matching contralaterally, accuracy was worse in older participants for target locations located to the side, which may reflect age-related changes in the perception of peripersonal space. In contrast to previous studies, accuracy did not differ between the preferred and non-preferred arms in either group. These results extend previous findings demonstrating age-related impairments in proprioceptively guided arm movements when interhemispheric transfer is required.

Keywords Aging · Proprioception · Upper limb · Reaching · Multi-joint reaching

T. S. Schaap · T. W. J. Janssen
Faculty of Human Movement Sciences, MOVE Research Institute Amsterdam, VU University, Amsterdam, The Netherlands

T. I. Gonzales · S. H. Brown (✉)
Motor Control Laboratory, School of Kinesiology, University of Michigan, Ann Arbor, MI 48103, USA
e-mail: shcb@umich.edu

T. W. J. Janssen
Amsterdam Rehabilitation Research Institute, Reade, The Netherlands

Introduction

Proprioception is the ability to perceive the relative position of our joints and limbs in space and is mediated by neural impulses originating from joint, cutaneous, and muscle receptors (for review, see Proske and Gandevia 2009). These signals are interpreted by the central nervous system to facilitate the prediction of muscle interaction torques (Sainburg et al. 1993), the coordination of multi-joint movements (Cordo 1990), and maintenance of internal body representations used in the planning of voluntary movements (Haggard et al. 2003; Haggard and Wolpert 2005).

The ability to utilize proprioceptive information in the absence of vision can be affected by various factors. When making proprioceptively guided matching movements to remembered targets, large movement amplitudes are associated with greater endpoint errors (Goble and Brown 2009). This association may be related to target location relative to the body, since position matching errors have been found to increase as movement endpoints move further from the body midline (Wilson et al. 2010; Fuentes and Bastian 2010; Rincon-Gonzalez et al. 2011). Other factors which may affect proprioceptive performance include motor expertise (Lin et al. 2006) and developmental level (Goble et al. 2005), as evidenced by improved position sense in adolescents compared with children. Considerable data also exist for a left-hand proprioceptive advantage in right-handed young adults (Goble and Brown 2007, 2008, 2009). This is thought to reflect a non-preferred limb/hemisphere specialization in the ability to use proprioceptive feedback (Sainburg 2002; Goble et al. 2006) which may be reduced in older adults (Przybyla et al. 2011).

It is well established that somatosensory function declines with aging. Age-related changes in lower-limb proprioceptive function are associated with decreased postural control (Horak 2006) and increased fall risk (Sorock and Labiner 1992). In contrast, the effects of aging on upper limb proprioceptive function are less well understood. Kokmen et al. (1978) found that aging had a negligible effect on the ability to detect passive finger joint motion. Similarly, Lovelace and Aikens (1990) found that the accuracy of a remembered pointing task was similar between young and older adults. However, proprioceptive deficits about the elbow (Adamo et al. 2007) and wrist (Adamo et al. 2009; Wright et al. 2011) have been reported in elderly individuals, especially for tasks requiring interhemispheric transfer of proprioceptive information. More recently, Langan (2014) found that upper limb proprioceptive accuracy decreased when older adults performed self-guided reaching movements with extrinsic sensory feedback.

Most studies have used single-joint or planar paradigms to examine age-related changes in upper limb proprioceptive function. It is unclear whether these changes can be generalized to more complex, unrestrained multi-joint movements, where additional sensory feedback may influence proprioceptive performance. For example, King et al. (2013) found no differences in matching accuracy between the preferred and non-preferred arms when young adults performed a proprioceptive reaching task in the vertical plane, demonstrating the effects of increased sensory feedback on motor lateralization. Further, multi-joint movement requires precise control of joint interaction torques (Gribble and Ostry 1999), thought to be centrally mediated by proprioceptive feedback (Sainburg et al. 1995, Verschueren et al. 1999). Older adults may be unable to sufficiently compensate for interaction torques due to age-related degeneration of the cerebellum (Zhang et al. 2010), an important site for proprioceptive information integration (Jueptner and Willer 1998). Since age-related declines in cognitive function may impair the ability to integrate multiple sources of sensory feedback (Brauer et al. 2001; Goble et al. 2009), differences in proprioceptive acuity between young and older adults may persist when performing multi-joint matching movements. These differences may be most pronounced when additional sensory feedback is generated at larger movement extents, particularly when movement endpoints are located further from the body midline. Indeed, Ghafouri and Lestienne (2000) demonstrated that older adults made marked spatial errors when reproducing elliptical hand paths in the horizontal plane, where movements deviated most from the midline. These findings were interpreted as possibly reflecting age-related degradation of peripersonal space, defined as the neural representation of space immediately surrounding the body.

Given the aforementioned factors which have been shown to influence proprioceptively guided movements, the purpose of this study was to examine the effects of aging, hand preference, and target location on reaching to remembered targets in three-dimensional space. We hypothesized that, in both young and older adults, matching errors would be greater for movements made to targets located further away from the midline, with errors greater in the older group. We also hypothesized that a non-preferred arm position matching advantage would be seen in the young adults with reduced asymmetries between the preferred and non-preferred arms in older adults. Lastly, we hypothesized that more complex tasks requiring interhemispheric transfer of proprioceptive information would lead to greater errors in older compared with young adults.

