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

3
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18
19 **Keywords:** Kinaesthesia – Multisensory perception Aging - Illusion – Muscle proprioception
20 – Touch - Vision

21
22 **Running Title:** Multisensory self-movement perception in elderly

23
24 **Highlights:**

- 25 • Kinesthesia is altered in the elderly
26 • Sensory stimulation results in differential perceptual effects across age groups
27 • Age-related decline in muscle proprioception is greater than other senses
28 • Elderly rely more on visual and tactile afferents for hand-movement perception.
29 • Multisensory integration is preserved despite the decline of aging sensory systems

30 **Abstract**

31 To perceive self-hand movements, the central nervous system (CNS) relies on multiple
32 sensory inputs mainly derived from vision, touch, and muscle proprioception. However, how
33 and to what extent the CNS relies on these sensory systems to build kinesthetic percepts as the
34 systems decline with age remain poorly understood. Illusory sensations of right hand rotation
35 were induced by separately stimulating these three sensory modalities at two intensity levels.
36 A mechanical vibrator applied to the *pollicis longus* muscle, a textured disk for touching, and a
37 visual pattern rotating under the participant's hand were used to activate muscle proprioception,
38 touch, and vision, respectively. The perceptual responses of 19 healthy elderly adults (60-88
39 yrs) were compared to those of 12 younger adults (19-40 yrs). In the younger group, the three
40 types of stimulation elicited similar kinesthetic illusions at each intensity level applied. The
41 same visual and tactile stimuli elicited more salient and faster illusions in older adults than in
42 younger adults. In contrast, the vibration-induced illusions were significantly fewer, less salient
43 and delayed in the older adults. For the three modalities considered, increasing the intensity of
44 stimulation resulted in smaller increases in illusion velocity in older adults than in younger
45 adults. Lastly, a similar improvement in the perceptual responses was observed in older and
46 younger adults when several stimulations were combined and older participants reported more
47 salient illusions than younger participants only in the visuo-tactile condition. This study
48 suggests that reliance on sensory inputs for kinesthetic purposes is profoundly reshaped with
49 aging. The elderly may rely more on visual and tactile afferents for perceiving self-hand
50 movements than younger adults likely due to relatively greater muscle proprioception
51 degradation. In addition, multisensory integration seems preserved but not enhanced to
52 compensate for the global decline of all sensory systems with age.

53 **1. Introduction**

54 To perceive self-hand movements, the central nervous system (CNS) relies on multiple
55 sensory information mainly derived from vision, touch, and muscle proprioception. The
56 contribution of each these sensory modalities has been advantageously studied in younger
57 adults using specific stimuli inducing illusion of self-body movements (see review
58 Kavounoudias 2017). That muscle proprioception plays a crucial role in kinesthesia is attested
59 by a large amount of studies showing that applying vibration to motionless subjects' muscle
60 tendons selectively activates muscle receptors (Roll & Vedel 1982) and induces illusory
61 movements of the body in the direction of the lengthening muscle (Albert et al., 2006; Goodwin
62 et al., 1972; Blanchard et al. 2011; 2013). In addition, the visual system also contributes to the
63 sense of movement, as evidenced by thevection phenomenon, i.e., a kinesthetic percept elicited
64 by a visual moving scene scrolling in front of a participant (Brandt and Dichgans 1972; Guerraz
65 and Bronstein 2008) or under one's limb (Blanchard et al., 2011, 2013; Chancel et al., 2016a,
66 Tardy-Gervet et al., 1984). Visually induced illusions of an arm movement were also observed
67 during reflection in the mirror of the passively displaced contralateral arm, the so-called mirror
68 paradigm (Ramachandran and Altschuler 2009; Guerraz et al. 2012; Chancel et al. 2016b).
69 Touch, like vision, also conveys kinesthetic information since illusions of self-body movements
70 can be elicited using a tactile stimulus rotating under the palm of the hand (Blanchard et al.
71 2011, 2013; Chancel et al. 2016a) and illusory finger movement sensations have also been
72 reported to occur in response to stretching of the skin over the metacarpophalangeal joints of
73 the hand (Collins et al., 2000).

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

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

99 Most of the above mentioned studies investigated alterations of each sensory modality in
100 isolation. However, it is well known that kinaesthesia is by nature multisensory, each actual
101 limb movement giving rise to multiple concomitant sensory inputs. Several studies have
102 stressed the need to integrate convergent cutaneous, muscular and visual inputs to properly
103 assess limb positions and movements in healthy younger adults (Aimonetti et al., 2012;
104 Blanchard et al., 2011, 2013; Chancel et al., 2016b; Cordo et al., 2011; Guerraz et al., 2012;
105 Tardy-Gervet et al., 1986; van Beers et al., 2002). In addition, it is generally admitted that the
106 different sensory modalities do not contribute equally to these integrative mechanisms. In
107 accordance with the Bayesian framework, many modelling studies have provided evidence that
108 the multisensory estimate of an event such as a self-body movement is given by the reliability-
109 weighted average of each single-cue estimate (Chancel et al., 2016a; Fetsch et al., 2009; Prsa
110 et al., 2012; Reuschel et al., 2009; Vidal and Bühlhoff, 2010). This Bayesian like mechanism
111 seems to rule multisensory integration for elderly as well, even when facing sensorimotor
112 decline. Indeed, Bayesian optimal adaptation between sensory reliability and a priori
113 information efficiently describes age-related changes in visuomotor behavior, both for an object
114 tracking task (Sherback et al., 2010) and multisensory reflexes such as the vestibulo-ocular
115 reflex (Karmali et al., 2018). This also holds true regarding the integration of visual and haptic
116 cues in a subjective vertical perception task, which follows the same Bayesian principles in
117 younger and older individuals (Braem et al. 2014). On the other hand, during a navigation task

