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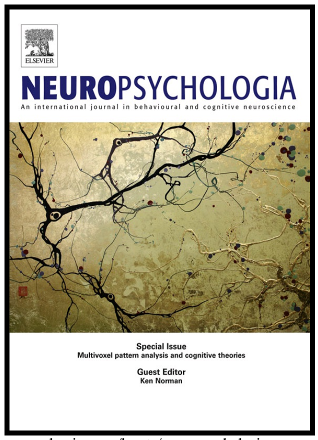

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M. Chancel, C. Landelle, C. Blanchard, O. Felician, M. Guerraz, A. Kavounoudias

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Hand movement illusions show changes in sensory reliance and preservation of multisensory integration with age for kinaesthesia

Chancel M[1,6], Landelle C[1], Blanchard C[2,3], Felician O[4,5], Guerraz M[6], Kavounoudias A[1*].

[1]Laboratoire de Neurosciences Sensorielles & Cognitives (UMR7260), Aix-Marseille Université, CNRS, 3 Place Victor Hugo, 13003 Marseille, France

[2]Division of Clinical Neuroscience, Queen's Medical Centre, University of Nottingham, Nottingham, UK.

[3]Sir Peter Mansfield Imaging Centre, School of Medicine, University of Nottingham, Nottingham, UK.

[4]Aix Marseille Univ, Inserm, INS UMR_S 1106, 13005, Marseille, France

[5]Service de Neurologie et Neuropsychologie, CHU Timone, APHM, 13005, Marseille, France

[6]Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LPNC, 38000 Grenoble, France

***Correspondence:** Anne Kavounoudias, Anne.Kavounoudias@univ-amu.fr

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Abstract

To perceive self-hand movements, the central nervous system (CNS) relies on multiple sensory inputs mainly derived from vision, touch, and muscle proprioception. However, how and to what extent the CNS relies on these sensory systems to build kinesthetic percepts as the systems decline with age remain poorly understood. Illusory sensations of right hand rotation were induced by separately stimulating these three sensory modalities at two intensity levels. A mechanical vibrator applied to the *pollicis longus* muscle, a textured disk for touching, and a visual pattern rotating under the participant's hand were used to activate muscle proprioception, touch, and vision, respectively. The perceptual responses of 19 healthy elderly adults (60-88 yrs) were compared to those of 12 younger adults (19-40 yrs). In the younger group, the three types of stimulation elicited similar kinesthetic illusions at each intensity level applied. The same visual and tactile stimuli elicited more salient and faster illusions in older adults than in younger adults. In contrast, the vibration-induced illusions were significantly fewer, less salient and delayed in the older adults. For the three modalities

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considered, increasing the intensity of stimulation resulted in smaller increases in illusion velocity in older adults than in younger adults. Lastly, a similar improvement in the perceptual responses was observed in older and younger adults when several stimulations were combined and older participants reported more salient illusions than younger participants only in the visuo-tactile condition. This study suggests that reliance on sensory inputs for kinesthetic purposes is profoundly reshaped with aging. The elderly may rely more on visual and tactile afferents for perceiving self-hand movements than younger adults likely due to relatively greater muscle proprioception degradation. In addition, multisensory integration seems preserved but not enhanced to compensate for the global decline of all sensory systems with age.

Keywords: Kinaesthesia – Multisensory perception Aging - Illusion – Muscle proprioception – Touch - Vision

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1. Introduction

To perceive self-hand movements, the central nervous system (CNS) relies on multiple sensory information mainly derived from vision, touch, and muscle proprioception. The contribution of each these sensory modalities has been advantageously studied in younger adults using specific stimuli inducing illusion of self-body movements (see review Kavounoudias 2017). That muscle proprioception plays a crucial role in kinesthesia is attested by a large amount of studies showing that applying vibration to motionless subjects' muscle tendons selectively activates muscle receptors (Roll & Vedel 1982) and induces illusory movements of the body in the direction of the lengthening muscle (Albert et al., 2006; Goodwin et al., 1972; Blanchard et al. 2011; 2013). In addition, the visual system also contributes to the sense of movement, as evidenced by the vection phenomenon, i.e., a kinesthetic percept elicited by a visual moving scene scrolling in front of a participant (Brandt and Dichgans 1972; Guerraz and Bronstein 2008) or under one's limb (Blanchard et al., 2011, 2013; Chancel et al., 2016a, Tardy-Gervet et al., 1984). Visually induced illusions of an arm movement were also observed during reflection in the mirror of the passively displaced contralateral arm, the so-called mirror paradigm (Ramachandran and Altschuler 2009; Guerraz et al. 2012; Chancel et al. 2016b). Touch, like vision, also conveys kinesthetic information since illusions of self-body movements can be elicited using a tactile stimulus rotating under the palm of the hand (Blanchard et al. 2011, 2013; Chancel et al. 2016a) and illusory finger movement sensations have also been reported to occur in response to stretching of the skin over the metacarpophalangeal joints of the hand (Collins et al., 2000).

Ageing is associated with a decline in all these sensory systems at multiple levels from the peripheral receptors to the central processing of sensory afferents. Age-related changes in the optics of the eye and in the neural processing of visual inputs have been well documented (see reviews Andersen, 2012; Owsley, 2011). The deterioration of the somatosensory system, including touch and proprioception, has also been well described in numerous neurophysiological studies from peripheral sensors to central structures. (see reviews Goble et al., 2009; Ribeiro and Oliveira, 2007; Shaffer and Harrison, 2007). In the CNS, global structural alterations such as a reduction of grey matter volume (Good et al., 2001) including sub-cortical regions like the thalamus (Serbruyns et al., 2015) and of the white matter especially the corpus callosum (Lebel et al., 2012) with advancing age have been clearly shown to occur in the human brain.

The extent to which peripheral and central sensory damages lead to kinesthetic alteration, particularly the ability to perceive hand movements, is therefore relevant to ask. In fact, whereas alteration in fine motor hand dexterity has been well established in the elderly, less attention has been paid to their kinesthetic hand functions. The functional kinesthetic deficits observed in older individuals has been mainly investigated using passively imposed movements at the lower limbs, showing a decreased ability to detect a passive movement at the knee and the ankle (see review Goble et al. 2009). Hay et al. (1996) investigated illusory movements induced by muscle vibration in elders and reported that after 60 years, whole-body tilt illusions induced by ankle muscle vibrations in standing subjects are reduced in amplitude. Regarding visual motion perception, studies have shown that older observers are less able to perceive the direction of self-motion from optical flow (Haibach et al., 2009; Warren et al., 1989) than younger observers. As for the kinesthetic contribution of touch, it has not been studied so far to our knowledge but it could be altered since the ability to detect a tactile stimulus applied to the surface of the skin decreases with age (Desrosiers et al., 1999).

Most of the above mentioned studies investigated alterations of each sensory modality in isolation. However, it is well known that kinaesthesia is by nature multisensory, each actual limb movement giving rise to multiple concomitant sensory inputs. Several studies have

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stressed the need to integrate convergent cutaneous, muscular and visual inputs to properly assess limb positions and movements in healthy younger adults (Aimonetti et al., 2012; Blanchard et al., 2011, 2013; Chancel et al., 2016b; Cordo et al., 2011; Guerraz et al., 2012; Tardy-Gervet et al., 1986; van Beers et al., 2002). In addition, it is generally admitted that the different sensory modalities do not contribute equally to these integrative mechanisms. In accordance with the Bayesian framework, many modelling studies have provided evidence that the multisensory estimate of an event such as a self-body movement is given by the reliability-weighted average of each single-cue estimate (Chancel et al., 2016a; Fetsch et al., 2009; Prsa et al., 2012; Reuschel et al., 2009; Vidal and Bülthoff, 2010). This Bayesian like mechanism seems to rule multisensory integration for elderly as well, even when facing sensorimotor decline. Indeed, Bayesian optimal adaptation between sensory reliability and a priori information efficiently describes age-related changes in visuomotor behavior, both for an object tracking task (Sherback et al., 2010) and multisensory reflexes such as the vestibulo-ocular reflex (Karmali et al., 2018). This also holds true regarding the integration of visual and haptic cues in a subjective vertical perception task, which follows the same Bayesian principles in younger and older individuals (Braem et al. 2014). On the other hand, during a navigation task requiring visual and/or self-motion cues, Bates & Wolbers (2014) observed that performances of the older adults were sub-optimal since they relied less than optimally predicted on visual information. Therefore, the question remains as to whether multisensory integration rules regarding self-body perception survive during aging. In particular, it is of interest to determine to what extent age-related declines in the sensory modalities like vision, muscle proprioception and touch are associated with a sensory reweighting to build a consistent percept and/or whether enhancing multisensory integration could at least partly overcome sensory decline.