Methods

Participants

Twelve young (six male; six female, mean age 22 ± 2.3 years) and twelve older (six male; six female, mean age 76 ± 5.6 years) individuals participated in the study. All participants were right-handed, lived independently in the community, and were free of any neuromuscular or neurological conditions that might hinder task performance. None had a long-standing history of highly skilled motor activity or sports involving precise upper limb control. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield 1971). Cognitive function was assessed in the older group using the Mini Mental State Examination (Folstein et al. 1975), where all participants scored >27. Participants were instructed to abstain from any strenuous upper limb activity 4 h prior to testing. Informed consent was obtained prior to testing according to procedures established by the Institutional Review Board of the University of Michigan.

Experimental procedure

Participants were comfortably seated on an adjustable straight-back chair in front of a table. Initial arm position was 90° elbow flexion and 10° shoulder abduction with the fingers touching the edge of the table. The index and middle fingers were held in an extended position while all other, digits were flexed. Participants were instructed to keep their trunk upright and in contact with the chair during testing and were blindfolded for all trials.

The task involved reaching to remembered target locations from a seated position. The target location was defined by having participants actively move their arm to a self-determined position in three-dimensional space, located either directly in front of the participant or approximately 45° to the side. Target locations were at shoulder height and were equal to approximately 85 % of the participant's maximum reach distance. The arm, hand, and fingers were held in the target location for 3 s. The arm was then returned to the edge of the table where the experimenter assisted the participant in repositioning his or her hand to the designated starting position. The target location was matched by actively moving the arm to the previous target location after a 3-s delay. Participants were instructed to move using one continuous motion at a preferred movement speed, to keep the head stationary and facing forward, and to attend to the spatial position of the hand. Prior to testing, each participant was familiarized with reaching target locations (i.e., front, side) by performing visually guided practice trials to a target board. The reach distance to the target board was adjusted to reflect approximately 85 % of each participant's maximum reach distance.

The target location was matched with either the same (i.e., ipsilateral) or opposite (i.e., contralateral) arm. In the contralateral condition, the target location was reproduced by moving the matching arm in space so that it mirrored the memorized position of the reference arm relative to the body midline. Matching conditions were conducted with either the non-preferred (left) or preferred (right) hand performing the matching movement. Four different matching tasks (ipsilateral-left, ipsilateral-right, contralateral-left, contralateral-right) were performed in a pseudorandomized order to control for order effects. For each matching task, four trials were performed to the front target location and four trials to the side position. A 2-min rest period was provided between conditions.

Experimental setup

An electromagnetic tracking system (Ascension Technology, Burlington, VT, USA) with Motion Monitor software (Innovative Sports Training, Chicago, IL, USA) was used to record upper limb kinematics. Three electromagnetic sensors were used throughout testing. One sensor was taped on the distal dorsal aspect of the middle and index fingers of each hand to track the end point position of the hand. Both fingers were taped together prior to the placement of the hand sensors. The third sensor was attached to the sternum. All sensors and connecting wires were secured to the arm with foam wrap to minimize movement artifacts.

Data acquisition and analysis

Position data in the x (anterior/posterior), y (lateral) and z (vertical) directions were obtained from the motion capture sensors. Signals were digitized at 100 Hz and filtered (Butterworth filter, cutoff frequency 6 Hz) prior to data analysis. Absolute positional error, a measure of endpoint accuracy (Adamovich et al. 1999), was calculated according to the following formula:

$$\text{Absolute positional error} = \left(d_x^2 + d_y^2 + d_z^2\right)^{1/2}$$

where d_x, d_y, and d_z are the differences between the target and matched endpoint positions in the x direction (anterior/posterior), the y direction (lateral), and the z direction (vertical). Both target and matched endpoint positions were determined using a threshold detection algorithm of ±2 SD from the baseline (zero) velocity signal. Absolute and constant radial, inclination, and azimuth errors were calculated in a spherical reference frame with the origin located at the position of the sternal sensor (see Fig. 1). Evidence suggests that a spherical coordinate system best approximates the internal representation of the position of the hand when making reaching movements to targets in space (Soechting and Flanders 1989; Vetter et al. 1999). Movement amplitude (i.e., the absolute distance between the initial and endpoint positions of the matching hand) and movement time were also compared between age groups.

Statistical analysis

An initial comparison of performance between males and females indicated no differences in matching performance. We, therefore, pooled data across sexes for all subsequent analyses. Main and two-way interaction effects were determined for the three within-subject independent factors (condition, direction, matching hand) using a repeated measures mixed model analysis of variance where age was chosen as the between-subject factor. Data were analyzed using SPSS (version 17.0; SPSS Inc, Chicago, IL, USA). Statistical significance was set at $p < 0.05$.