118 requiring visual and/or self-motion cues, Bates & Wolbers (2014) observed that performances
119 of the older adults were sub-optimal since they relied less than optimally predicted on visual
120 information. Therefore, the question remains as to whether multisensory integration rules
121 regarding self-body perception survive during aging. In particular, it is of interest to determine
122 to what extent age-related declines in the sensory modalities like vision, muscle proprioception
123 and touch are associated with a sensory reweighting to build a consistent percept and/or whether
124 enhancing multisensory integration could at least partly overcome sensory decline.

125 Outside the field of kinesthesia, numerous studies have recently shown that, despite age-
126 related degradation in single sensory systems, multisensory integration processing does not
127 seem to be diminished but rather enhanced (see reviews, Freiherr et al., 2013, Kuehn et al.,
128 2017, de Dieuleveult et al., 2017). This has been largely reported in studies using visual-
129 auditory paradigms (de Boer-Schellekens and Vroomen, 2014; Diaconescu et al., 2013;
130 Diederich et al., 2008; Hugenschmidt et al., 2009; Laurienti et al., 2006; Mahoney et al., 2012;
131 Peiffer et al 2007). For instance, Laurienti and colleagues (2006) found in an audiovisual
132 discrimination task that despite larger response times for unisensory targets in older adults
133 compared to younger adults, the gain of the bisensory responses observed when the two types
134 of stimuli were simultaneously presented was greater for the older group than the younger one.
135 These results suggest at first glance that older individuals may take greater advantage of
136 redundant multisensory information (same content conveyed by various sensory inputs) than
137 younger adults by increasing the efficiency of integrative processing. However, when the
138 different stimuli are incoherent in time or space, older people always integrate them
139 inappropriately, while young adults correctly segregate the different messages, considering that
140 they do not originate from the same event. Consequently, as reported for instance by Poliakoff
141 and coll (2006), older adults tested in a crossmodal selective attention task have more difficulty
142 in focusing on one sensory modality while ignoring a concomitant distractor presented in
143 another modality. Therefore, the facilitation of multisensory integration in older adults may be
144 an advantage when stimuli belong to the same event, but become a disadvantage when
145 information from multiple sources should not be associated (Poliakoff et al., 2006; Setti et al.,
146 2011). As to studies investigating multisensory integration in sensorimotor tasks, they rather
147 support the general, though controversial, hypothesis that the elderly would have more
148 difficulty in quickly adapting the weighting of the different sensory information to sudden
149 environmental changes (Allison et al 2006; Eikema et al. 2014; Horak et al., 1989; Teasdale
150 and Simoneau, 2001).

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

163

164 **2. Method**

165 *2.1 Participants*

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

178 *2.2 Stimuli (Fig. 1A)*

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

180 The muscle proprioceptive stimulation was a lab-customed mechanical vibrator and
181 consisted of a biaxial DC motor with eccentric masses, forming a cylinder that was 5 cm long

182 and 2 cm diameter. A 0.5-mm peak-to-peak mechanical vibration was applied to the right
183 *pollicis longus* tendon at two constant frequencies: 30 or 60Hz. Low-amplitude mechanical
184 vibration applied on a muscle tendon is well known to specifically activate muscle spindle
185 primary endings, as evidenced through microneurographic recordings (Roll and Vedel, 1982;
186 Fig. 1B).

