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Research article

Age-related differences in proprioceptive asymmetries

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ABSTRACT

Age-related differences in proprioceptive asymmetries have received little attention. This study aimed to determine differences in asymmetry of the right/left upper limb proprioceptive systems between younger and older adults. Asymmetries were compared in two "eyes closed" experiments involving the same elbow joints. Position sense was tested in two matching conditions: ipsilateral remembered and contralateral concurrent. Movement sense was tested while reproducing with the opposite forearm the illusory movement elicited by distal tendon vibration applied to the reference forearm. Older adults exhibited a larger error when matching with the non-dominant than dominant forearm in the ipsilateral remembered condition and a disparate asymmetry in the contralateral condition when compared to younger adults. In addition, in older adults, the velocity of reproduced illusory movements was slower, and asymmetry in movement perception was not significant. The difference in proprioceptive asymmetry between younger and older adults might be attributed to a significant reduction of the sensory system gain affecting, more particularly, the left non-dominant arm sensory system via several physiological and neurophysiological mechanisms.

1. Introduction

Functional/behavioral differences in upper limb position and movement sense have been observed in young adults. Their interpretations have been based on structural and neurophysiological differences stemming from hemisphere dominance and gender, also referred to as asymmetries. Yamauchi, et al. [44] posited that the difference in position perception, in the context of a left limb advantage, was ascribable to differences in hemispheric specialization in the processing of kinesthetic data. However, Adamo and Martin [2] showed that the difference in position perception was the result of a difference in the overall *gain* of the respective proprioceptive sensory-motor loops, where *gain* represents the input-output relationship of a system in terms of magnitude (here: perceived–achieved movement outcome). In their study [2], upper limb position sense was investigated in right-handed young adults performing a wrist position matching when the reference position was provided by the ipsilateral or contralateral limb. The constant error in the ipsilateral condition was similar for the right and left-hand matching. However, in contralateral matching, the right-hand overshot, while the left-hand undershot the opposite-hand reference [2]. The deduced gain difference hypothesis, explaining this asymmetry, was strongly supported by a linear model representing both sensorimotor systems and by morphological and physiological data [23].

Asymmetry of vibration-induced elbow movement illusions between dominant and non-dominant limbs, further implied a difference in internal movement/kinesthetic representation between the upper limb/hemisphere systems [5]. This difference stemmed from a combination of differences in cortical structure and information processing common to each hemisphere and gender. These asymmetries, associated with hand/hemisphere dominance [2,4,5,36], can be considered intrinsic. Vibration-induced activity of muscle proprioceptors has been extensively used to demonstrate their contribution to position sense [16,34] and movement control [24]. However, in these studies, the equivalence of proprioceptive information from homologous body segments did not receive attention. The first approach was likely by Adamo and Martin [2]. Position sense and movement sense asymmetries were revealed by the direction of the constant error in matching tasks in which information provided by the reference limb was reproduced by the contralateral limb. The difference in gain was associated with known brain morphological (cortical area sizes) and physiological data. For example, the sensory thumb-little finger hand representation presented a small difference between the two hemispheres [40] and the non-dominant hand

Abbreviations: IR, ipsilateral remembered; CC, contralateral concurrent; HAROLD, Hemispheric Asymmetry Reduction in Older Adults; AE, absolute error; CE, constant error; MT, movement time; MV, movement velocity; RVLM, right vibration left match; LVRM, left vibration right match.

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may use a different activation method than the dominant for left and right-handers [22].

Age-related degradations in proprioceptive based performance, including daily living activities, arise from anatomical and physiological changes in the central and peripheral nervous systems [18]. According to Goble, et al. [14], prevalent sensory declines in older adults negatively impact daily living activities as central processing abilities decrease and the peripheral nervous system alters with age. Several studies also showed decrease in proprioceptive acuity with age [19,43]. Adamo, et al. [3] examined age-related changes in forearm proprioceptive perception via an elbow extension position matching task requiring memory and/or interhemispheric transfer. The matching errors, movement time, and movement smoothness were significantly degraded in older adults. This evidenced cognitive and sensorimotor declines associated with aging. However, the effects of age on asymmetry were not investigated.