Results

All participants were able to perform reaching movements as instructed. Movement amplitudes associated with targets located to the side were approximately 7 cm greater than those located in the forward direction for both age groups. Matching movement time was significantly greater

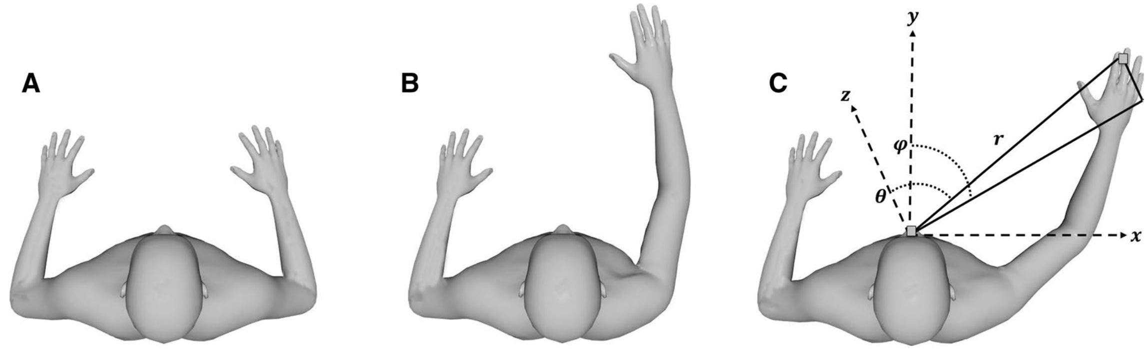

Fig. 1 *Top–down* perspective of the experimental setup. Position of the arms initially (**a**), when reaching forward (**b**), and when reaching to the side (**c**). Radial distances (r) were the absolute distance between the sternal and finger sensors. Inclination angles (θ) were the angular distances between the *sagittal plane* (z) and *line* segment between the positions of the sternal and finger sensors. Azimuth angles (φ) were the angular distances in the *horizontal plane* between the midline (y) and the position of the finger sensor

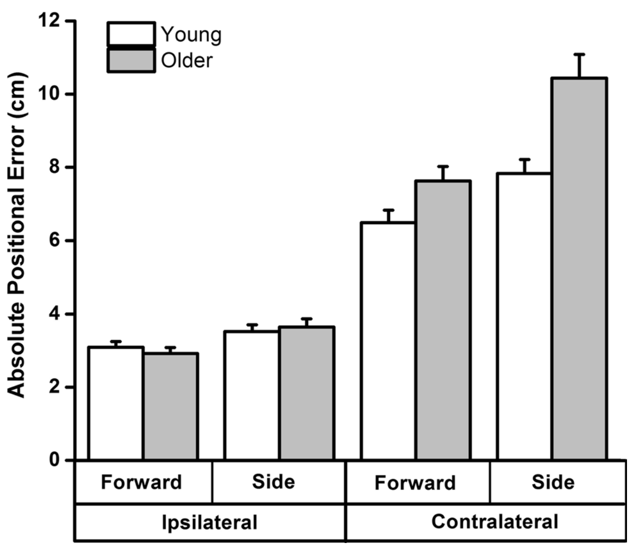

Fig. 2 Mean ± 1 SE absolute positions errors when matching remembered forward and side arm positions with the ipsilateral and contralateral arm. *Open bars* represent data from young participants; *filled bars* older participants

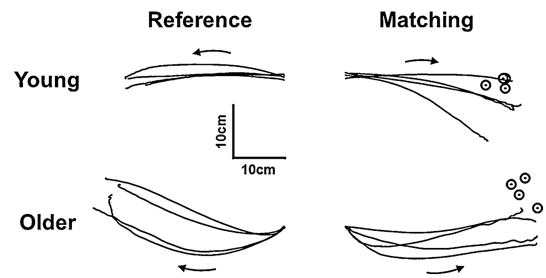

Fig. 3 *Top–down* perspective of hand trajectories from a young (*upper record*) and older (*lower record*) participant for four consecutive trials during the contralateral-side condition. Reference targets (*circled dots*), mirrored from *left* to *right* with respect to the *midsagittal plane*, were indicated by the *left hand* and matched with the *right*. *Arrows* indicate the direction of the movement

in older (2.17 ± 0.13 s) compared with young adults (1.70 ± 0.09 s) ($p < 0.01$).

Absolute errors

Absolute positional errors (Fig. 2) were similar between young and older participants in the ipsilateral matching condition, regardless of target location. By comparison, absolute positional errors were greater in the contralateral matching condition for both groups ($p < 0.001$), with errors greater in the older group compared with the younger group ($p < 0.001$) (Fig. 3). Errors in the older group were most pronounced in the contralateral matching condition when matching to the side ($p < 0.05$). No significant differences in absolute positional error were found between the non-preferred and preferred hands in either group.