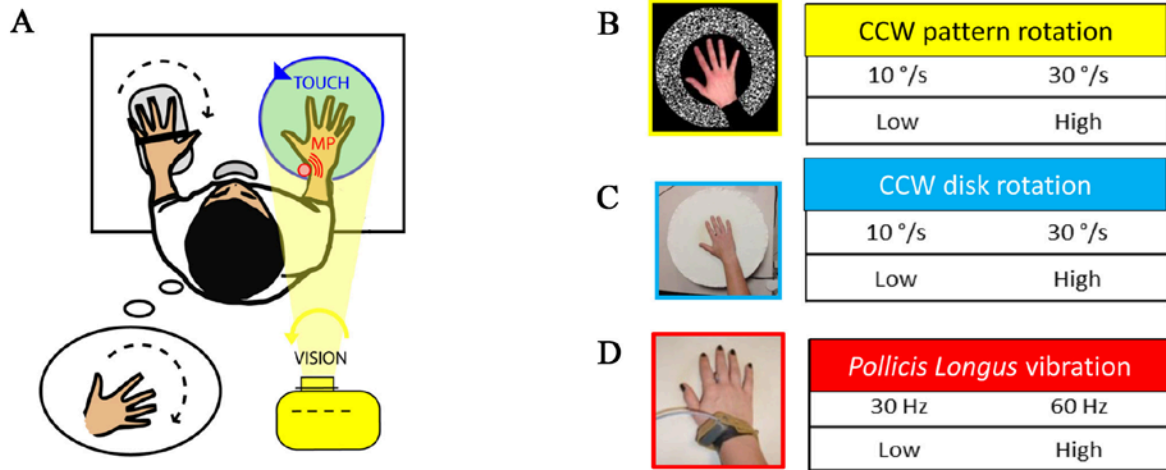
187 The tactile stimulation was delivered by a motorized disk (40 cm in diameter, developed
188 by Rematique company, Saint-Etienne, France) covered with cotton twill (8.5 ribs/cm). This
189 material was used because a microneurographic study showed that it can efficiently activate
190 cutaneous receptors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

193 Visual stimulation consisted of a projection of a black and white pattern on the disk. To
194 give the participant the feeling that the pattern was moving in the background, i.e., under his/her
195 hand, a black mask adjusted to the size of each participant's hand was included in the video that
196 prevented the pattern from being projected onto the participant's hand. The pattern was rotating
197 around the participant's right hand with a constant counterclockwise angular velocity set to 10
198 or 30 °/s (Fig. 1D).

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

206

Figure 1 (2 columns) (color online only)



207

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

214

215 **2.3 Procedure**

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

229

230

231 *2.3.1 Pre-test phase*

232 Before proceeding to the main study, participants were required to complete a pre-test
233 task to ensure that they were able to estimate and copy a movement passively imposed. Indeed,
234 the experimental task required the participant to copy with the left hand an illusory movement
235 perception of the right hand. It was therefore necessary to first assess the capacity of the elderly
236 participants to copy with his/her left hand an actual passively imposed movement of his/her
237 right hand. During the pre-test, participants' right hand was attached to a mechanical disk and
238 passively rotated in the clockwise direction, either at 5 °/s or at 10 °/s. These velocities of
239 movement were chosen because we know from previous studies performed in younger adults
240 (Balnchard et al., 2013) that the unisensory stimulations used in the main experiment induce
241 illusory clockwise hand rotations perceived with a velocity of 5 °/s and 10 °/s approximatively
242 for the low and the high intensity, respectively. Participants had to copy on real time the
243 movement imposed on their right hand with their left hand attached to a linear potentiometer
244 (50 kΩ, 1W) mounted on a rectangular plate. By turning the hand, the axis of the potentiometer
245 in rotation made it possible to record the angular deviation of the wrist of the participant. It was
246 used to measure the latency and velocity of the left hand movement. The velocity error of the
247 movement copy was computed as the difference between velocities of the right hand/passive
248 movement and the left hand/reproduction movement. The performances of participants of the
249 older group were compared to those of the younger group as a reference. No participant of the
250 older group displayed a mean velocity error more than two standard deviations away from the
251 mean reference value obtained for the younger group. We also verified that the latencies before
252 the beginning of the left-hand movement were not significantly different between the younger
253 and older groups. This test was conducted to ensure that the differences observed between older
254 and younger individuals in the present study, if any, were not due to an inability of the elderly
255 to reproduce a movement of one hand with the other hand.

256 *2.3.2 Experimental test*

257 Participants included in the experiment then underwent a training session composed of
258 15 trials of each stimulation condition to familiarize them with the stimuli and the reproduction
259 task.

260 Then, the experimental sessions were run, which included seven stimulation conditions
261 randomly intermixed: three unisensory conditions (muscle proprioceptive P, tactile T, visual
262 V), three bisensory conditions (proprio-tactile PT, visuo-proprioceptive VP, visuo-tactile VT)

263 and one trisensory condition (visuo-tactilo-proprioceptive VTP). During each stimulation
264 condition, participants were asked to copy with their left hand and in real time any illusory
265 movements they perceived. At the end of each trial, participants were also asked to rate the
266 saliency of the illusory movement they perceived from 0 (“No sensation of movement was felt”)
267 to 4 (“A clear sensation of movement was perceived, as if it was real”). The subjective rating
268 was given orally and the experimenter wrote it down by hand. Each session consisted of six
269 repetitions of the seven stimulation conditions performed at two intensity levels (7 conditions
270 * 2 intensities * 6 trials). Each trial lasted 10 s (1 s of rest and 9 s of stimulation). A total of
271 three sessions of 15 minutes were performed on two different days (at the same time during the
272 day).

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

279 Analogic signals were recorded using a National Instruments card (NI PCI-6229) piloted
280 with in-house software implemented in LabView (V.2010). Regardless of the experimental
281 condition, the stimulation started 750 ms after the onset of the data acquisition period and lasted
282 for 9 s.