Outside the field of kinesthesia, numerous studies have recently shown that, despite age-related degradation in single sensory systems, multisensory integration processing does not seem to be diminished but rather enhanced (see reviews, Freiherr et al., 2013, Kuehn et al., 2017, de Dieuleveult et al., 2017). This has been largely reported in studies using visual-auditory paradigms (de Boer-Schellekens and Vroomen, 2014; Diaconescu et al., 2013; Diederich et al., 2008; Hugenschmidt et al., 2009; Laurienti et al., 2006; Mahoney et al., 2012; Peiffer et al 2007). For instance, Laurienti and colleagues (2006) found in an audiovisual discrimination task that despite larger response times for unisensory targets in older adults compared to younger adults, the gain of the bisensory responses observed when the two types of stimuli were simultaneously presented was greater for the older group than

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the younger one. These results suggest at first glance that older individuals may take greater advantage of redundant multisensory information (same content conveyed by various sensory inputs) than younger adults by increasing the efficiency of integrative processing. However, when the different stimuli are incoherent in time or space, older people always integrate them inappropriately, while young adults correctly segregate the different messages, considering that they do not originate from the same event. Consequently, as reported for instance by Poliakoff and coll (2006), older adults tested in a crossmodal selective attention task have more difficulty in focusing on one sensory modality while ignoring a concomitant distractor presented in another modality. Therefore, the facilitation of multisensory integration in older adults may be an advantage when stimuli belong to the same event, but become a disadvantage when information from multiple sources should not be associated (Poliakoff et al., 2006; Setti et al., 2011). As to studies investigating multisensory integration in sensorimotor tasks, they rather support the general, though controversial, hypothesis that the elderly would have more difficulty in quickly adapting the weighting of the different sensory information to sudden environmental changes (Allison et al 2006; Eikema et al. 2014; Horak et al., 1989; Teasdale and Simoneau, 2001).

Therefore, although the beneficial impact of concomitant multisensory inputs for kinesthetic purposes in healthy younger adults is now well documented (Blanchard et al., 2013; Collins et al., 2000), it is still unclear whether age-related changes occur in the way the CNS optimizes central integrative processing to overcome sensory system declines for kinaesthesia. In a previous study performed in younger adults, we quantified hand movement illusions induced by three types of stimulation (muscle proprioception, vision and touch) and the improvement in the perceptual responses elicited by combining congruent multisensory stimulation (Blanchard et al., 2013). The present study aimed to investigate whether and how ageing impacts the ability of the elderly to perceive self-hand movements based on multisensory feedback from these three different modalities. In particular, we addressed whether sensory reweighting occurs and/or whether the multisensory processing of different kinesthetic cues is altered in elders when perceiving self-hand movement.

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2. Method

2.1 Participants

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Nineteen right-handed elderly individuals aged 60 to 88 years (4 men; mean: 71 ± 7 yrs of age) with normal or corrected-to-normal vision took part in the experiment. None of them had history of neurological or sensori-muscular diseases. A Minimum Mental State (MMS) score of 26 and preserved daily life autonomy were required to participate in the study. Daily life autonomy was assessed through a brief interview before the experimental session during which we ensured that the participants will come by their own means to the laboratory, come back for a second session, which required a good ability to move and manage a schedule. Thirteen right-handed younger adults also participated to this study (5 men; mean: 29 ± 10 yrs of age) and met the same inclusion criteria. All participants gave a written informed consent, conforming to the Helsinki declaration, and the experiment was approved by the local ethics committee (CCP Marseille Sud 1 #RCB 2010-A00359-30). All participants were financially compensated for their time.

2.2 Stimuli (Fig. 1A)

Three kinds of stimulation were applied to the right hand of each participant.

The muscle proprioceptive stimulation was a lab-customed mechanical vibrator and consisted of a biaxial DC motor with eccentric masses, forming a cylinder that was 5 cm long and 2 cm diameter. A 0.5-mm peak-to-peak mechanical vibration was applied to the right *pollicis longus* tendon at two constant frequencies: 30 or 60Hz. Low-amplitude mechanical vibration applied on a muscle tendon is well known to specifically activate muscle spindle primary endings, as evidenced through microneurographic recordings (Roll and Vedel, 1982; Fig. 1B).

The tactile stimulation was delivered by a motorized disk (40 cm in diameter, developed by Rematique company, Saint-Etienne, France) covered with cotton twill (8.5 ribs/cm). This material was used because a microneurographic study showed that it can efficiently activate cutaneous receptors without reaching a saturation plateau within the velocity range used in the present study (Breugnot et al. 2006). The disk rotated under the participant's right hand in a counterclockwise direction at two constant velocities: 10 or 30 °/s (Fig. 1C).

Visual stimulation consisted of a projection of a black and white pattern on the disk. To give the participant the feeling that the pattern was moving in the background, i.e., under his/her hand, a black mask adjusted to the size of each participant's hand was included in the

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video that prevented the pattern from being projected onto the participant's hand. The pattern was rotating around the participant's right hand with a constant counterclockwise angular velocity set to 10 or 30 °/s (Fig. 1D).

These three types of stimulation were delivered for 9s either separately (unisensory conditions) or simultaneously (multisensory condition) at two intensity levels (low or high). The intensity levels of the three stimuli were chosen based on a previous experiment performed in younger adults showing that these stimulation intensities of the three sensory modalities efficiently induced similar illusions of clockwise self-hand rotation (Blanchard et al., 2013). The stimuli were delivered using a National Instruments card (NI PCI-6229) and a specifically designed software implemented in LabView (V.2010).

Figure 1 (2 columns) (color online only)

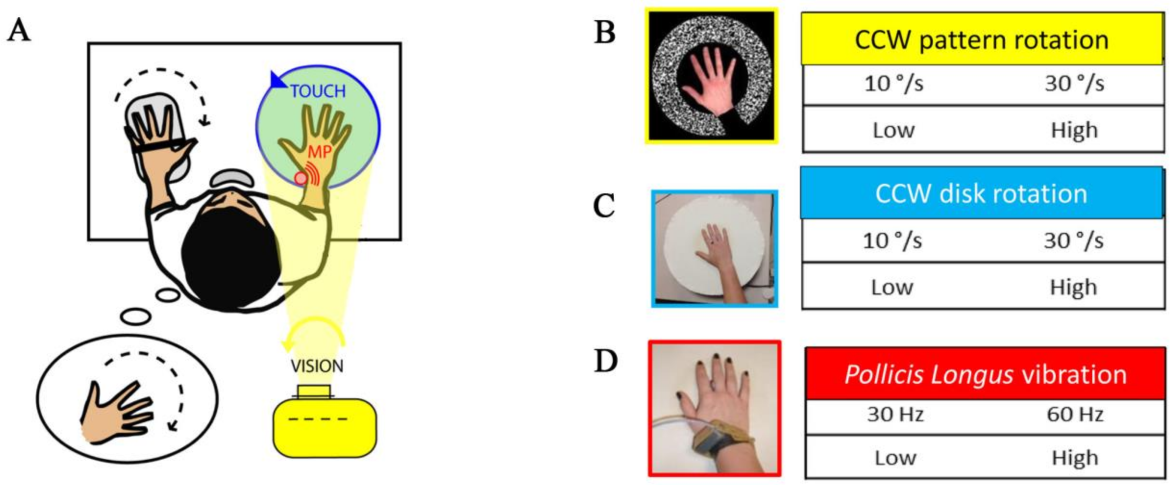

Figure 1: Experimental setup (A) and stimulation devices (B-D) applied at two intensity levels (Low or High) on the participant's right hand. *B*: visual pattern displayed by a video projector (see *A*). *C*: the textured disk used as tactile stimulation. *D*: mechanical vibrator applied onto the tendon of the pollicis longus muscle of participants' right wrist. Participants held a potentiometer in their left hands to copy on line any illusory sensation they perceived in their rights hands. Angular deviation of the potentiometer was recorded. MP: muscular proprioception; CCW: counterclockwise.

2.3 Procedure

Participants sat on an adjustable chair in front of a fixed table with the arm rests immobilizing the participant's forearms, his/her left hand resting on the table and his/her right hand on the motorized disk. A small abutment in the disk center placed between the index and middle fingers kept the right hand from moving with the disk when it rotated. Head movements were limited by a chin- and chest-rest allowing participants to relax and sit comfortably. The experiment occurred in the dark, and participants wore headphones to block external noise. Shutter glasses were also worn to partially occlude the participant's visual field, reducing it only to the disk surface. Although the experiment was carried out in darkness, participants were asked to close their eyes at the beginning of each trial, except during the conditions involving visual stimulation (visual alone, visuo-proprioceptive, visuo-tactile and trimodal combinations). Having their eyes open may have impacted upon their perception even in absence of visual meaningful content (Brodoehl et al., 2015), therefore we ensure the instruction of closing their eyes was carefully respected when required.