To understand whether absolute positional errors were directionally dependent, we analyzed absolute errors in terms of their spherical coordinates (i.e., radial, inclination, and azimuth). Absolute radial errors (Fig. 4a) were greater when matching with the contralateral hand compared with the ipsilateral hand ($p < 0.001$). A small, but statistically significant difference in absolute radial error was found between target locations ($p < 0.05$), where matching was less accurate when reaching to targets located to the side. No significant differences were found between age groups or matching hand. Absolute inclination errors (Fig. 4b) were also greater in the contralateral matching condition compared with the ipsilateral condition ($p < 0.001$). In the contralateral condition, older adults had greater inclination errors compared with younger adults ($p < 0.05$), especially when reaching to the side ($p < 0.001$). No significant differences in absolute inclination error were found between

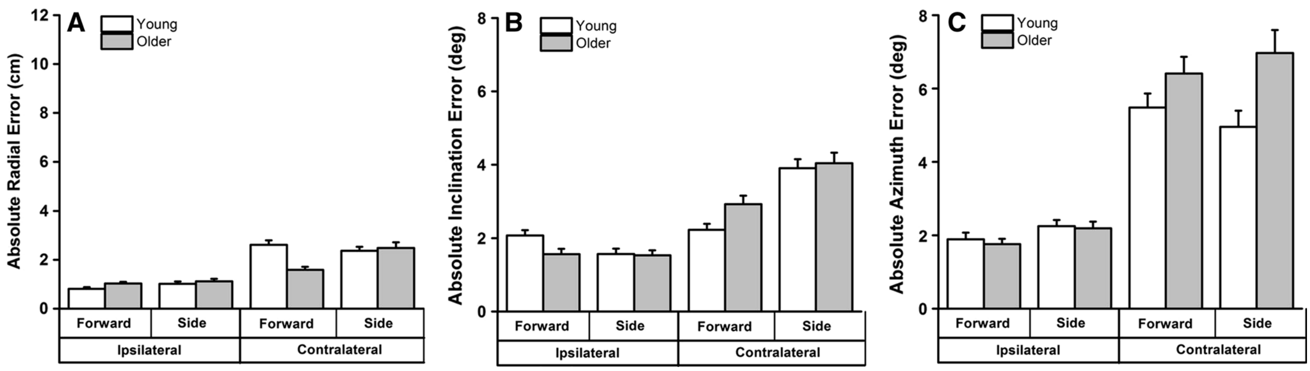

Fig. 4 Mean ± 1 SE absolute radial (**a**), inclination (**b**), and azimuth (**c**) errors when matching remembered forward and side arm positions with the ipsilateral and contralateral arm. *Open bars* represent data from young participants; *filled bars* older participants

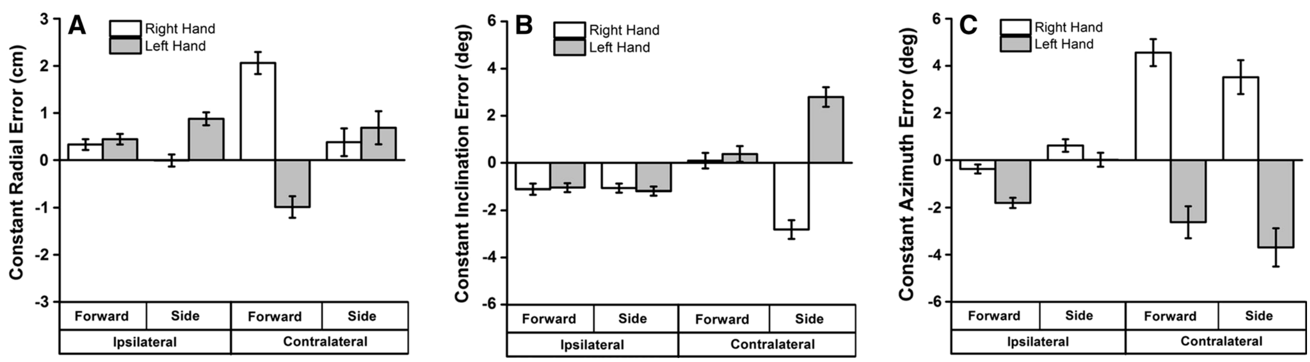

Fig. 5 Mean ± 1 SE constant radial (**a**), inclination (**b**), and azimuth (**c**) errors when matching remembered forward and side arm positions with the ipsilateral and contralateral arm. *Open bars* represent data when the target position was matched with the right arm; *filled bars* with the left arm

matching hands. Absolute azimuth errors (Fig. 4c) were greater in the contralateral matching condition compared with the ipsilateral condition for both groups. Errors were greater in the older group compared with the younger group ($p < 0.001$), which were most pronounced in the contralateral condition ($p < 0.001$). Absolute positional errors were most influenced by errors in the azimuth direction in both tasks and target locations ($p < 0.001$), with no observed differences between matching hands.

Constant errors

To determine where matching errors were localized in space relative to target positions, we calculated constant errors from the spherical error measures. Inspection of constant error measures revealed no statistically significant differences between older and younger participants. Therefore, constant error data were collapsed across groups. Significant differences in constant radial error (Fig. 5a) were found between matching hands ($p < 0.01$). In the contralateral matching condition, participants overestimated target distance when matching with the right hand and underestimated distance when matching with the left hand when reaching forward, but not to the side ($p < 0.001$). Differences were not significant in the ipsilateral condition, and no differences were found between age groups. Constant inclination errors (Fig. 5b) indicated that participants overestimated target height when matching with the right hand and underestimated height when matching with the left hand during the contralateral matching condition when matching to the side, but not forward ($p < 0.001$). Differences between matching hands were not significant in the ipsilateral condition or between age groups. Constant azimuth errors (Fig. 5c) indicated that participants overestimated target rotational position when matching with the right hand and underestimated when matching with the left hand in the contralateral matching task when reaching forward and to the side ($p < 0.001$). Differences in error between matching hands were not significant in the ipsilateral condition or between age groups.