283 *2.4 Data and statistical analysis*

284 All the variables used in this study are gathered in Table 1 together with the type of
285 statistical analysis performed. For binary or ordinal dependent variables, or when continuous
286 dependent variables did not satisfy normality and variance homogeneity hypotheses, non-
287 parametric statistical analyses were performed (Mann-Whitney or Wilcoxon tests). Otherwise,
288 continuous dependent variables were analyzed using three-way mixed-design ANOVAs to
289 assess the main effects and interactions of age, modality (P, T, V), and intensity (Low, High)
290 on the participants’ illusions. These mixed-design analyses allowed us to take into account for
291 the variability within and between subjects, by means of fixed (age, modality and intensity) and
292 random effects (subject), respectively. When interactions between fixed factors were
293 significant, LSD Fisher post-hoc tests were performed. For all statistical analyses, the level of
294 significance was corrected for multiple comparisons using the Bonferroni’s correction. In the

295 text we reported corrected p-values (i.e. p-values uncorrected multiplied by the number of
 296 comparisons) and we considered the result to be statistically significant at the corrected p value
 297 < .05.

298 **Table 1:** Summary of the analyzed variables in the present study.
 299

	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

300

301 *2.4.1 General assessment of stimulation*

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

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

307 The degree of saliency of the illusion sensations was also assessed: participants were
 308 asked to rate the vividness/clarity of their illusions on an analog scale ranging from 0 (“No
 309 sensation of movement was felt”) to 4 (“A clear sensation of movement was perceived, as if it
 310 was real”) after each trial. Note that the saliency index was independent of the velocity of the
 311 perceived illusion as a high saliency may coincide with a slow illusory movement. This allowed

312 us to verify that the participants had a sufficiently clear perception of the movement they had
313 to reproduce, whatever its velocity.

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

317 *2.4.2 Potentiometric data*

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

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

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

$$339 \quad RVI = \frac{Velocity(high) - Velocity(low)}{Velocity(low)} \times 100$$

340

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

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

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

$$351 \quad MSI = \frac{\text{Multisensory velocity} - \text{highest unisensory velocity}}{\text{highest unisensory velocity}} \times 100$$

352 A positive MSI value reflects a perceptual benefit in the multisensory condition over the best
353 unisensory condition. To test whether multisensory integration occurred in all multisensory
354 conditions, the MSIs were first compared to 0 using one-sample Wilcoxon tests for each group
355 independently. Then, to test whether older adults took greater advantage of multisensory
356 information as suggested by previous studies in the literature (see Introduction), the MSI values
357 obtained in each multisensory condition were compared between the younger and the older
358 groups using Mann-Whitney tests.

359

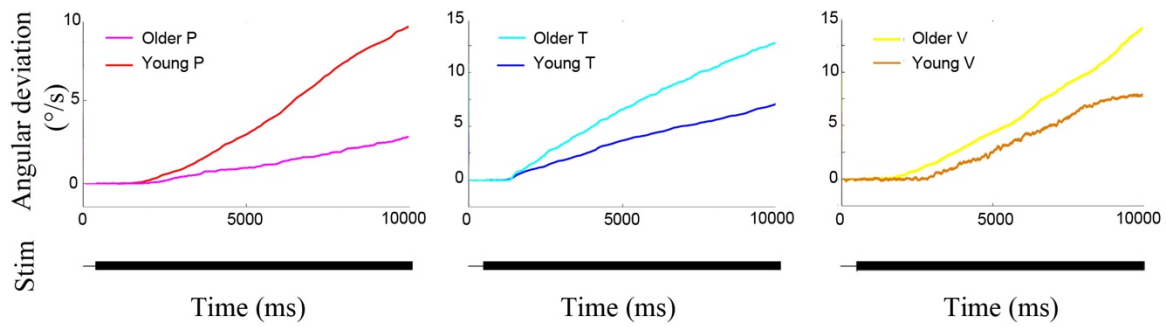
360 **3. Results**

361 *3.1 Unisensory stimulation: comparisons within and between groups*

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

364

365 **Figure 2 (2 columns) (print color)**



366

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

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

376

377 *3.1.1 Illusion occurrence*

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

383 When comparing groups using Mann-Whitney statistical tests, a significant difference
 384 was found in the occurrence of the proprioceptive illusions that dropped down to 61 % and 74
 385 % in the older group compared to the 97 % and 99 % in the younger group for the low ($p =$
 386 $.003$) and high ($p = .019$) stimulation intensity, respectively (Table 2). Conversely, tactile
 387 illusions were significantly more frequently evoked in the older group (100%) than in the
 388 younger group (95%) at the low intensity ($p = .03$). More precisely, four older participants and
 389 one younger adult did not feel any illusion when a low-intensity proprioceptive stimulation was
 390 applied, and one of these older participants did not feel any illusion when a high-intensity
 391 proprioceptive stimulation was applied.