This study aimed to determine age-related differences on asymmetry of the right/left upper limb proprioceptive systems. As the relationship between proprioceptive perception (the input) and its motor outcome (the output) can be represented by the gain of the sensorimotor system, it is hypothesized that age-related variations in the gain of the sensory component of the system modify the intrinsic sensory asymmetry of the upper limbs. It is speculated that an asymmetry reduction in older adults, resulting from a decrease in gain, could reflect an interaction of both the decrease in sensory acuity with age and the postulated compensation of age effects on information processing [7] and motor tasks [27,30,41] by bilateral activation of the hemispheres. This understanding of the age-related differences in proprioception is relevant to the design of rehabilitation procedures and preventive programs aimed at reducing the effects of aging and neurological disorders on an individual's awareness of upper limb spatial position and movement.

2. Material and methods

2.1. Participants

Fourteen younger adults (6 females, 8 males; mean age 25.3 ± 2.9 years) and fourteen older adults (7 females, 7 males; mean age 63.0 ± 8.2 years), right-handed with mean laterality index of 0.8 ± 0.1 (range: 0.6–1.0) and 0.9 ± 0.1 (range: 0.6–1.0), respectively, as determined by the Edinburgh Handedness Inventory [28], and free of upper limb neurological and musculoskeletal disorders, participated in this study. The study was approved by the University of Michigan (UM) Health and Behavioral Sciences Institutional Review Board (HUM00106283). All participants signed an informed consent form before the experiment.

2.2. Experimental set-up and procedure

A custom-designed electronically controlled chair and LabVIEW software were used to move the forearm passively to predefined positions and record the active forearm displacement. The horizontal levers (forearm supports) were equipped with precision encoders to measure elbow joint rotation and servo-motors to impose a forearm displacement and return to the initial position after a controlled delay. An electromagnetic clutch coupled and decoupled the motor allowing the participant, when required, to move the forearm freely with negligible force. The movement speed imposed by the motor was set to 20°/sec for all trials. For movement sense, an electrodynamic vibrator (LDS® V203) equipped with a polycarbonate probe (2 × 15 mm rounded edge) was driven by a power amplifier connected to a waveform generator to elicit the illusion of elbow flexion by stimulation of the distal tendons of the upper-arm extensor muscles [5,23].

The procedure was partially replicated from previous studies [2,3,5,23]. Participants were seated with the upper arms positioned in 60° abduction, 40° horizontal shoulder flexion with elbows included angle initially set to 120° extension. The forearms, in wrist pronation, were supported by the horizontal levers. The axis of elbow joint rotation was aligned with the axis of the corresponding lever, and the forearms and hands were stabilized using a cohesive bandage. All trials were conducted eyes closed. To ascertain that perception was solely based on proprioception all "movement" references were imposed passively. Trials and blocks were separated by 0.25 and 5 min rest breaks, respectively, during which participants were encouraged to open their eyes and "shake out" their hands or produce isometric muscle contractions to reset muscle proprioception and/or eliminate residual post-vibration effects [29].

2.2.1. Position sense

A passively imposed reference position of 20° elbow flexion was actively matched in two conditions illustrated in Fig. 1: 1) ipsilateral remembered (IR) – the reference and matching movements were performed with the same forearm, and 2) contralateral concurrent (CC) – the reference forearm was held in the reference position while the movement was reproduced with the opposite forearm. In the IR condition, the reference position was maintained for 2 s before the forearm was returned automatically to the initial position. For each condition and forearm, two practice trials preceded five test trials. Both forearms were used in alternated blocks to provide the reference. Blocks (10 trials: 5 IR and 5 CC) were randomized between participants.

2.2.2. Movement sense

The opposite arm was used to match the perceived illusory elbow flexion movement elicited by an 80-Hz sinusoidal vibration (displacement amplitude ≈100 μm, 10 s duration) of the reference arm distal tendon of the triceps muscles [5]. The probe-skin contact location was marked to ensure accurate repositioning (see Fig. 2). Participants were encouraged to remain relaxed to facilitate illusory movement perception. Sensitivity to movement illusions was determined in practice trials. If vibration did not elicit any illusion, which is not uncommon [5,34], this experiment was not pursued. Eleven out of twenty-eight participants (3 younger, 8 older) did not experience movement illusions.