Discussion

The present study compared proprioceptive acuity between young and older adults when matching remembered arm positions in three-dimensional space. We found that performance was similar between young and older adults when matching movements were performed with the same arm. For movements requiring interhemispheric transfer, declines in performance were greater in the older compared with young adults, especially for movement endpoints located to the side away from the body midline. In contrast to previous work demonstrating a proprioceptive specialization in the non-preferred limb (Sainburg 2002; Goble et al. 2006), limb asymmetries in proprioceptive acuity were not found in both young and older adults.

Proprioceptive acuity was similar between young and older adults during the ipsilateral matching condition, regardless of target location from the body midline. These findings contrast with those reported by Adamo et al. (2007, 2009), who found that older adults had significantly greater matching errors when replicating joint angles with the same and opposite arms. Methodological differences may account for conflicting findings, since Adamo et al. (2007, 2009) conducted single-joint position matching tasks in a gravity-eliminated environment. In the present study, we used a multi-joint position matching task which allowed gravitational forces to influence arm movements. The perception of arm orientation, thought to rely upon a subjective gravitational reference frame (Darling et al. 2008), may have been enhanced by moving in three-dimensional space. Indeed, evidence suggests that the central nervous system generates an internal representation of interactions between gravity and arm movement dynamics, which may facilitate sensorimotor control and movement planning (Papaxanthis et al. 2005; Gentili et al. 2007). Reaching in three-dimensional space, compared with single-joint movements, increases proprioceptive feedback from multiple limb segments. It is possible that proprioceptive feedback used to establish an internal representation of the desired movement may indirectly influence sense of effort, which has been implicated as a factor to enhance position matching ability in the presence of the force of gravity (Winter et al. 2005; Gandevia et al. 2006). Furthermore, age-related changes in proprioceptor function are known to increase the amount of spontaneous, unwanted neuronal activity (i.e., noise) in sensory feedback (Shaffer and Harrison 2007). This has been suggested as a factor that could influence the magnitude of errors in single-joint studies of elderly upper limb proprioceptive function (Adamo et al. 2007, 2009). There is evidence that the central nervous system encodes limb endpoint positions by integrating sensory feedback from combinations of joint segments (Helms Tillery et al. 1996, Bosco et al. 2000). The effects of sensory noise on limb position estimation may be mitigated when multiple sources of proprioceptive information are provided (Kuo 2005), therefore allowing for a more accurate internal representation of limb position.

We demonstrated marked increases in position matching errors for reaching tasks that required interhemispheric transfer of memory-based proprioceptive information (i.e., contralateral matching condition). In contrast to the ipsilateral matching condition, the magnitudes of matching errors were greater in older compared with young adults. Our findings are corroborated by other investigations of age-related differences in proprioceptive ability between young and older individuals (Adamo et al. 2007, 2009; Herter et al. 2014). These results may be explained by deterioration of cognitive processes involved in sensorimotor function (Li and Lindenberger 2002) and reduced hemispheric connectivity caused by corpus callosum degeneration (Abe et al. 2002). Indeed, declines in working memory and psychomotor speeds have been associated with age-related atrophy of the anterior region of the corpus callosum (Fling et al. 2011). Sex may also influence corpus callosum morphology (Suganthy et al. 2003) and contribute to differences in bimanual coordination between men and women (Shetty et al. 2014). In the present study, however, sex was not associated with differences in proprioceptive acuity due to our small sample size.

Interestingly, absolute position matching errors were most pronounced when older adults reached to the side in the contralateral matching condition. Previous work has demonstrated that upper limb proprioceptive acuity decreases as target distances are located further from the body midline (Wilson et al. 2010; Fuentes and Bastian 2010; Rincon-Gonzalez et al. 2011). We observed this effect only when interhemispheric transfer of proprioceptive information was required, suggesting that known age-related degradation of the corpus callosum (Abe et al. 2002) may have decreased the signal-to-noise ratio of the transferred information. Degeneration of other cognitive structures involved in the processing of interhemispherically transferred sensory information may also be involved. Decreased matching accuracy for contralateral matching movements to the side may reflect degenerative processes associated with the perception of hand position in peripersonal space (Ghafouri and Lestienne 2000). Age-related impairment of peripersonal space representations of the hand alters the allocation of attentional resources during the planning and execution of movements, resulting in increased arm movement response times (Bloesch et al. 2013). This has implications for older adults when motor behaviors require the arm to be moved away from the body midline. For example, reaching to the side can serve a protective role when maintaining postural control or deflecting impact forces exerted on the body when falling. Young adults initiate protective arm movement 50–100 ms after a tripping perturbation (Pijnappels et al. 2010). Based on previous work demonstrating greater response time latency and variability in older versus young adults during reaction time tasks (Hultsch et al. 2002), it is likely that this protective response becomes delayed with age. This may be reflected by age-related differences in arm movement mechanics and recovery strategies during falls (Roos et al. 2008). Elevated fall risk (Woollacott et al. 1986; Sorock and Labiner 1992) and fall morbidity (Sattin 1992) in older adults may therefore be partially due to diminished peripersonal space representations of arm position. Future investigations are needed to substantiate this argument.