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2.3.1 Pre-test phase

Before proceeding to the main study, participants were required to complete a pre-test task to ensure that they were able to estimate and copy a movement passively imposed. Indeed, the experimental task required the participant to copy with the left hand an illusory movement perception of the right hand. It was therefore necessary to first assess the capacity of the elderly participants to copy with his/her left hand an actual passively imposed movement of his/her right hand. During the pre-test, participants' right hand was attached to a mechanical disk and passively rotated in the clockwise direction, either at 5 °/s or at 10 °/s. These velocities of movement were chosen because we know from previous studies performed in younger adults (Balnchard et al., 2013) that the unisensory stimulations used in the main experiment induce illusory clockwise hand rotations perceived with a velocity of 5 °/s and 10 °/s approximatively for the low and the high intensity, respectively. Participants had to copy on real time the movement imposed on their right hand with their left hand attached to a linear potentiometer (50 kΩ, 1W) mounted on a rectangular plate. By turning the hand, the axis of the potentiometer in rotation made it possible to record the angular deviation of the wrist of the participant. It was used to measure the latency and velocity of the left hand movement. The velocity error of the movement copy was computed as the difference between velocities of the right hand/passive movement and the left hand/reproduction movement. The performances of participants of the older group were compared to those of the younger group as a reference. No participant of the older group displayed a mean velocity error more than

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two standard deviations away from the mean reference value obtained for the younger group. We also verified that the latencies before the beginning of the left-hand movement were not significantly different between the younger and older groups. This test was conducted to ensure that the differences observed between older and younger individuals in the present study, if any, were not due to an inability of the elderly to reproduce a movement of one hand with the other hand.

2.3.2 Experimental test

Participants included in the experiment then underwent a training session composed of 15 trials of each stimulation condition to familiarize them with the stimuli and the reproduction task.

Then, the experimental sessions were run, which included seven stimulation conditions randomly intermixed: three unisensory conditions (muscle proprioceptive P, tactile T, visual V), three bisensory conditions (proprio-tactile PT, visuo-proprioceptive VP, visuo-tactile VT) and one trisensory condition (visuo-tactilo-proprioceptive VTP). During each stimulation condition, participants were asked to copy with their left hand and in real time any illusory movements they perceived. At the end of each trial, participants were also asked to rate the saliency of the illusory movement they perceived from 0 (“No sensation of movement was felt”) to 4 (“A clear sensation of movement was perceived, as if it was real”). The subjective rating was given orally and the experimenter wrote it down by hand. Each session consisted of six repetitions of the seven stimulation conditions performed at two intensity levels (7 conditions * 2 intensities * 6 trials). Each trial lasted 10 s (1 s of rest and 9 s of stimulation). A total of three sessions of 15 minutes were performed on two different days (at the same time during the day).

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To assess the spatio-temporal characteristics of the illusions, we asked participants to copy in real time with their left hand attached to a potentiometer any perceived movements of their right stimulated hand. To facilitate the matching task, the axis of the potentiometer was collinear with the left wrist axis. Participants were asked to pay specific attention to the latency and the velocity of the perceived movement they had to copy. The potentiometer data were sampled at 1 kHz.

Analogic signals were recorded using a National Instruments card (NI PCI-6229) piloted with in-house software implemented in LabView (V.2010). Regardless of the

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experimental condition, the stimulation started 750 ms after the onset of the data acquisition period and lasted for 9 s.

2.4 Data and statistical analysis

All the variables used in this study are gathered in Table 1 together with the type of statistical analysis performed. For binary or ordinal dependent variables, or when continuous dependent variables did not satisfy normality and variance homogeneity hypotheses, non-parametric statistical analyses were performed (Mann-Whitney or Wilcoxon tests). Otherwise, continuous dependent variables were analyzed using three-way mixed-design ANOVAs to assess the main effects and interactions of age, modality (P, T, V), and intensity (Low, High) on the participants' illusions. These mixed-design analyses allowed us to take into account for the variability within and between subjects, by means of fixed (age, modality and intensity) and random effects (subject), respectively. When interactions between fixed factors were significant, LSD Fisher post-hoc tests were performed. For all statistical analyses, the level of significance was corrected for multiple comparisons using the Bonferroni's correction. In the text we reported corrected p-values (i.e. p-values uncorrected multiplied by the number of comparisons) and we considered the result to be statistically significant at the corrected p value < .05.

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Table 1: Summary of the analyzed variables in the present study.

	Dependent Variable	Type	Collected data	Normality	Test for variance homogeneity (Fligner-Killen)	Statistical Analysis
	Occurrence	Binary	Oral report (Yes/No)	No	-	Mann-Whitney
Unisensory stimulation	**Saliency**	Ordinal	Oral report (0 to 4)	No	-	Mann-Whitney
	Latency	Continuous	Potentiometric data	Yes	Yes	mixed design ANOVA
	Velocity	Continuous	Potentiometric data	Yes	Yes	mixed design ANOVA
	RVI	Continuous	Ratio between potentiometric data	Yes	Yes	mixed design ANOVA
Multisensory stimulation	**Saliency**	Ordinal	Oral report (0 to 4)	No	-	Mann-Whitney
	Latency	Continuous	Potentiometric data	Yes	Yes	mixed design ANOVA
	Velocity	Continuous	Potentiometric data	Yes	Yes	mixed design ANOVA
	RVI	Continuous	Ratio between potentiometric data	Yes	No	Mann-Whitney
	MSI_Velocity	Continuous	Ratio between potentiometric data	No	Yes	Mann-Whitney Wilcoxon

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2.4.1 General assessment of stimulation

To assess the general efficiency of the stimulation, two measurements were used: the occurrence and the saliency of the illusions.

The occurrence of the illusions, i.e., the percentage of illusory hand movements perceived by the participants with respect to the number of trials for each stimulation condition, were computed for the two levels of intensity of each stimulation tested.

The degree of saliency of the illusion sensations was also assessed: participants were asked to rate the vividness/clarity of their illusions on an analog scale ranging from 0 ("No sensation of movement was felt") to 4 ("A clear sensation of movement was perceived, as if it was real") after each trial. Note that the saliency index was independent of the velocity of the perceived illusion as a high saliency may coincide with a slow illusory movement. This allowed us to verify that the participants had a sufficiently clear perception of the movement they had to reproduce, whatever its velocity.

For each stimulation condition (unisensory and multisensory conditions), Mann-Whitney tests were used to compare the occurrence and saliency indexes between younger and older individuals.

2.4.2 Potentiometric data

For each trial, the angular deviation recorded from the potentiometer was first centered on the mean initial hand position measured during the 750-ms phase prior to the stimulation onset. The direction, latency, and mean velocity of the illusions of the 32 participants were extracted from the centered angular data. The response latency (ms) was automatically determined at + 2 standard deviations (SD) above the mean pre-stimulus level. This arbitrary threshold helped us to accurately determine the start of subject left-hand reproduction, although a systematic check by the experimenter was carried out to verify the validity of the automatic processing. The velocity of the illusion (°/s) was calculated from the onset of the illusion up to the maximum angular deviation as measured with the potentiometer using the least square method to obtain a linear regression of the data.

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Effects of unisensory and multisensory conditions have been analyzed separately. First, age-related differences between illusions induced by the three unisensory conditions (P, T or V) were investigated. Mean latencies and velocities of the illusions were compared using three-way mixed-design ANOVAs to assess the main effects and interactions of age (Young, Old), modality (P, T, V), and intensity (Low, High) on the participants' illusions followed by post-hoc tests corrected for multiple comparisons when interactions were significant (Table 1).

Because we found a significant interaction between the intensity of stimulation and the age on illusion velocities, another index was computed a posteriori to further estimate the participant's ability to encode the increase in stimulation intensities: we computed the rate of velocity increase (RVI), which is the percentage of increase in illusion velocity between the high and low levels of stimulation, as described by the following equation:

$$RVI = \frac{Velocity(high) - Velocity(low)}{Velocity(low)} \times 100$$

For each unisensory stimulation, Pearson correlation coefficients were calculated to test whether individual RVI values correlated with the age of the participants within the older group.

Age-related differences between illusions induced by the multisensory conditions were also examined. As for the unisensory conditions, mean latencies and velocities of the illusions were compared using three-way mixed-design ANOVAs to assess the main effects and interactions of age, modality (PT, VP, VT, VTP), and intensity (Low, High) on the participants' illusions followed by post-hoc tests corrected for multiple comparisons (Table 1).

In addition, the proportional enhancement or depression of the multisensory responses over the best unisensory response was computed for each participant using the multisensory index (MSI) as defined by Stein et al. (2009):

$$MSI = \frac{Multisensory\ velocity - highest\ unisensory\ velocity}{highest\ unisensory\ velocity} \times 100$$

A positive MSI value reflects a perceptual benefit in the multisensory condition over the best unisensory condition. To test whether multisensory integration occurred in all multisensory

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conditions, the MSIs were first compared to 0 using one-sample Wilcoxon tests for each group independently. Then, to test whether older adults took greater advantage of multisensory information as suggested by previous studies in the literature (see Introduction), the MSI values obtained in each multisensory condition were compared between the younger and the older groups using Mann-Whitney tests.

3. Results

3.1 Unisensory stimulation: comparisons within and between groups

As expected, all the illusions were oriented in the counter-clockwise direction, whatever the stimulation condition applied (Fig. 2).