2.3. Data processing and analysis

The elbow joint rotation signals were digitized at 100-Hz, and low

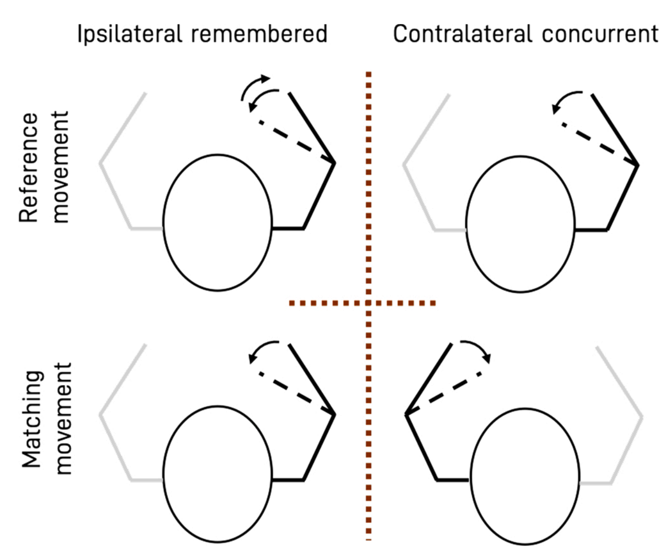

Fig. 1. Schematic of the forearm position matching conditions in a top view representation. The top panel shows the reference movement in two conditions. The bottom panel shows the matching movement when reproduced with the same (ipsilateral) or opposite (contralateral concurrent) arm. Arrows indicate the direction of the movements. Both right and left arm provided the preference. Right arm reference positions are shown here.

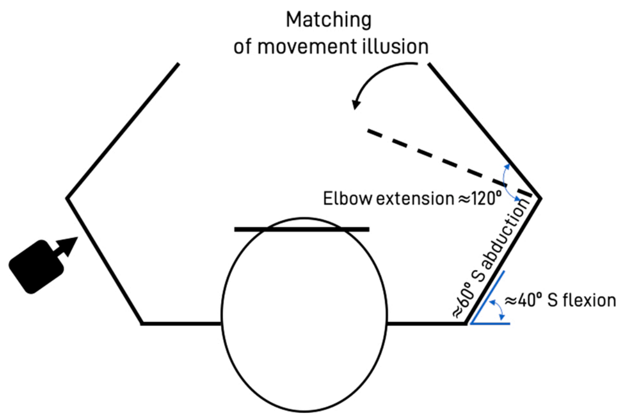

Fig. 2. Schematic of the movement sense testing as viewed from above. Vibration is applied to the distal tendons of either the right or left triceps (left vibration illustrated), while the forearm support was immobilized. The contralateral arm matches the vibration-induced movement illusion concurrently (S = shoulder).

pass filtered with a fourth-order Butterworth filter with a 6-Hz cut-off frequency.

2.3.1. *Position sense*

Absolute (AE) and constant errors (CE) evaluations were relative to the reference movement and quantified over five repetitions of each condition. The AE was calculated as the absolute angular difference between reference and matching positions. The CE was calculated as the direction of the matching error relative to the reference position. Matching position amplitude greater than the reference represented an overshoot while the opposite represented an undershoot. The matching movement time (MT) was also computed. MT was defined as the time between the movement onset and offset, respectively defined as the times at which the elbow movement velocity (differentiated position signal) raised above or dropped below 2.5°/sec. The analysis was stratified. A linear mixed model was conducted to consider the repeated structure of the data. The fixed effects were condition (IR, CC) and matching forearm (right, left). The random effect was the group (younger, older). The model was applied for each dependent variable (AE, CE, MT).

2.3.2. *Movement sense*

The matching movement velocity (MV) was quantified over five repetitions. This velocity was determined by the average of the slopes of primarily continuous movement segments, as defined in Adamo, et al. [5]. A linear mixed model was conducted to consider the repeated structure of the data for MV. The fixed effect was forearm (right, left). The random effect was group (younger, older). The model included data from the 17 participants who perceived movement illusions (11 younger, 6 older). However, the interpretation considers all participants since the more frequent (2.6 times greater) absence of illusion in older adults might result from an aging effect.

Minitab 18.0 was used to perform the statistical analyses. Significance was set at $P \leq 0.05$. To determine which factors influenced the main and interaction effects, Tukey HSD post hoc multiple comparisons were conducted. Student's t-tests were used to distinguish differences between arms or groups. Means ± standard errors are reported.