392 Table 2: Occurrence of illusions (% mean \pm SD) and subjective rate of the illusion saliency
 393 (mean \pm SD) for the three unisensory conditions (P, T, V) at two intensity levels in the older
 394 and younger groups. Statistics are between-groups comparisons using Mann-Whitney tests. * p
 395 $< .05$; ** $p < .01$; *** $p < .001$.

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

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398 3.1.2 Illusion saliency (Table 2)

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

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

406 3.1.3 Illusion latencies (Fig.3)

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

409 We examined the impact of aging on the latency of the perceived illusions, and whether
 410 this impact differed depending on which sensory modality was stimulated (proprioception,
 411 touch, or vision) at which intensity (Low or High). The three-way mixed ANOVA showed a

412 main effect of age [$F(1, 29) = 16.68, p = .0003, \eta^2 = 0.36$]: for the three unisensory conditions
413 and the two intensity levels considered, younger participants reported their illusory sensations
414 earlier with a mean \pm SD latency of 1008 ± 654 ms compared to older individuals who had
415 longer mean \pm SD latency of 2773 ± 1841 ms.

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

428 A significant main effect of intensity was observed for the three unisensory stimuli, i.e.,
429 latencies were on average longer in response to low intensity than to high intensity [$F(1, 29) =$
430 $7.16, p = .012, \eta^2 = 0.20$] with no significant interactions between intensity * age [$F(1, 29) =$
431 $0.29, p = .59, \eta^2 = 0.009$] or intensity * modality [$F(2, 58) = 0.31, p = .74, \eta^2 = 0.01$] nor between
432 age* modality * intensity [$F(2, 58) = 1.62, p = .21, \eta^2 = 0.05$].

433

434

Figure 3 (1 column) (print color)

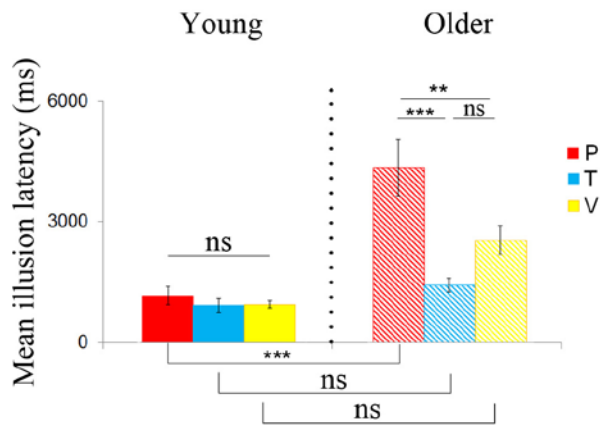


Figure 3: Mean illusion latencies (\pm SEM) for young (solid fill) and older (striped fill) participants in response to muscle proprioceptive (P, red), tactile (T, blue) and visual (V, yellow) stimuli for the two stimulation intensities confounded. ns: non-significant $p_{\text{corr}} > .05$; *: $p_{\text{corr}}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

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437 3.1.4 Illusion velocities (Fig. 4)

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

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

443 Increasing the stimulation intensity led to a faster perceived illusion in both younger and
444 older groups all modalities confounded [Main effect of intensity: $F(1, 30) = 45.36, p < .0001,$
445 $\eta^2 = 0.60$] with no significant interaction between intensity and age [$F(1, 30) = 0.33, p = .57,$
446 $\eta^2 = 0.011$] or between intensity and modality [$F(2, 60) = 0.07, p = .93, \eta^2 = 0.049$].

447 Moreover, the effect of age was significantly different depending on the stimulated
448 modality [Interaction age * modality $F(2, 60) = 17.7, p < .0001, \eta^2 = 0.37$] and on the intensity
449 of stimulation [Interaction age * modality * intensity $F(2, 60) = 5.92, p = .004, \eta^2 = 0.16$]. Post
450 hoc analysis showed that as previously observed for the latencies, no significant difference was
451 observed in the illusion velocities between the stimulation conditions (P, T and V) at the two
452 stimulation intensities within the younger group. On the contrary, in the older group, tactile
453 illusions were perceived faster than the visual illusions, and both were faster than proprioceptive
454 illusions for the low and the high intensities of stimulation ($p_{\text{corr}} < .0001$; Fig. 4). Interestingly,
455 the illusion velocity for the tactile stimulation was significantly greater for the older group
456 compared to the younger group at both intensities (Old > Young: $T_{\text{Low}}, p_{\text{corr}} = .027; T_{\text{High}}, p_{\text{corr}}$

457 = .007) while the visual and proprioceptive illusions did not significantly differ on this
 458 parameter between the two groups ($p_{\text{corr}} > .05$).