Figure 2 (2 columns) (print color)

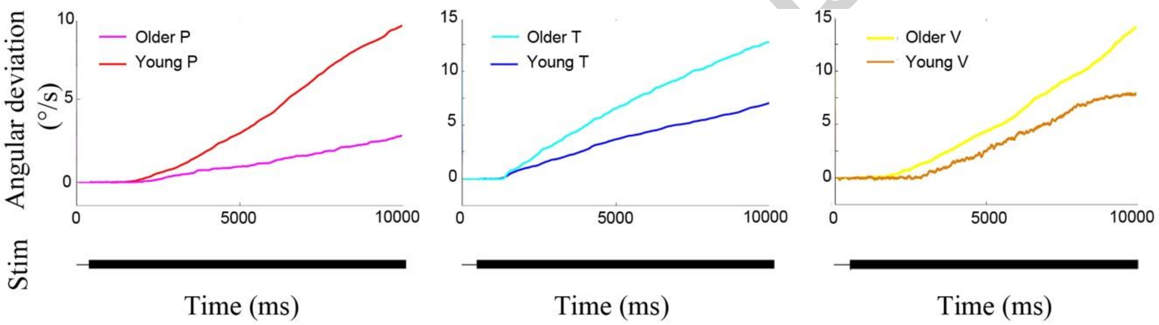

Figure 2: Typical individual data from an older and a younger participant during unisensory proprioceptive (left panel), tactile (middle panel) or visual (right panel) conditions applied at a high intensity level.

At the bottom : Timing of the stimulation (Stim) over the 10,000 ms-duration of the trial; At the top: Potentiometric recordings showing clockwise angular deviations (°/s) copied on line with the left hand by the two participants; Note that although the intensity of stimulation was the same for the two participants, the younger participant has a stronger proprioceptive illusion compared to the older participant; conversely, the perceptual responses elicited by the tactile or the visual stimulation were greater in the older than in the younger participant.

3.1.1 Illusion occurrence

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To obtain a rough assessment of the efficiency of the stimulation applied on both groups, the percentage of occurrence of the movement illusions among the 6 trials performed per condition at each intensity was computed. All the stimulation conditions, except the proprioceptive stimuli, gave rise to an illusory perception of movement in more than 90 % of the trials in the older participants and 95% of the trials in the younger group (Table 2).

When comparing groups using Mann-Whitney statistical tests, a significant difference was found in the occurrence of the proprioceptive illusions that dropped down to 61 % and 74 % in the older group compared to the 97 % and 99 % in the younger group for the low (p = .003) and high (p = .019) stimulation intensity, respectively (Table 2). Conversely, tactile illusions were significantly more frequently evoked in the older group (100%) than in the younger group (95%) at the low intensity (p = .03). More precisely, four older participants and one younger adult did not feel any illusion when a low-intensity proprioceptive stimulation was applied, and one of these older participants did not feel any illusion when a high-intensity proprioceptive stimulation was applied.

Table 2: Occurrence of illusions (% mean ± SD) and subjective rate of the illusion saliency (mean ± SD) for the three unisensory conditions (P, T, V) at two intensity levels in the older and younger groups. Statistics are between-groups comparisons using Mann-Whitney tests. * $p < .05$; ** $p < .01$; *** $p < .001$.

		ILLUSION OCCURRENCE (%)				**ILLUSION SALIENCY**			
		Mean ± SD		**Young vs. Old**		**Mean** ± SD		**Young vs. Old**	
		Young	**Old**	**U**	***p***	**Young**	**Old**	**U**	***p***
Low Intensity	**P**	97 ± 7	61 ± 39	196	.003**	1.96 ± 1.1	1.49 ± 1.3	91.5	.42
	T	95 ± 8	100 ± 0	95	.03*	2.00 ± 0.5	3.33 ± 0.8	13	< .001***
	V	98 ± 5	91 ± 19	141	.3	3.21 ± 0.6	3.08 ± 1.1	71	.80
High Intensity	**P**	99 ± 4	74 ± 36	174	.019*	2.85 ± 0.4	2.00 ± 1.3	103.5	.14
	T	97 ± 7	97 ± 6	121	.9	2.19 ± 0.7	3.45 ± 0.7	15	.001***
	V	98 ± 5	93 ± 14	146	.2	3.08 ± 0.7	3.11 ± 1.1	67	.65

3.1.2 Illusion saliency (Table 2)

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The illusion saliency measures the clarity with which the participant perceived the illusion, regardless of its kinematic components (latency and velocity). On a scale from 0 to 4, the average subjective ratings (± SD) are reported in the Table 2 for both the younger and older groups.

No significant difference was found between the two groups for the saliency index, except for the tactile illusions (low and high intensities), which were perceived as more salient by the older participants compared to the younger participants (Mann-Whitney tests $p \leq .001$).

3.1.3 Illusion latencies (Fig.3)

To avoid biases (over-weighting in the mean due to maximal value of 9 000 ms), trials for which the participants felt no illusion were removed from this analysis.

We examined the impact of aging on the latency of the perceived illusions, and whether this impact differed depending on which sensory modality was stimulated (proprioception, touch, or vision) at which intensity (Low or High). The three-way mixed ANOVA showed a main effect of age [$F(1, 29) = 16.68$, $p = .0003$, $\eta^2 = 0.36$]: for the three unisensory conditions and the two intensity levels considered, younger participants reported their illusory sensations earlier with a mean ± SD latency of 1008 ± 654 ms compared to older individuals who had longer mean ± SD latency of 2773 ± 1841 ms.

As shown in Figure 3, a significant interaction between age and modality was observed [$F(2, 58) = 6.39$, $p = .0031$, $\eta^2 = 0.18$]. In the younger group, post hoc analysis showed that there were no significant differences regarding the latencies between any of the three stimulated sensory modalities (P vs T: $p_{corr}= 1$; P vs V: $p_{corr}= 1$; T vs V: $p_{corr}= 1$; see Table 7 in supplementary data). Interestingly, the mean illusion latencies in the older group for proprioceptive stimulation were significantly longer than for visual stimulation and even longer compared to tactile stimulation (P vs V: $p_{corr}= .008$; P vs T: $p_{corr}< .0001$), while the latencies did not significantly differ between the tactile and visual conditions (T vs P: $p_{corr}= .60$). There was no significant difference between older and younger groups concerning the latencies in response to tactile and visual stimulation (T: $p_{corr}= 1$; V: $p_{corr}= .34$; Fig. 3) while for the proprioceptive stimulation, the latency in the older group was significantly longer than in the younger group ($p_{corr} < .0001$).

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A significant main effect of intensity was observed for the three unisensory stimuli, i.e., latencies were on average longer in response to low intensity than to high intensity [$F(1, 29) = 7.16$, $p = .012$, $\eta^2 = 0.20$] with no significant interactions between intensity * age [$F(1, 29) = 0.29$, $p = .59$, $\eta^2 = 0.009$] or intensity * modality [$F(2, 58) = 0.31$, $p = .74$, $\eta^2 = 0.01$] nor between age* modality * intensity [$F(2, 58) = 1.62$, $p = .21$, $\eta^2 = 0.05$].

Figure 3 (1 column) (print color)

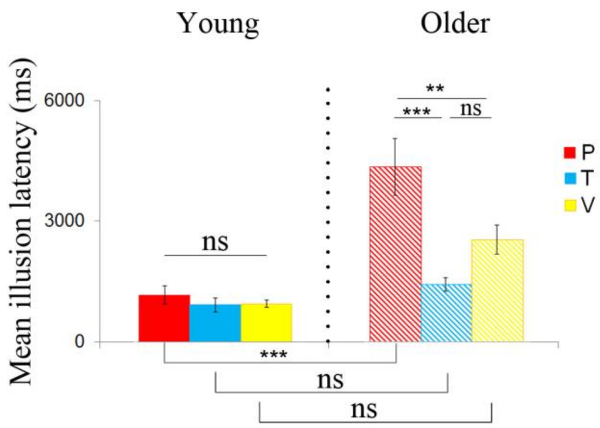

Figure 3: Mean illusion latencies (± SEM) for young (solid fill) and older (striped fill) participants in response to muscle proprioceptive (P, red), tactile (T, blue) and visual (V, yellow) stimuli for the two stimulation intensities confounded. ns: non-significant $p_{corr} > .05$; *: $p_{corr} < .05$; **: $p_{corr} < .01$; ***: $p_{corr} < .001$ (p corrected for multiple comparisons)

3.1.4 Illusion velocities (Fig. 4)

We compared the perceived velocity of the movement illusion between the two age groups, and examined how this age-related differences varied depending on the stimulation condition and its intensity.

Significant differences were observed between the two age groups in the velocities of the illusions [main effect of age $F(1, 30) = 8.06$, $p = .008$, $\eta^2 = 0.21$].