3. Results

3.1. *Position sense*

The AE corresponding to each condition and matching forearm for both age groups are compared in Fig. 3. The main effect of group ($F_{(25.68)} = 8.73$, $p = 0.007$, 95 %CI [0.333,1.313]) and condition ($F_{(502.82)} = 29.53$, $p < 0.001$, 95 %CI [0.348,0.715]), as well as a group x condition ($F_{(502.82)} = 20.53$, $p < 0.001$, 95 %CI [0.2118,0.5800]) interaction effect were significant. The AE was 1.8 ± 0.3° smaller for the IR than CC condition for older adults ($p < 0.001$) and 2.2 ± 0.5° smaller for older than younger adults in the CC condition ($p < 0.001$).

The CE corresponding to each condition and matching forearm for both age groups are compared in Fig. 4. The interaction effect of matching forearm x group ($F_{(502.10)} = 7.92$, $p = 0.005$, 95 %CI [0.133, 0.688]) was significant. In the IR condition, the CE was 1.3 ± 0.5° greater for the left than the right forearm for older adults ($p = 0.016$). However, the mean difference of -0.2 ± 0.5° between the left and the right forearm was not significant for younger adults ($p = 0.613$). In the CC condition, the CE was 0.9 ± 0.4° greater for the right than the left forearm for younger adults ($p = 0.031$). The mean difference -1.1 ± 0.7° between the

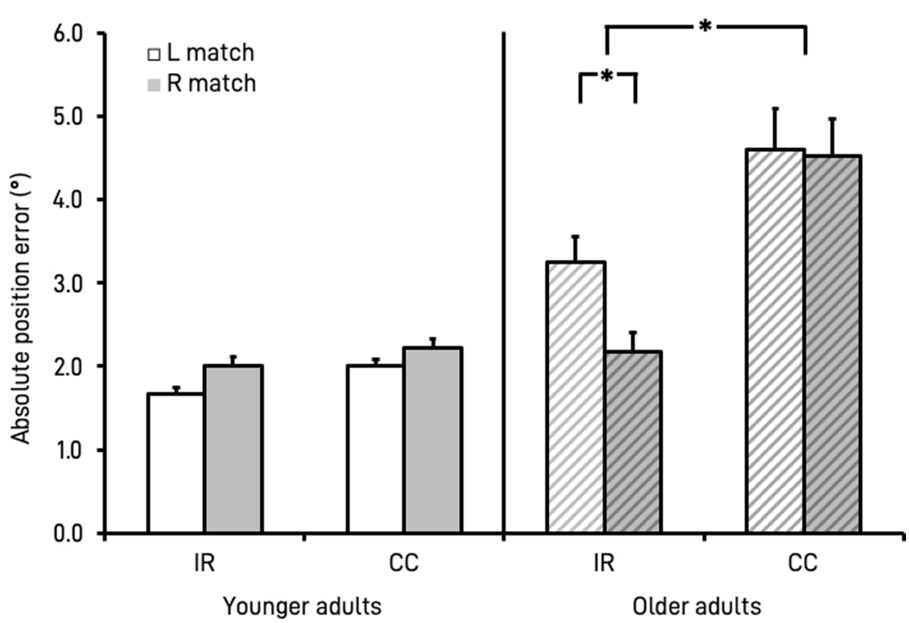

Fig. 3. Mean (+SE) absolute error (degrees) in each matching condition (IR – ipsilateral remembered, CC – contralateral concurrent) for younger adults (n = 14, left panel) and older adults (n = 14, right panel ▨) when matching with the left (□) and the right (■) arms. * $p < 0.05$.