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

463

464

Figure 4 (1 column) (color online only)

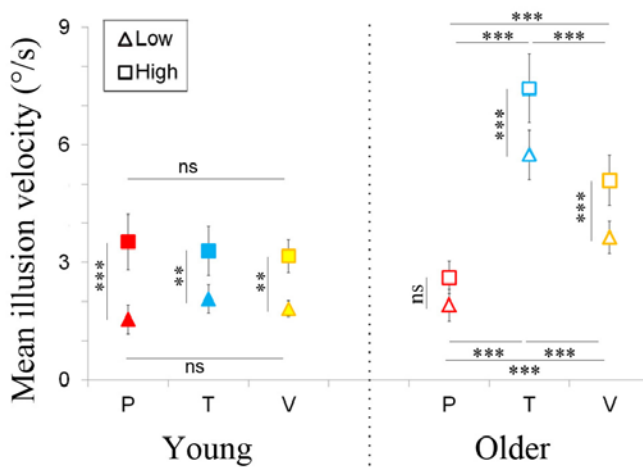


Figure 4: Mean illusion velocity (\pm SEM) perceived by the young (solid fill) and older (solid line) participants in response to muscle proprioceptive (P, red), tactile (T, blue) and visual (V, yellow) stimulations at low (triangle symbol) and high (square symbol) intensities. ns: non-significant $p_{\text{corr}} > .05$; *: $p_{\text{corr}} < .05$; **: $p_{\text{corr}} < .01$; ***: $p_{\text{corr}} < .001$ (p_{corr} : p corrected for multiple comparisons)

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466

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

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

480 **Figure 5 (1 column) (color online only)**

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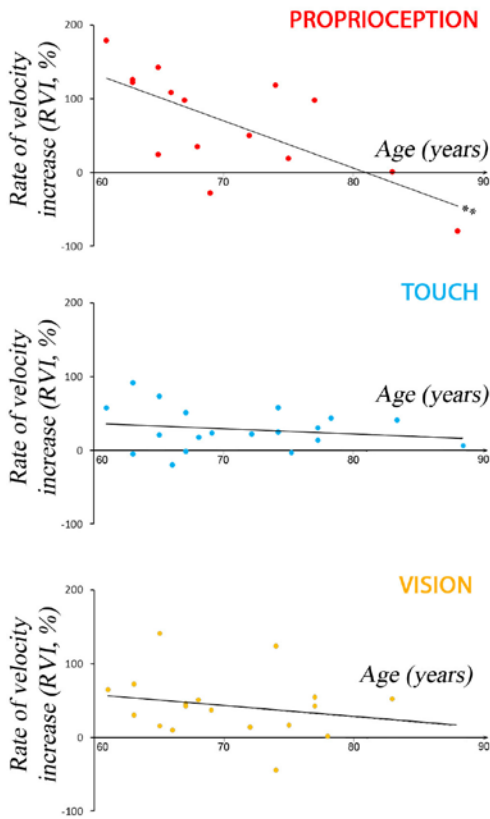


Figure 5: Correlations between individual RVI values and Age within the older group for the proprioceptive (higher panel), the tactile (middle panel), and the visual stimulation (lower panel).

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

483 **3.2 Multisensory stimulation: comparisons within and between groups**

484 **3.2.1 Illusion occurrence**

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

487 **3.2.2 Illusion saliency**

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

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

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

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3.2.3 Illusion latencies

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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 [$F(3, 90) = 2.04$, $p = .11$, $\eta^2 = 0.06$].

508

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Table 4: Illusion latencies (mean \pm 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).

511

512

		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

513

514 3.3.4 Illusion velocities (Fig. 6)

515 Comparisons in the velocities of the illusions between the two groups and between the
516 different multisensory conditions applied at high and low velocities were tested using a three-
517 way mixed design ANOVA. On the whole, older participants perceived faster illusions (mean
518 ± SD = 6.40 ± 2.89 °/s) than younger participants (mean ± SD = 3.32 ± 2.11 °/s) for the four
519 multisensory conditions confounded [Main effect of age: F(1, 30) = 15.43, p = .0005, η^2 =
520 0.34]. However, this effect of age differed according to the multisensory stimulation
521 [Interaction age * modality F(3, 90) = 6.31, p = .0006, η^2 = 0.17] and the intensity of the
522 stimulation [Interaction age * modality * intensity : F(3, 90) = 6.07, p = .0008, η^2 = 0.17].