Increasing the stimulation intensity led to a faster perceived illusion in both younger and older groups all modalities confounded [Main effect of intensity: $F(1, 30) = 45.36$, $p <$

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.0001, η^2 = 0.60] with no significant interaction between intensity and age [F(1, 30) = 0.33, p = .57, η^2 = 0.011] or between intensity and modality [F(2, 60) = 0.07, p = .93, η^2 = 0.049].

Moreover, the effect of age was significantly different depending on the stimulated modality [Interaction age * modality F(2, 60) = 17.7, p < .0001, η^2 = 0.37] and on the intensity of stimulation [Interaction age * modality * intensity F(2, 60) = 5.92, p = .004, η^2 = 0.16]. Post hoc analysis showed that as previously observed for the latencies, no significant difference was observed in the illusion velocities between the stimulation conditions (P, T and V) at the two stimulation intensities within the younger group. On the contrary, in the older group, tactile illusions were perceived faster than the visual illusions, and both were faster than proprioceptive illusions for the low and the high intensities of stimulation (p_{corr}< .0001; Fig. 4). Interestingly, the illusion velocity for the tactile stimulation was significantly greater for the older group compared to the younger group at both intensities (Old > Young: T_{Low}, p_{corr} = .027; $T_{High,}$ p_{corr} = .007) while the visual and proprioceptive illusions did not significantly differ on this parameter between the two groups (p_{corr} > .05).

Note that for both groups, stimulation at the higher intensity always gave rise to faster illusions than for the lower ones for all stimulation conditions except for the proprioceptive stimulation in the older group (P_{low} vs P_{high}: p_{corr} = .27). The complete statistical table of these post-hoc tests can be found in the supplementary data (Table 8).

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Figure 4 (1 column) (color online only)

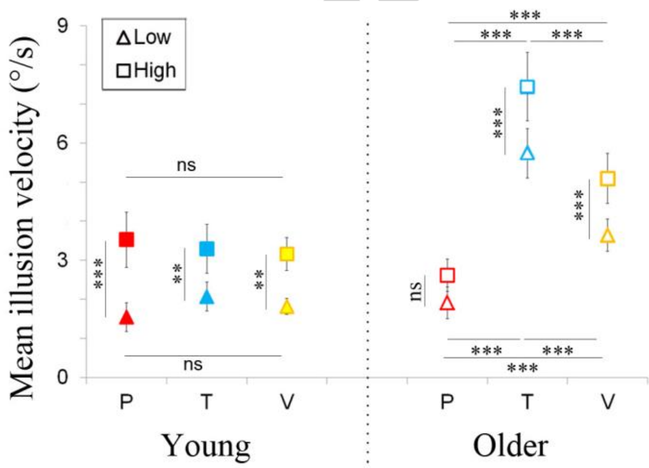

Figure 4: Mean illusion velocity (± SEM) perceived by the young (solid fill) and older (solid line) participants in response to muscle proprioceptive (P, red), tactile (T, blue) and visual (V, yellow)

stimulations at low (triangle symbol) and high (square symbol) intensities. ns: non-significant $p_{corr} > .05$; *: $p_{corr} < .05$; **: $p_{corr} < .01$; ***: $p_{corr} < .001$ (p_{corr} : p corrected for multiple comparisons)

.

In order to investigate the impact of increased intensities of stimulation in both groups independently of how fast the illusions were perceived, we computed the rate of velocity increase (RVI). The RVI is the percentage of illusion velocity increase between the high and low stimulation intensities. On average, for the three unisensory conditions, RVI was greater in the younger group than in the older group for all stimulation conditions considered [Main effect age: $F(1,25) = 7.599$, $p = .011$, $\eta^2 = 0.23$, Interaction age * modality $F(2,50) = 1.98$, $p = 0.15$]. Indeed, with respect to the illusion velocity perceived at the low intensity level, the increase in illusion velocity between the low and the high stimulation intensity was greater in the younger (Mean RVI 102%) than in the older group (Mean RVI 44 %).

Interestingly, as shown in Figure 5, for muscle proprioception stimulation, the RVIs were inversely correlated with age in the older group (Pearson $r = -0.70$, $p = .004$) but not in the younger group ($r = .27$, $p = .40$). No significant correlation was found with age for the RVI obtained in the visual and tactile stimulation conditions.

Figure 5 (1 column) (color online only)

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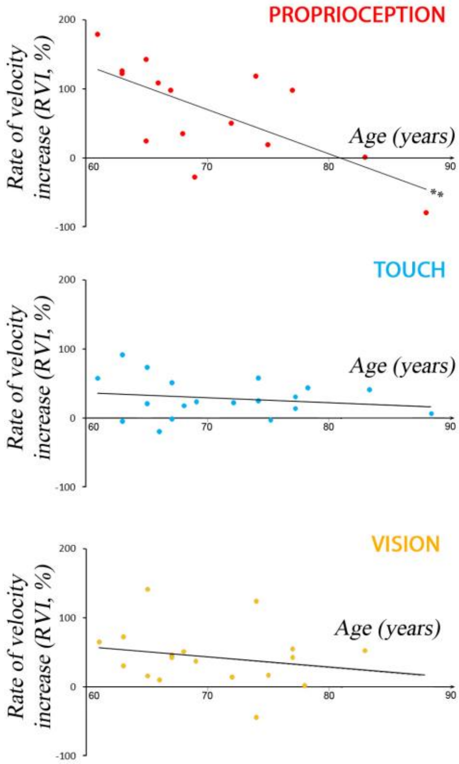

Figure 5: Correlations between individual RVI values and Age within the older group for the proprioceptive (higher panel), the tactile (middle panel), and the visual stimulation (lower panel).

Note that the negative correlation was significant only for the proprioceptive condition ($p = .004$).

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3.2 Multisensory stimulation: comparisons within and between groups

3.2.1 Illusion occurrence

For all multisensory conditions (PT, VP, VT, VTP) and the two intensity levels (low and high), illusions occurred in 100 % of the trials in both the younger and the older groups.

3.2.2 Illusion saliency

For the four multisensory stimulation conditions, both older and younger participants reported high subjective rates (on average > 2.5). These rates were significantly higher for the older group than the younger group except for the visuo-proprioceptive illusions and the high intensity proprio-tactile illusions (Table 3).

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Table 3: Subjective ratings (mean ± SD) of illusion saliency and group comparison (Younger vs Older groups) using U Mann Whitney tests for multisensory conditions (PT, VP, VT, VTP) at low and high intensities. * $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$.

		ILLUSION SALIENCY			
		Mean ± SD		**Young vs. Old**	
		Young	**Old**	**U**	***p***
Low Intensity	**PT**	2.52 ± 0.5	3.32 ± 0.6	23	.005*
	VP	3.08 ± 0.3	3.36 ± 0.7	49	.15
	VT	3.13 ± 0.4	3.68 ± 0.4	25	.006**
	VTP	2.98 ± 0.6	3.60 ± 0.5	29.5	.013*
High Intensity	**PT**	3.00 ± 0.4	3.41 ± 0.5	41.5	.069
	VP	3.21 ± 0.3	3.46 ± 0.6	43.5	.084
	VT	3.25 ± 0.5	3.79 ± 0.3	18	.0019**
	VTP	3.58 ±0.4	3.88 ± 0.2	37	.027*

3.2.3 Illusion latencies

Comparisons in the latencies of the illusions between the two groups and between the different multisensory conditions applied at high and low velocities were tested using a three-way mixed design ANOVA. As shown in Table 4, age had a significant impact on the perception of our participants since for all multisensory conditions, the illusion latency was significantly longer for older compared to younger participants ($p = .005$, $\eta^2 = 0.23$). Nevertheless, this main effect of age did not interact with the type of stimulation ($p = .06$, $\eta^2 = 0.08$). If increasing the stimulation intensity leads to a significant decrease in the latency (Main effect intensity: $p = .0005$, $\eta^2 = 0.34$), this effect did not significantly differ between groups (Interaction age * intensity $p = .78$, $\eta^2 = 0.002$). The triple interaction age * modality * intensity was not significant neither [$F(3, 90) = 2.04$, $p = .11$, $\eta^2 = 0.06$].

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Table 4: Illusion latencies (mean ± SD) in younger and older groups for multisensory conditions (PT, VP, VT and VTP) at low and high intensities. Statistical results were obtained by a three-way mixed design ANOVA (Age*Modality*Intensity).