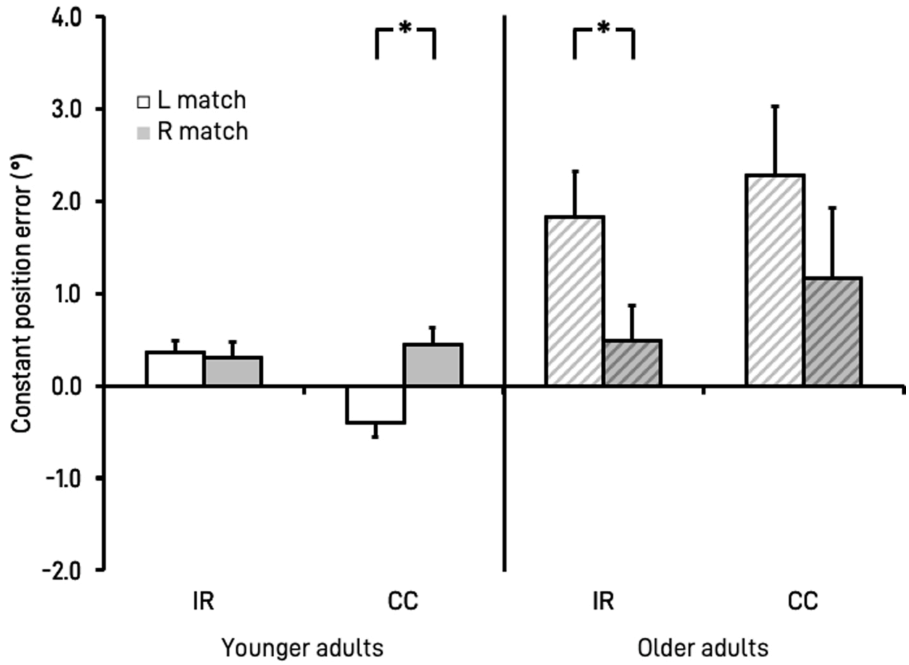

Fig. 4. Mean (+SE) constant error (degrees) in each position matching condition (IR – ipsilateral remembered, CC – contralateral concurrent) for younger adults (n = 14, left panel) and older adults (n = 14, right panel ▨) when matching with the left (□) and the right (■) arms. * p < 0.05.

left and the right forearm was not significant for older adults (p = 0.111).

For MT, the main effect of condition ($F_{(489.83)} = 15.13$, $p < 0.001$, 95 %CI [0.032, 0.099]) was significant. In the IR condition, MT was -0.12 ± 0.06 s slower for the right than the left forearm for younger adults (p = 0.03). However, the mean difference of 0.08 ± 0.06 s between the right and the left forearm was not significant (p = 0.14) for older adults. In the CC condition, the mean differences between the right and left forearms were not significant for younger and older adults (p = 0.66 and p = 0.99, respectively).

3.2. Movement sense

The MV of each matching condition are illustrated in Fig. 5. The main

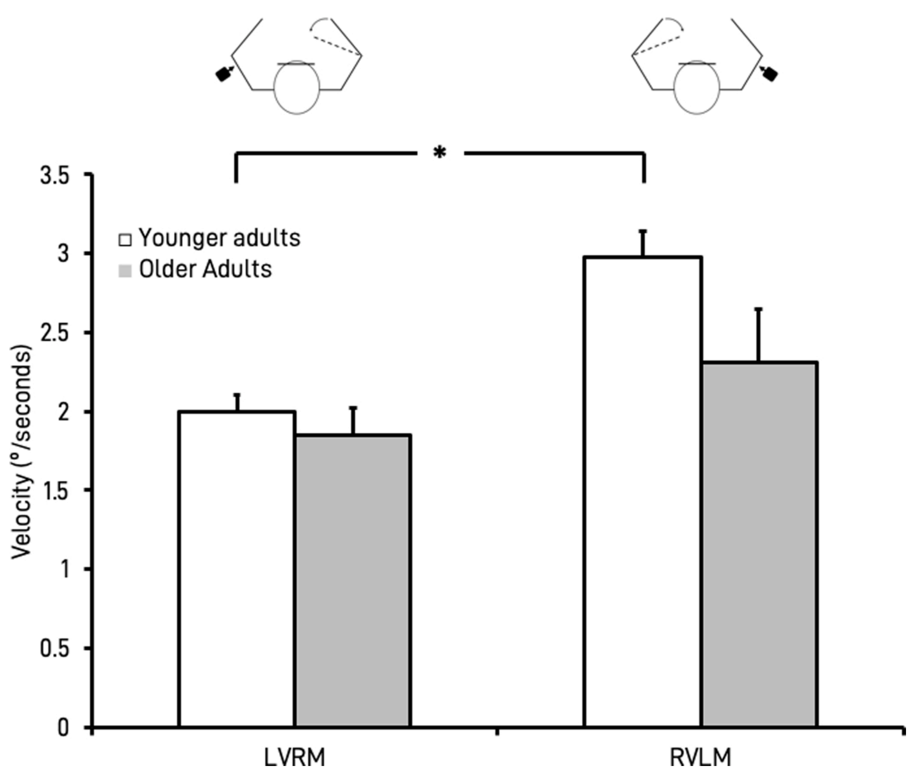

Fig. 5. Mean (+SE) matching velocity for younger adults (n = 11, □) and older adults (n = 6, ■) in the left vibration right match (LVRM) and the right vibration left match (RVLM) conditions. The vibration did not elicit an illiusion of movement for 3 younger adults and 8 older adults. * p < 0.05.