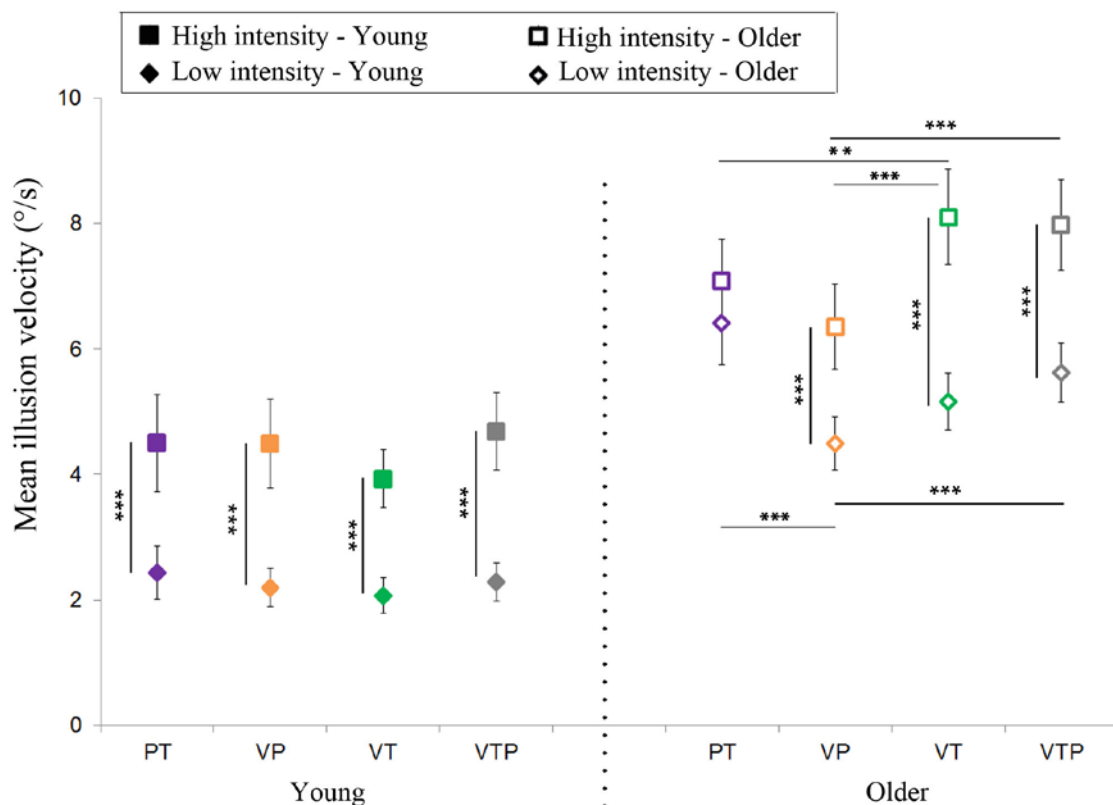
523 Post-hoc analysis (see Table 9 in supplementary data) showed that in younger adults,
524 whatever the level of stimulation intensity, comparisons among the various multisensory
525 conditions did not reveal any significant difference. In addition, high intensity stimulations lead
526 systematically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

527 By contrast, in the older group, the visuo-proprioceptive stimulation gave rise to slower
528 illusions with respect to the proprio-tactile at low intensity (VP_{low} vs PT_{low} : p_{corr} < .0001).

529 Visuo-proprioceptive illusions were also slower than visuo-tactile illusion at the high intensity
 530 (VP_{high} vs VT_{high} : $p_{corr} < .0001$), as well as slower than the trisensory illusions at the high (VP_{high}
 531 vs VTP_{high} : $p_{corr} < .0001$) and low intensity (VP_{low} vs VTP_{low} : $p_{corr} = .012$). In other words,
 532 most of multisensory conditions including a tactile stimulation had a greater effect than the
 533 visuo-proprioceptive conditions. Conversely, adding a tactile stimulation to the visuo-
 534 proprioceptive stimulation leads to an increased illusion while this did not hold true for the
 535 other bisensory conditions.

536 In addition, like for the unisensory stimulations, increasing the stimulation intensity
 537 leads to an increased perceived velocity in both groups [Main effect of intensity $F(1, 30) = 99.1$,
 538 $p < .0001$, $\eta^2 = 0.77$]. This effect of the intensity did not significantly interact with age
 539 [Interaction age * intensity $F(1, 30) = 0.24$, $p = .63$, $\eta^2 = 0.0075$] but varied according to the
 540 stimulation type [Interaction intensity * modality ($F(3, 90) = 5.4$, $p = .0018$, $\eta^2 = 0.15$]. Post
 541 hoc analysis of the triple interaction revealed that only in the proprio-tactile condition, the older
 542 participants did not show a significant increase in illusion velocity between the low and the
 543 high intensity level after correction for multiple comparisons (PT_{high} vs PT_{low} : $p_{corr} = 1$, Fig. 6
 544 and see Table 9 supplementary data).

545 **Figure 6 (1.5 column) (color online only)**



546

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

551 Finally, we investigated the impact of increased intensities of stimulation in both groups
 552 independently of how fast the illusions were perceived via the percentage of illusion velocity
 553 increase (RVI) between the high and low stimulation intensities. Results on Figure 7 show that
 554 like for the unisensory stimulation, the RVI was significantly smaller in the older group
 555 compared to the younger group for all multisensory conditions (Mann-Whitney tests: PT: U =
 556 221, $p < .001$, VP: U = 260, $p = .04$, VTP: U = 203, $p < .001$) except for the visuo-tactile
 557 condition (U = 265, $p = .06$).