		Mean Latency (ms) ± SD		
		Young	**Old**	
Low Intensity	**PT**	751 ± 616	1438 ± 820	Intensity main effect F(1, 30) = 15.39, p = .0005
	VP	978 ± 440	1837 ± 1017	
	VT	791 ± 502	1398 ± 729	
	VTP	936 ± 569	1340 ± 871	
High Intensity	**PT**	745 ± 491	1077 ± 584	
	VP	816 ± 430	1760 ± 701	
	VT	590 ± 686	1141 ± 786	
	VTP	552 ± 402	1168 ± 598	
		Age main effect F(1, 30) = 9.16, p = .005		Age * Intensity F(1, 30) = 0.08, p = .78 Age * Modality F(3, 90) = 2.58, p = .06

3.3.4 Illusion velocities (Fig. 6)

Comparisons in the velocities of the illusions between the two groups and between the different multisensory conditions applied at high and low velocities were tested using a three-way mixed design ANOVA. On the whole, older participants perceived faster illusions (mean ± SD = 6.40 ± 2.89 °/s) than younger participants (mean ± SD = 3.32 ± 2.11 °/s) for the four multisensory conditions confounded [Main effect of age: $F(1, 30) = 15.43$, $p = .0005$, $\eta^2 = 0.34$]. However, this effect of age differed according to the multisensory stimulation [Interaction age * modality $F(3, 90) = 6.31$, $p = .0006$, $\eta^2 = 0.17$] and the intensity of the stimulation [Interaction age * modality * intensity : $F(3, 90) = 6.07$, $p = .0008$, $\eta^2 = 0.17$].

Post-hoc analysis (see Table 9 in supplementary data) showed that in younger adults, whatever the level of stimulation intensity, comparisons among the various multisensory conditions did not reveal any significant difference. In addition, high intensity stimulations lead systematically to faster perceived illusions than low intensity stimulations (Fig. 6).

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By contrast, in the older group, the visuo-proprioceptive stimulation gave rise to slower illusions with respect to the proprio-tactile at low intensity (VP_{low} vs PT_{low} : $p_{corr} < .0001$). Visuo-proprioceptive illusions were also slower than visuo-tactile illusion at the high intensity (VP_{high} vs VT_{high} : $p_{corr} < .0001$), as well as slower than the trisensory illusions at the high (VP_{high} vs VTP_{high} : $p_{corr} < .0001$) and low intensity (VP_{low} vs VTP_{low} : $p_{corr} = .012$). In other words, most of multisensory conditions including a tactile stimulation had a greater effect than the visuo-proprioceptive conditions. Conversely, adding a tactile stimulation to the visuo-proprioceptive stimulation leads to an increased illusion while this did not hold true for the other bisensory conditions.

In addition, like for the unisensory stimulations, increasing the stimulation intensity leads to an increased perceived velocity in both groups [Main effect of intensity $F(1, 30) = 99.1$, $p < .0001$, $\eta^2 = 0.77$]. This effect of the intensity did not significantly interact with age [Interaction age * intensity $F(1, 30) = 0.24$, $p = .63$, $\eta^2 = 0.0075$] but varied according to the stimulation type [Interaction intensity * modality ($F(3, 90) = 5.4$, $p = .0018$, $\eta^2 = 0.15$]. Post hoc analysis of the triple interaction revealed that only in the proprio-tactile condition, the older participants did not show a significant increase in illusion velocity between the low and the high intensity level after correction for multiple comparisons (PT_{high} vs PT_{low} : $p_{corr} = 1$, Fig. 6 and see Table 9 supplementary data).

Figure 6 (1.5 column) (color online only)

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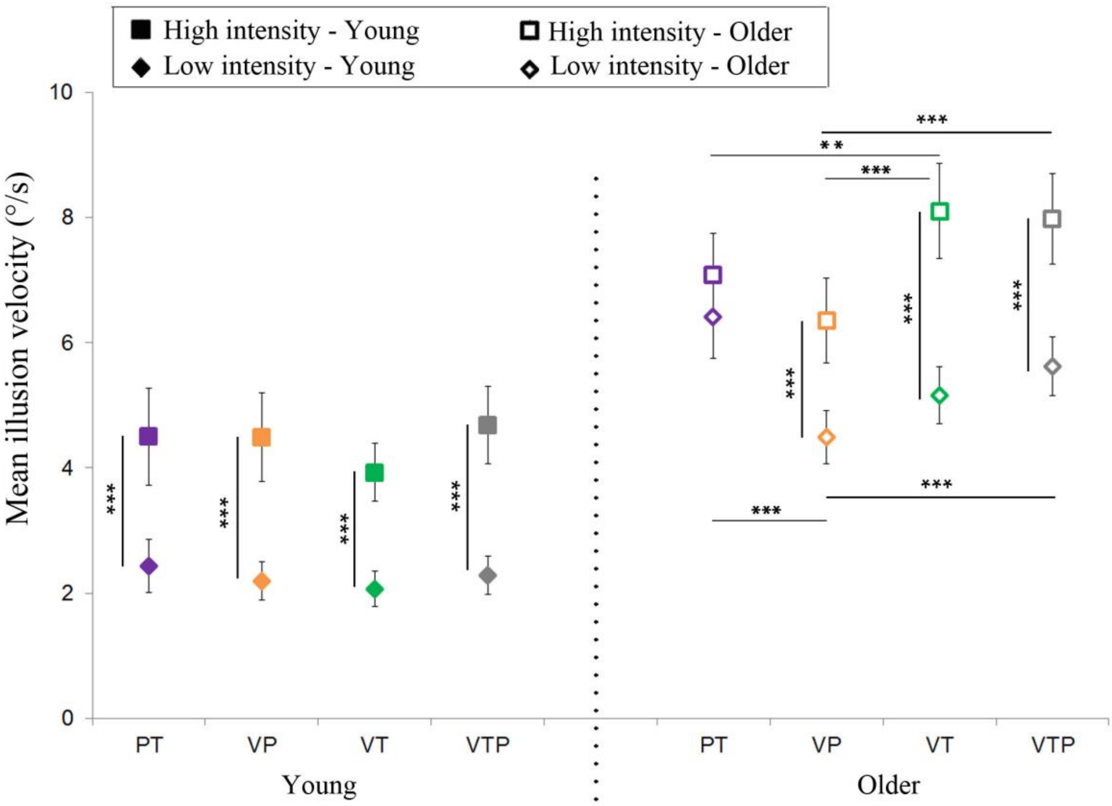

Figure 6: Mean illusion velocity (± SEM) perceived by the younger and older participants in response to proprio-tactile (PT, purple), visuo-proprioceptive (VP, orange), visuo-tactile (VT, green) and trisensory (VTP, grey) stimulations. *: $p_{corr}<.05$; **: $p_{corr}<.01$; ***: $p_{corr}<.001$ (p_{corr} : p corrected for multiple comparisons).

Finally, we investigated the impact of increased intensities of stimulation in both groups independently of how fast the illusions were perceived via the percentage of illusion velocity increase (RVI) between the high and low stimulation intensities. Results on Figure 7 show that like for the unisensory stimulation, the RVI was significantly smaller in the older group compared to the younger group for all multisensory conditions (Mann-Whitney tests: PT: U = 221, p < .001, VP: U = 260, p = .04, VTP: U = 203, p < .001) except for the visuo-tactile condition (U = 265, p = .06).

Figure 7 (1column) (color online only)

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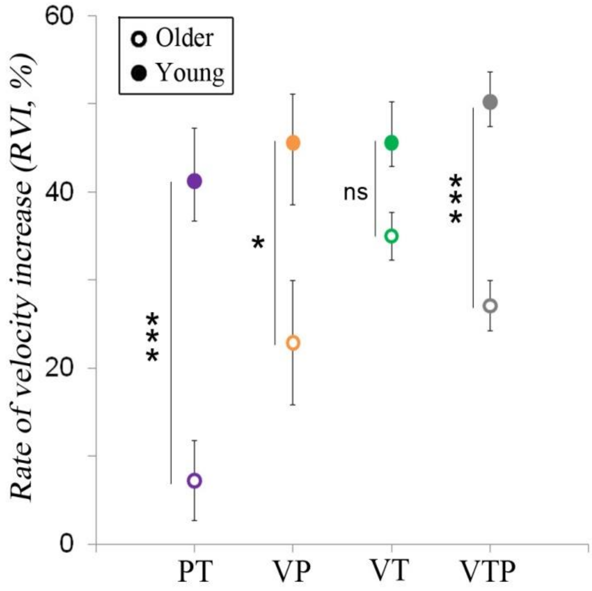

Figure 7: Rate of illusion velocity increase (± SEM) between the low and the high level of stimulation intensity in the four multisensory conditions observed in the younger (full dots) and older (empty dots) groups. PT: proprio-tactile (purple), VP: visuo-proprioceptive (orange), VT : visuo-tactile (green), and VTP: visuo-proprio-tactile (grey) conditions. ns: p > .05; *: p< .05; **: p < .01; ***: p < .001.

3.3.5 Multisensory index (MSI) for illusion velocities

To quantify the improvement of the perceptual responses induced by the multisensory stimulation with respect to the most efficient unisensory stimulation, the multisensory index (MSI) was individually estimated for each multisensory condition. A positive MSI value reflected a perceptual benefit of the multisensory condition over the best unisensory conditions. Perceptual benefits of multisensory stimulation were first tested using one-sample Wilcoxon tests comparing mean MSI values to zero. In the younger group, a perceptual benefit was significantly observed only at the high intensity level for all the multisensory conditions except for the visuo-tactile condition. In the older group, participants showed a perceptual benefit in most of multisensory conditions except for the visuo-tactile and visuo-proprio-tactile conditions at the low intensity level and for the proprio-tactile condition at the higher intensity level (see Table 5).