effect of matching forearm ($F_{(376.78)} = 10.89$, $p < 0.001$, 95 %CI [0.138, 0.544]) was significant. For younger adults, MV was 0.9 ± 0.2°/sec greater ($p = 0.007$) for the right vibration left match (RVLM) than the left vibration right match (LVRM) situation. For older adults, MV was not significantly different ($p = 0.45$) between RVLM and LVRM.

4. Discussion

When comparing age groups, position and movement sense degradation with age are indicated by (1) larger absolute position errors, (2) larger errors when matching with the left non-dominant forearm than the right dominant forearm in the IR condition, (3) a disparate asymmetry in the CC condition, translated by no significant position sense asymmetry, (4) perception of a slower velocity of illusory movements, and (5) no significant asymmetry in movement perception. Sensory, motor and cognitive processes may all play a role in the disparity of age-related effects.

4.1. Position sense

The AE was small and similar in both IR and CC conditions for the younger adults, while it was greater in the CC than IR condition for the older adults. This difference is linked to the utilization by the matching arm system of proprioceptive information from the contralateral reference limb in the CC condition [2] and thus requires a comparison between information generated by two not quite similar hemisphere systems [36]. This is further demonstrated by the CE results.

Left-right asymmetry in position matching, indicated by CE differences between forearms in the CC condition, was significant for the younger but not for the older group. Position sense intrinsic asymmetry between the left and right upper limbs can be interpreted as a difference in gain between the right and left hemisphere sensory systems [2,5,23]. For each forearm/hemisphere system, the total gain, as defined in [2], is the product of the gain of each component of the system: perceptual (position information/representation), interhemispheric transfer (in contralateral matching), motor command and muscle. Considering all results concerning proprioception obtained from younger adults, the question is: is the absence of significant asymmetry in older adults an age issue or a paradox? The asymmetry pattern of left undershoot and right overshoot of the opposite-forearm reference observed here, was also found for younger adults in a study using the wrist in an otherwise identical task with an identical shoulder posture [2]. A similar intrinsic asymmetry was also observed for the sense of effort in younger adults performing isometric hand grasp exertions [4,37]. Furthermore, the degradation of muscle proprioception with age was also demonstrated in several studies [3,13,17]. Hence, considering the ensemble of these results, a transformation of asymmetry with age was hypothesized, that could be viewed as an exacerbation, regardless of numerical values decrease or increase.

It was demonstrated [2] that the left undershoot of the right reference position pattern is due to a sensory gain higher for the left than right hand. Such a difference was assumed to reflect the difference in structural representation between the two hands [8,21] as a result of cortical plasticity associated with hand utilization [11,32]. Hence, a number of age-related alterations can contribute to changes in gain. Structural and physiological changes are more pronounced with age (see [9] for review). Furthermore, a reduction in the number of muscle proprioceptors and Ia afferent fibers mediating muscle proprioceptive information occurs with age [39]. In addition, it has been also demonstrated that the degeneration of proprioceptive afferent fibers with age precedes muscle atrophy in mice [42]. Finally, a reduction of the cortical map size and more diffuse mapping of the limb was observed in older rats when compared to younger rats ("the rat model is approved in aging research"), and the degradation of perception was associated with large overlapping of areas [15,38]. In humans, the relative cortical representation of the right hand, but not the left, increases with age [20], which is attributed to more right-hand usage, and the relationship between map size and limb use has been established [10,31].

The degradation of position sense with age confirms the decrease in proprioceptive acuity found previously [3,13,17]. This alteration stems from several mechanisms, including a decrease in muscle stiffness, deterioration of stretch receptors, and the decrease in the number of receptors and Ia afferent fibers, which is a corollary of the muscle mass reduction and thus the number of fibers [39]. The latter may also be a consequence of the degradation of central processing of sensory information [13]. Indeed, the larger effect for the left non-dominant side than the right dominant side in the IR condition, appears congruent with less usage of the non-dominant hand for activities of daily living in older adults [1,3]. Less limb usage leads to the attrition/atrophy of corresponding cortical areas [6,32] and thus a reduction in accuracy, greater for the left non-dominant than the dominant right forearm. In older adults, the increase in bilateral processing indicated by the Hemispheric Asymmetry Reduction in Older Adults (HAROLD) model, which posits a compensatory increase in cognitive processing [7] to maintain acceptable performance, has been shown to apply to motor tasks [26] and to reduce motor asymmetry in older adults [27,30]. This bilateral recruitment process cannot be excluded, but may not be sufficient [33] to compensate for sensory degradations likely affecting more strongly the non-dominant limb.