No differences in absolute positional error were found between the preferred and non-preferred limbs for either young or older adults. This finding contrasts with previous work that demonstrated a non-preferred arm advantage for the localization of memorized proprioceptive targets when making single-joint movements (Goble et al. 2006; Goble and Brown 2007). Our results corroborate other multi-joint studies where no interlimb differences in proprioceptive acuity were found (Carson et al. 1990; Chapman et al. 2001; King et al. 2013). Increased sensory feedback generated across multiple limb segments may have attenuated differences in endpoint accuracy between the preferred and non-preferred arms when performing unrestrained proprioceptively guided movements. Alternatively, when making multi-joint movements, the central nervous system may use multiple redundant degrees of freedom to reduce differences in arm positioning errors between the preferred and non-preferred limbs (Karduna and Sainburg 2012). While our results imply that the central nervous system retains this ability through age, a comparison of intra-limb joint dynamics between young and older adults is warranted to support this postulation.

Our constant error results revealed a rightward horizontal bias in matching errors during the contralateral matching condition. With regard to the midsagittal plane, participants overestimated the horizontal angular distance of target positions indicated by the left hand when matching with the right hand, where the left hand underestimated the position of the right hand. Hand positioning biases have been reported previously (Haggard et al. 2000; Helms Tillery et al. 1994), although these studies required participants to reach across the midline to match target positions indicated by the contralateral arm. The pattern of constant errors revealed by the present study, then, may be introduced when spatial coordinates are bilaterally transformed across the midsagittal plane, potentially due to the utilization of different reference frames between the left and right arms (McGuire and Sabes 2009). Alternatively, the observed rightward bias may reflect a lifetime of dominant arm use. A leftward systemic bias in visuospatial processing has been extensively studied (for review see Brooks et al. 2014), which may be related to proprioceptive biases observed when matching contralaterally indicated arm positions.

It has been hypothesized that proprioceptive acuity is greater when using a hand positioning protocol compared with a joint angle protocol (van Beers et al. 1998). Recent reports indicated that differences in hand versus joint angle matching were not statistically significant (King and Karduna 2014) or were too small in magnitude to have a meaningful impact on results (Fuentes and Bastian 2010). We instructed participants to attend to hand position, rather than joint angle, when performing target reference and matching movements. Based on these previous investigations, we do not anticipate that our observed findings would be significantly different if participants were instructed to attend to joint angle.

Conclusion

Using a multi-joint matching paradigm in three-dimensional space, we found that proprioceptive ability was similar between young and older adults when tasks did not require interhemispheric transfer of position-related sensory feedback. This observation may reflect the benefits of increased feedback as a result of moving with or against gravity. The greatest age-related deficits were seen when moving to remembered targets located to the side and requiring interhemispheric transfer, suggesting workspace-related impairments during proprioceptively guided movements. Together these findings extend our understanding of the factors influencing proprioceptive acuity and are of value when considering, for example, movement-based exercises to improve sensorimotor coordination in older adults. Future work should include a detailed exploration of proprioceptive acuity in different parts of the workspace as well as understanding how standing posture, associated with many activities of daily living involving reaching movements, may influence task performance.

References

Abe O, Aoki S, Hayashi N, Yamada H, Kunimatsu A, Mori H, Yoshikawa T, Okubo T, Ohtomo K (2002) Normal aging in the central nervous system: quantitative MR diffusion-tensor analysis. Neurobiol Aging 23(3):433–441

Adamo DE, Martin BJ, Brown SH (2007) Age-related differences in upper limb proprioceptive acuity. Percept Mot Skills 104:1297–1309

Adamo DE, Alexander NB, Brown SH (2009) The influence of age and physical activity on upper limb proprioceptive ability. J Aging Phys Act 17:272–293

Adamovich SV, Berkinblit MB, Fookson O, Poizner H (1999) Pointing in 3D space to remembered targets I: kinesthetic versus visual target presentation. J Neurophysiol 79:2833–2846

Bloesch EK, Davoli CC, Abrams RA (2013) Age-related changes in attentional reference frames for peripersonal space. Psychol Sci 24(4):557–561

Bosco G, Poppele RE, Eian J (2000) Reference frames for spinal proprioception: limb endpoint based or joint-level based? J Neurophysiol 83(5):2931–2945

Brauer SG, Woollacott M, Shumway-Cook A (2001) The interacting effects of cognitive demand and recovery of postural stability in balance-impaired elderly persons. J Gerontol A Biol Sci Med Sci 56(8):M489–M496