Interestingly, by comparing the two groups, no significant difference between the MSI values was found for all multisensory conditions. As clearly shown in Figure 8 where individual MSI

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values were plotted for all multisensory conditions, the indexes of integration did not differ between the older and younger participants for the four multisensory conditions tested.

Table 5: Index of MSI velocity (mean ± SD) for the younger and the older groups for the four multisensory conditions. Statistical results were obtained by one sample Wilcoxon tests to compare each group's mean from 0 and by Mann Whitney tests to compare MSI values between groups (Young vs. Old). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

		MSI VELOCITY							
		Young			**Old**			**Young vs. Old**	
		Mean ± SD	**V**	***p***	**Mean** ± SD	**V**	***p***	**U**	***p***
Low Intensity	**PT**	13.62 ± 55.6	50	.39	14.07 ± 21.3	148	.016*	102	.42
	VP	6.34 ± 26.6	59	.19	12.48 ± 28.0	142	.03*	119	.88
	VT	-3.22 ± 28.5	40	.66	-7.56 ± 13.1	39	.10	136	.65
	VTP	-4.12 ± 26.0	36	.75	2.64 ± 20.6	100	.43	104	.47
High Intensity	**PT**	21.24 ± 46.8	69	.05*	1.92 ± 21.3	103	.38	155	.24
	VP	314.10 ± 19.7	75	.02*	21.56 ± 24.7	173	< .001***	103	.45
	VT	7.20 ± 20.9	62	.14	14.47 ± 25.8	144	.025*	101	.40
	VTP	18.32 ± 27.3	81	.005**	11.05 ± 18.2	149	.015*	134	.70

Figure 8 (1 column) (color online only)

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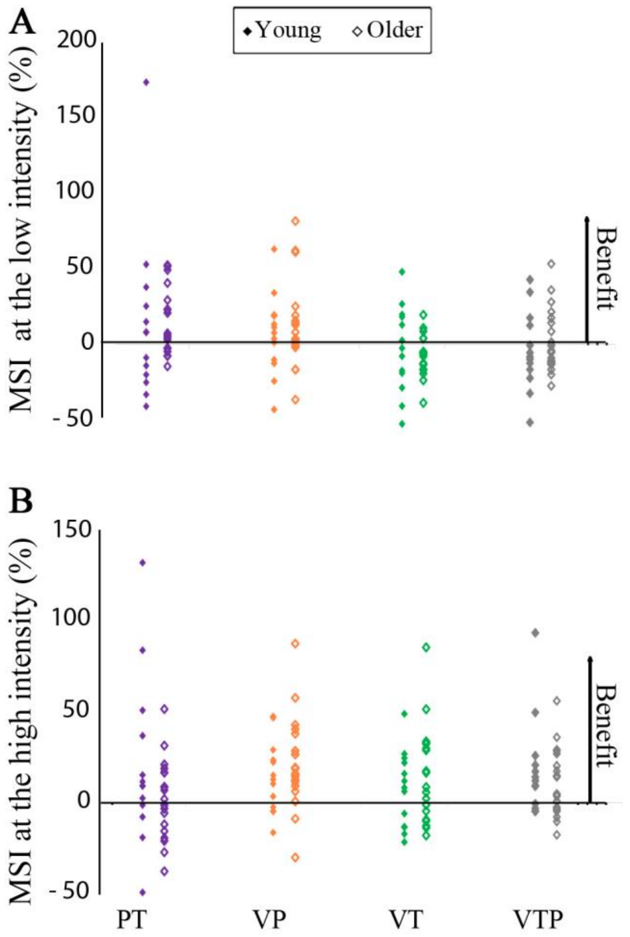

Figure 8: Individual multisensory index (MSI) for illusion velocities at low (A) and high (B) intensity of stimulation in the younger (full diamonds) and older (empty diamonds) groups in response to proprio-tactile (PT, purple), viuso-proprioceptive (VP, orange), visuo-tactile (VT, green) and trisensory (TPV, grey) stimulation. Note that for the four multisensory conditions, no significant differences were found between the two groups (Mann Whitney tests, $p > .05$).

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4. Discussion

This study aimed to investigate changes with age in the relative contribution of muscle proprioception, touch, and vision to kinaesthesia and their integration. To this end, we compared the latencies and perceived velocities of illusory movements of self-hand rotations induced by stimulating each of these sensory channels in isolation or in combination in a younger group and an older group (above 60 years old).

4.1 Reshaping of sensory reliance with age

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Although all sensory systems are structurally impaired during ageing (Borel and Alescio-Lautier, 2014; Desrosiers et al., 1999; Shaffer and Harrison, 2007), the extent of their deterioration may not be the same in each sensory modality, and the functional consequences for kinaesthesia may differ. The results from the present study support this view.

One of the main findings of the present study was that the same proprioceptive stimulation applied in younger or older participants did not elicit equivalent illusory movements. It was more difficult to elicit vibration-induced illusory sensations in the older participants (lower occurrence in the older group), and when they were present, the proprioceptive illusions were delayed and less salient than those reported by the younger participants. In addition, the increase in perceived illusion velocity in proprioceptive stimulation for increasing intensities of this stimulation declines with age (as attested by a negative correlation of the RVI values with age).

A first explanation of these altered proprioceptive induced illusory movements could be that the vibration stimulation used in the present study may not recruit muscle spindles endings to the same extent in older and younger adults due to physiological degradation of the skin and muscle tissues (skin and muscle elasticity deterioration…). If this is the case, motor consequences of muscle tendon vibration should also be altered in the same way as perceptual consequences. However, Quoniam et al. (1995) examined the tonic vibration reflex (TVR) induced by an 80 Hz vibration of the biceps and triceps muscles both in younger (20- to 44-year-old) and older (60- to 86-year-old) participants. This reflex is assumed to primarily utilize the same pathways as the stretch reflex. The latter authors showed that the latency and amplitude of the TVR did not depend on the age of the subject. This result suggests that the alteration of the perceptual illusions observed in the present study cannot be fully explained by a lesser activation of muscle spindles in elderly when the muscle tendon vibration was applied.

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Kinesthetic illusions induced by visual or tactile stimulation were also altered in elderly. Increasing the intensity level of the visual or tactile stimulation resulted in a smaller increase in the illusion velocity in the older adults compared with the younger adults (attested by lower RVI values in the older than the younger group). Because this was not observed for the tactile and visual stimulation for which the response latencies did not differ between older and younger participants, alterations in the perceptual responses observed in the present study cannot be fully explained by a nonspecific effect such as a general slowdown of central

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processing in the elderly nor by a deterioration of the motor system leading to difficulties in actively reproducing with their left hands what they perceive of their right hands. In addition, we ensured in the pre-testing session that older individuals included in this study were able to copy with their left hand a movement passively imposed on their right hand within the range of the younger participants' performances that were included in the present study; i.e., the latencies and velocities of the copied movements should not exceed the mean performance of the younger group from more than two standard deviations).

A noteworthy finding is the fact that the illusory sensations induced by visual and tactile stimulation were faster in the older participants than in the younger participants. The older participants also reported a greater saliency of the tactile illusions compared to the younger group. Therefore, a differential decline in the sensory systems seems more likely responsible for the differential perceptual effects found in this study, suggesting a greater degradation of the muscle proprioceptive modality compared to the visual and the tactile modality for kinaesthesia for those above 60 years of age.

The question that thus arises is determining whether the perceptual differences observed between older and younger adults result from peripheral and/or central processing changes. The degradation with age in the structural properties and density of mechanoreceptors (Kararizou et al., 2005) and in peripheral and central nerve conduction have been widely reported in the literature (Dorfman and Bosley, 1979; Swash and Fox, 1972). Although a peripheral origin can account for the difficulty to induce proprioceptive illusions as well as for the delayed perceptual responses observed in elderly, it does not seem sufficient to explain the greater tactile illusions elicited in the older participants compared to the younger participants. In addition, trisensory stimulation did not override the bisensory conditions that already included a tactile in older adults. Altogether, these results support the hypothesis of a central origin with changes in the sensory reliance in favour of touch and vision for kinesthetic purposes, likely due to a relative greater degradation of muscle proprioception in elderly. As reported in previous studies (Blanchard et al., 2013; Chancel et al., 2016a), the velocity of the visual and tactile illusions evoked in younger healthy adults is very low compared to the velocity of the stimulation applied. These very low perceptual gains can be explained by the conflicting proprioceptive feedback simultaneously indicating that the hand was not actually moving. Using a modelling Bayesian approach, Chancel et al. (2016a) demonstrated that discrimination of illusory hand movement velocity based on visuo-tactile information is sub-optimal due to an unpredicted over-weighting of muscle proprioceptive

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information. Conversely, the strengthening of visual and tactile illusions in the elderly despite the deterioration of these sensory systems might be explained by a relatively weaker weight attributed to resting proprioception cues with respect to the moving visual or tactile cues.