In sum, the apparent paradox of the overshoot of the left forearm matching the right forearm reference in older adults, when compared to younger adults, can be explained by a significant reduction of the sensory system gain with age and more particularly for the left forearm sensory system. The present results support this hypothesis as they render the absence of asymmetry coherent. Indeed, Martin and Adamo [2,23] argued that the gain of the sensory system was inversely proportional to the size of the cortical map since a smaller cortical size needs to be associated with higher gain than a larger representation. Hence, it is proposed that a gain reduction occurs in both limb/hemisphere systems with age. This reduction could be associated with the remapping and diffuse reorganization of the somatosensory cortex and the reduction of proprioceptive information due to the attrition of muscle proprioceptors and Ia fibers. For the dominant right forearm, the reduction in gain may be less severe due to arm utilization patterns, as plasticity (translated by a lesser decrease in cortical representation in the left hemisphere) is likely competing with the natural structural and neurophysiological attrition effects of aging.

4.2. Movement sense

Movement sense results are also in agreement with the hypothesis that the gain reduction may be less severe in the dominant right forearm due to arm utilization effects. A general decrease in proprioceptive sensitivity in older adults is expressed by a lack of asymmetry and an average movement speed in the RVLM condition, 1°/sec slower (≈ 2 vs. 3°/sec) for older than younger adults, and unsuccessful attempts to elicit movement illusion in 8/14 older, but only in 3/14 younger adults. Besides structural and physiological changes mentioned above, older adults' sensitivity may also be affected by the observed decrease in tissue stiffness, which is a likely consequence of muscle mass loss. This softness reduces mechanical transmissibility to the sensory receptors and thus the number of stretch receptors activated. Hence, in light of our previous work and model [2–5] the age effects can be associated with a broad decrease in sensory gain when compared to younger adults. Nevertheless, the HAROLD model effects [7], observed indirectly by more symmetric movement trajectories in older than younger adults [30] and directly by bilateral activation of the primary motor cortex [27] and sensorimotor areas [41], may also be considered in the absence of asymmetry in the active reproduction of sensory perceptions. However, the extent of the effect associated with this phenomenon may be limited in our sensory tasks since force exertion was quite small, and movement trajectory did not need to be strictly/efficiently controlled. A limitation of the interpretation of these results is the small sample size; however, the behaviors remained consistent.

Finally, degradation of MT with age is well-known. However, in position matching, we observed a strong tendency ($p = 0.055$) towards shorter MT for the older than younger adults and a matching accuracy greater for the younger than older adults. Instructions were to match the reference "displacement," which includes moving at the same velocity. Due to the decrease in proprioceptive sensitivity with age, it may be assumed that to elicit the same perception of "movement"/"displacement speed" when performing the match, the matching movement speed had to be increased to raise the firing frequency of Ia afferents, which encode movement velocity [34,35]. This assumption is also supported by the slower speed of illusion matching movements in older than younger adults, and the increase in final position error since they both stem from the same decrease in sensitivity/acuity, as discussed above. The result also follows the general speed-accuracy tradeoff [12,25], in which the degradation of cognitive processing and sensorimotor noise plays a role. This interpretation is also supported by the position matching result where the matching movement speed was likely slowed down to achieve a more accurate final position.

5. Conclusions

Upper limb proprioceptive asymmetry is reduced with age. This reduction may stem more from a degradation of the sensory system leading to a significant decrease in its gain, than from compensation associated with bilateral cortical activations. The marked decrease in gain with age might explain a transformation of the asymmetry in older adults. Finally, the primarily curvy profile of movements matching the vibration-induced illusions observed in older adults is expected to reflect the decrease in proprioceptive sensitivity.

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CRediT authorship contribution statement

Yadrianna Acosta-Sojo: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Bernard J. Martin:** Conceptualization, Methodology, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors report no declarations of interest.

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