Brooks JL, Della Sala S, Darling S (2014) Representational pseudoneglect: a review. Neuropsychol Rev 24(2):148–165

Carson RG, Elliott D, Goodman D, Dickinson J (1990) Manual asymmetries in the reproduction of a 3-dimensional spatial location. Neuropsychologia 28(1):99–103

Chapman CD, Heath MD, Westwood DA, Roy EA (2001) Memory for kinesthetically defined target location: evidence for manual asymmetries. Brain Cogn 46(1–2):62–66

Cordo PJ (1990) Kinesthetic control of a multijoint movement sequence. J Neurophysiol 63(1):161–172

Darling WG, Viaene AN, Peterson CR, Schmiedeler JP (2008) Perception of hand motion direction uses a gravitational reference. Exp Brain Res 186(2):237–248

Fling BW, Peltier SJ, Bo J, Welsh RC, Seidler RD (2011) Age differences in interhemispheric interactions: callosal structure, physiological function, and behavior. Front Neurosci 5:38

Folstein MF, Folstein SE, McHugh PR (1975) “Mini-mental state”: a practical method for grading cognitive state of patients for the clinician. J Psychiatr Res 12(3):189–198

Fuentes CT, Bastian AJ (2010) Where is your arm? Variations in proprioception across space and tasks. J Neurophysiol 103(1):164–171

Gandevia SC, Smith JL, Crawford M, Proske U, Taylor JL (2006) Motor commands contribute to human position sense. J Physiol 571(Pt 3):703–710

Gentili R, Cahouet V, Papaxanthis C (2007) Motor planning of arm movements is direction-dependent in the gravity field. Neuroscience 145(1):20–32

Ghafouri M, Lestienne FG (2000) Altered representation of peripersonal space in the elderly human subject: a sensorimotor approach. Neurosci Lett 289(3):193–196

Goble DJ, Brown SH (2007) Task-dependent asymmetries in the utilization of proprioceptive feedback for goal-directed movement. Exp Brain Res 180(4):693–704

Goble DJ, Brown SH (2008) The biological and behavioral basis of upper limb asymmetries in sensorimotor performance. Neurosci Biobehav Rev 32(3):598–610

Goble DJ, Brown SH (2009) Dynamic proprioceptive target matching behavior in the upper limb: effects of speed, task difficulty and arm/hemisphere asymmetries. Behav Brain Res 200(1):7–14

Goble DJ, Lewis CA, Hurvitz EA, Brown SH (2005) Development of upper limb proprioceptive accuracy in children and adolescents. Hum Movement Sci 24(2):155-170

Goble DJ, Lewis CA, Brown SH (2006) Upper limb asymmetries in the utilization of proprioceptive feedback. Exp Brain Res 168(1–2): 307–311

Goble DJ, Coxon JP, Wenderoth N, Van Impe A, Swinnen SP (2009) Proprioceptive sensibility in the elderly: degeneration, functional consequences and plastic-adaptive processes. Neurosci Biobehav Rev 33(3):271–278

Gribble PL, Ostry DJ (1999) Compensation for interaction torques during single- and multijoint limb movement. J Neurophysiol 82(5):2310–2326

Haggard P, Wolpert DM (2005) Disorders of body scheme. In: Freund H, Jeannerod M, Hallett M, Leigaruda R (eds) Higher order motor disorders. Oxford University Press, Oxford, pp 261–271

Haggard P, Newman C, Blundell J, Andrew H (2000) The perceived position of the hand in space. Percept Psychophys 62(2):363–377

Haggard P, Taylor-Clarke M, Kennett S (2003) Tactile perception, cortical representation and the bodily self. Curr Biol 13(5):R170–R173

Helms Tillery SI, Flanders M, Soechting JF (1994) Errors in kinesthetic transformations for hand apposition. NeuroReport 6(1):177–181

Helms Tillery SI, Soechting JF, Ebner TJ (1996) Somatosensory cortical activity in relation to arm posture: nonuniform spatial tuning. J Neurophysiol 76(4):2423–2438

Herter TM, Scott SH, Dukelow SP (2014) Systematic changes in position sense accompany normal aging across adulthood. J Neuroeng Rehabil 11:43. doi:10.1186/1743-0003-11-43

Horak FB (2006) Postural orientation and equilibrium: what do we need to know about neural control of balance to prevent falls? Age Ageing 35(Suppl 2):ii7–ii11

Hultsch DF, MacDonald SW, Dixon RA (2002) Variability in reaction time performance of younger and older adults. J Gerontol B Psychol Sci Soc Sci 57(2):P101–P115

Jueptner M, Willer C (1998) A review of differences between basal ganglia and cerebellar control of movements as revealed by functional imaging studies. Brain 121(8):1437–1449

Karduna AR, Sainburg RL (2012) Similarities in the neural control of the shoulder and elbow joints belie their structural differences. PLoS ONE 7(10):e45837. doi:10.1371/journal.pone.0045837

King J, Karduna A (2014) Joint position sense during a reaching task improves at targets located closer to the head but is unaffected by instruction. Exp Brain Res 232(3):865–874