The hypothesis that central mechanisms have been developed in the elderly to compensate for sensory deterioration is supported by several other studies. For instance, Peters et al. (2016) assessed vestibular function in younger and older individuals using a direction discrimination task of real and virtual self-rotations. Overall, the authors observed elevated discrimination thresholds in the older adults compared to the younger adults, in accordance with the well-known structural deterioration of the peripheral vestibular apparatus. However, the elderly performed as well as the younger adults for some rotations imposed at a particular frequency. The authors concluded that a central frequency-specific processing gain may occur to compensate for the degradation of the vestibular system with age.

Changes in sensory reliance with age have also been reported in non-motor related cognitive domains, such as in semantic classification tasks, where visual dominance over audition has been specifically observed in the elderly (Diaconescu et al., 2013). Indeed, when participants must judge whether presented stimuli belong to animate or inanimate categories, auditory object categorization is enhanced by concomitant presentation of congruent visual stimuli, although this effect is not symmetric. Adding a congruent auditory stimulus does not increase the performance of older participants in categorizing a visual object. The authors concluded that elderly become more visually dependent in categorization tasks compared to younger individuals.

Finally, the relative greater decline in muscle proprioception may also be related to a generally more frequent lack of physical activity in the elderly. Indeed, we did not precisely assess the daily physical activity of our participants, either for the older or the younger ones. The informal interview that we had with every participant before the experiment confirmed that they had really different daily occupations (volunteering in association, regular hiking, gardening, sewing, amateur musician…) and came from different lines of work. Some of the elderly were very active while others had little physical exercise a day. This disparity between our participants reduced the possibility of a systematic bias. In addition, elderly participants in the present study did not exhibit manual motor deficits when they reproduced a passively imposed rotation using their contralateral hand as evidenced by the pre-testing session.

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Nevertheless, the hypothesis of an aging-related reduced engagement in physical activity cannot be fully ruled out, and this issue should be further investigate in follow-up works.

4.2 Preservation of multisensory integration processing in elderly

Perceptual enhancement of the responses induced by the multisensory stimulation with respect to the most efficient unisensory stimulation occurred only for the highest intensity of stimulation in the younger group whereas the older group showed a perceptual benefit in most of multisensory conditions including the lowest intensity of stimulation. Although it seemed more frequent in the older group, the beneficial impact of multisensory stimulation in the elderly group was of the same order as that observed in the younger group: improvements in velocity illusion during multisensory conditions in comparison with the most efficient unisensory response did not significantly differ between the two groups, as attested by similar MSI values. Nevertheless, as for unisensory conditions, the performances of the elderly in the four multisensory conditions remained lower than those of the younger adults with greater illusion latencies and slower rates of illusion increase between the low and high levels of stimulation intensity (except for the visuo-tactile condition). These results suggest that the capacity of the elderly to integrate multisensory information for kinaesthesia seems preserved. The present findings converge with a large amount of previous studies showing that although unisensory performance is lower in older adults compared to younger adults, multisensory integration for perceptual purposes is not reduced, but rather enhanced in the elderly (de Boer-Schellekens and Vroomen, 2014; Diaconescu et al., 2013; Diederich et al., 2008; Hugenschmidt et al., 2009; Laurienti et al., 2006; Mahoney et al., 2012; Peiffer et al 2007). The hypothesis of a preservation of multisensory processes in older adults is also supported by recent findings that as in younger adults, a Bayesian framework successfully predicted multisensory integration in the elderly (Braem et al., 2014; Karmali et al., 2018; Sherback et al., 2010). For instance, Braem et al. (2014) found that integration of visual and haptic cues in a subjective vertical perception task follows the same Bayesian principles in younger and older individuals. Indeed, when participants had to align a rod with the gravitational vertical using visual and/or haptic information, participants' performances in the bisensory condition were predictable by a weighted average of their unisensory performances, regardless of age.

During a sensorimotor task such as maintaining upright balance, stance perturbation provoked by a privation of one of the vestibular, proprioceptive or visual systems is generally

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found to be more severe in the elderly who respond with larger body excursions than younger adults (Abrahamova and Hlavacka, 2008; Peterka and Black, 1990; Quoniam et al., 1995; Speers et al., 2002; Whipple et al., 1993). This instability remains greater in elderly when two sensory systems are simultaneously deprived (Horak et al., 1989; Whipple et al., 1993). However, it is not clear from deprivation experiments whether impairments in postural control result from a degradation of the remaining sensory systems or from a decline in their central integrative processing. The postural consequences induced by multisensory stimulation rather than deprivation have been poorly studied. By applying variable concomitant visual and tactile stimulation in upright standing subjects, Allisson et al. (2006) showed that older participants performed as well as younger participants in adapting the relative weight of one sensory cue with respect to another, i.e., elderly demonstrated an intact inter-sensory reweighting to vision and touch for postural control. This previous study brings into question the general assumption that elderly would have more difficulty in quickly adapting the weighting of the different sensory information to sudden environmental changes ('sensory reweighting adaptation') resulting in greater imbalance and risk of fall in elderly (Horak et al., 1989; Teasdale and Simoneau, 2001).

The interpretation of such preservation or facilitation of multisensory processing in the elderly is a matter of debate. In another context outside of sensorimotor control and kinaesthesia like during visual and auditory discrimination tasks, older individuals take greater advantage of redundant audio-visual stimuli than younger adults, suggesting that by increasing the efficiency of integrative processing, elderly may compensate for the decline of sensory systems. Nevertheless, when different stimuli are temporally or spatially incongruent, the crossmodal benefit is no longer observed in older adults (Poliakoff et al., 2006; Setti et al., 2011). It has been suggested that the larger time window of integration in older adults than in younger adults facilitates multisensory integration, resulting in a beneficial effect when stimuli are congruent and in distractibility and inadequate co-processing of incongruent stimuli when stimuli are incongruent (Diederich et al., 2008; Setti et al., 2011). Mozolic et al (2012) recently proposed another hypothesis and postulated that multisensory enhancement in elderly might be a consequence of increase internal noise in the nervous system. According to this last view, if the sensory inputs are irrelevant, older adults are less able to suppress the information, but when it is relevant they have larger benefits to integrate multisensory inputs than younger adults.

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With regard to the neuronal basis of multisensory integration in the elderly, there is physiological evidence of compensatory mechanisms at the brain level. Despite the alteration of central structures, such as the reduction of grey (Good et al., 2001; Resnick et al., 2003) and white matter (Lebel et al., 2012) in the brain of the elderly, functional neuroplastic changes occur, and this modulation of brain activity can be correlated with cognitive and sensorimotor decline in older adults. The most general view is that older adults might first compensate for weak cognitive and sensorimotor deficits by increasing related brain network activity (Cabeza et al., 2002; Ward and Frackowiak, 2003) and by extending activations into the ipsilateral hemisphere (Ward, 2006; Kalisch et al. 2009; Brodoehl et al 2013). As an example, during a peripheral tactile stimulation, older adults display an enlarged activation in the contralateral primary somatosensory cortex (SI) and a lesser deactivation of the homologous ipsilateral region (Lenz et al., 2012). A general reduction of inhibitory phenomenon in the brain of elderly is supposed to facilitate such hemispheric asymmetrical reduction in particular between cortical sensorimotor regions (Cabeza et al., 2002; Lenz et al., 2012). In addition to recruit more brain areas, older people seem to have a loss of specialization of specific brain circuits. At the neural level, it is attested by a reduction in stimulus selectivity as evidenced in older monkeys by a degradation of visual orientation and direction selectivity in the visual cortex (Schmolesky et al., 2000). Although the exact neural bases are still debated, the authors seem to converge towards the idea that multisensory integration is maximized in the elderly, which is an advantage when the information is relevant, but a disadvantage when it is not relevant or simply noise.

To conclude, the present findings confirm that kinaesthesia is impaired with ageing likely due to the degradation of all sensory systems. However, such degradation might not be equivalent depending on the sensory system, and the weights of sensory modalities might change with ageing: elderly people might rely more on visual and tactile afferents for perceiving self-hand movements than younger adults due to a relatively greater degradation of muscle proprioception. In addition, to partly compensate for sensory declines, the capacity of elderly to integrate multisensory cues seems to be preserved if not enhanced.

Conflict of interest

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The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author contributions

Conceived and designed the work: AK, MG, OF. Acquired and analyzed the data: MC, CL, CB. Wrote the paper: AK and MC. All authors revised the work for important intellectual content. All of the authors have read and approved the final version of the manuscript. All authors agree to be accountable for the content of the work.

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Highlights:

- Kinesthesia is altered in the elderly
- Sensory stimulation results in differential perceptual effects across age groups
- Age-related decline in muscle proprioception is greater than other senses
- Elderly rely more on visual and tactile afferents for hand-movement perception.

Multisensory integration is preserved despite the decline of aging sensory systems

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