King J, Harding E, Karduna A (2013) The shoulder and elbow joints and right and left sides demonstrate similar joint position sense. J Mot Behav 45(6):479–486

Kokmen E, Bossemeyer RW Jr, Williams WJ (1978) Quantitative evaluation of joint motion sensation in an aging population. J Gerontol 33(1):62–67

Kuo AD (2005) An optimal state estimation model of sensory integration in human postural balance. J Neural Eng 2(3):S235–S249

Langan J (2014) Older adults demonstrate greater accuracy in joint position matching using self-guided movements. Hum Mov Sci 36C:97–106

Li K, Lindenberger U (2002) Relations between aging sensorimotor and cognitive functions. Neurosci Biobehav Rev 26(7):777–783

Lin CH, Lien YH, Wang SF, Tsauo JY (2006) Hip and knee proprioception in elite, amateur, and novice tennis players. Am J Phys Med Rehabil 85(3):216–221

Lovelace EA, Aikens JE (1990) Vision, kinesthesis, and control of hand movement by young and old adults. Percept Mot Skills 70(3 Pt 2):1131–1137

McGuire LM, Sabes PN (2009) Sensory transformations and the use of multiple reference frames for reach planning. Nat Neuroscience 12(8):1056–1063

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113

Papaxanthis C, Pozzo T, McIntyre J (2005) Kinematic and dynamic processes for the control of pointing movements in humans revealed by short-term exposure to microgravity. Neuroscience 135(2):371–383

Pijnappels M, Kingma I, Wezenberg D, Reurink G, van Dieën JH (2010) Armed against falls: the contribution of arm movements to balance recovery after tripping. Exp Brain Res 201(4):689–699

Proske U, Gandevia SC (2009) The kinaesthetic senses. J Physiol 587(17):4139–4146

Przybyla A, Haaland KY, Bagesteiro LB, Sainburg RL (2011) Motor asymmetry reduction in older adults. Neurosci Lett 489(2):99–104

Rincon-Gonzalez L, Buneo CA, Helms Tillery SI (2011) The proprioceptive map of the arm is systematic and stable, but idiosyncratic. PLoS ONE 6(11):e25214. doi:10.1371/journal.pone.0025214

Roos PE, McGuigan MP, Kerwin DG, Trewartha G (2008) The role of arm movement in early trip recovery in younger and older adults. Gait Posture 27(2):352–356

Sainburg RL (2002) Evidence for a dynamic-dominance hypothesis of handedness. Exp Brain Res 142(2):241–258

Sainburg RL, Poizner H, Ghez C (1993) Loss of proprioception produces deficits in interjoint coordination. J Neurophysiol 70(5):2136–2147

Sainburg RL, Ghilardi MF, Poizner H, Ghez C (1995) Control of limb dynamics in normal subjects and patients without proprioception. J Neurophysiol 73(20):820–835

Sattin RW (1992) Falls among older persons: a public health perspective. Annu Rev Public Health 13:489–508

Shaffer SW, Harrison AL (2007) Aging of the somatosensory system: a translational perspective. Phys Ther 87(2):193–207

Shetty AK, Shankar MS, Annamalai N (2014) Bimanual coordination: influence of age and gender. J Clin Diagn Res 8(2):15–16

Soechting JF, Flanders M (1989) Errors in pointing are due to approximations in sensorimotor transformations. J Neurophysiol 62(2):595–608

Sorock GS, Labiner DM (1992) Peripheral neuromuscular dysfunction and falls in an elderly cohort. Am J Epidemiol 136(5):584–591

Suganthy J, Raghuram L, Antonisamy B, Vettivel S, Madhavi C, Koshi R (2003) Gender- and age-related differences in the morphology of the corpus callosum. Clin Anat 16(5):396–403

van Beers RJ, Sittig AC, van der Gon JJD (1998) The precision of proprioceptive position sense. Exp Brain Res 122(4):367–377

Verschueren SM, Swinnen SP, Cordo PJ, Dounskaia NV (1999) Proprioceptive control of multijoint movement: bimanual circle drawing. Exp Brain Res 127(2):182–192

Vetter P, Goodbody SJ, Wolpert DM (1999) Evidence for an eye-centered spherical representation of the visuomotor map. J Neurophysiol 81(2):935–939

Wilson ET, Wong J, Gribble PL (2010) Mapping Proprioception across a 2D horizontal workspace. PLoS ONE 5(7):e11851. doi:10.1371/journal.pone.0011851

Winter JA, Allen TJ, Proske U (2005) Muscle spindle signals combine with the sense of effort to indicate limb position. J Physiol 568(3):1035–1046

Woollacott MH, Shumway-Cook A, Nashner LM (1986) Aging and posture control: changes in sensory organization and muscular coordination. Int J Aging Hum Dev 23(2):97–114

Wright ML, Adamo DE, Brown SH (2011) Age-related declines in the detection of passive wrist movement. Neurosci Lett 500(2):108–112

Zhang C, Zhu Q, Hua T (2010) Aging of cerebellar Purkinje cells. Cell Tissue Res 341(3):341–347