558 **Figure 7 (1column) (color online only)**

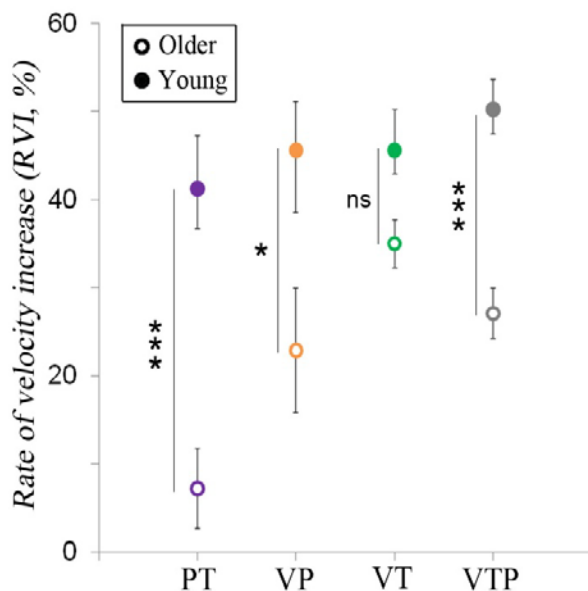


Figure 7: Rate of illusion velocity increase (\pm SEM) between the low and the high level of stimulation intensity in the four multisensory conditions observed in the younger (full dots) and older (empty dots) groups.

PT: proprio-tactile (purple), VP: visuo-proprioceptive (orange), VT : visuo-tactile (green), and VTP: visuo-proprio-tactile (grey) conditions. ns: $p > .05$; *: $p < .05$; **: $p < .01$; ***: $p < .001$.

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560

561 3.3.5 Multisensory index (MSI) for illusion velocities

562 To quantify the improvement of the perceptual responses induced by the multisensory
 563 stimulation with respect to the most efficient unisensory stimulation, the multisensory index
 564 (MSI) was individually estimated for each multisensory condition. A positive MSI value
 565 reflected a perceptual benefit of the multisensory condition over the best unisensory conditions.
 566 Perceptual benefits of multisensory stimulation were first tested using one-sample Wilcoxon
 567 tests comparing mean MSI values to zero. In the younger group, a perceptual benefit was
 568 significantly observed only at the high intensity level for all the multisensory conditions except

569 for the visuo-tactile condition. In the older group, participants showed a perceptual benefit in
 570 most of multisensory conditions except for the visuo-tactile and visuo-proprio-tactile conditions
 571 at the low intensity level and for the proprio-tactile condition at the higher intensity level (see
 572 Table 5).

573 Interestingly, by comparing the two groups, no significant difference between the MSI values
 574 was found for all multisensory conditions. As clearly shown in Figure 8 where individual MSI
 575 values were plotted for all multisensory conditions, the indexes of integration did not differ
 576 between the older and younger participants for the four multisensory conditions tested.

577

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

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

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Figure 8 (1 column) (color online only)

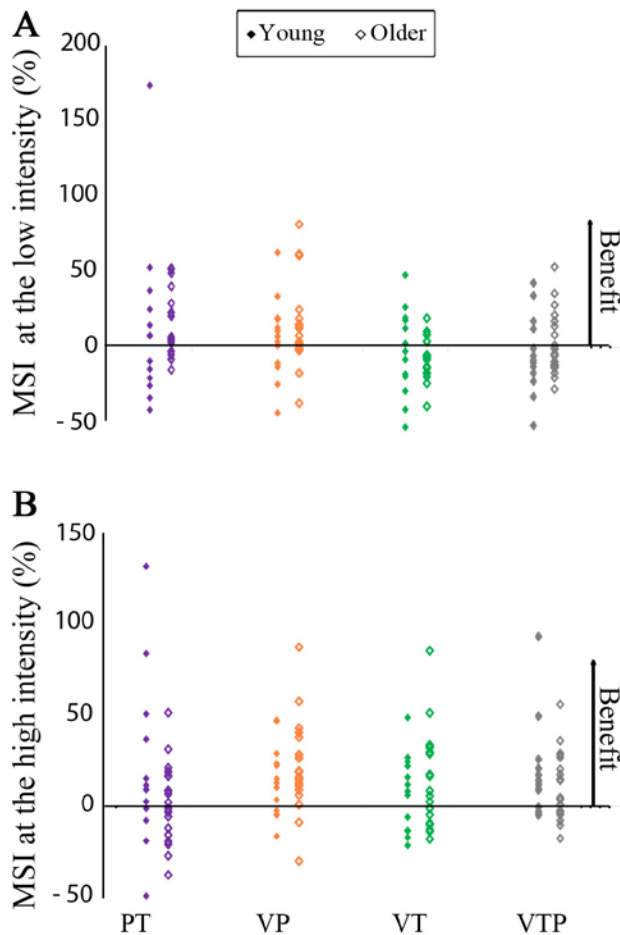


Figure 8: Individual multisensory index (MSI) for illusion velocities at low (A) and high (B) intensity of stimulation in the younger (full diamonds) and older (empty diamonds) groups in response to proprio-tactile (PT, purple), visuo-proprioceptive (VP, orange), visuo-tactile (VT, green) and trisensory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

585

586 4. Discussion

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

592

593 4.1 Reshaping of sensory reliance with age

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

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

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

618 Kinesthetic illusions induced by visual or tactile stimulation were also altered in elderly.
619 Increasing the intensity level of the visual or tactile stimulation resulted in a smaller increase in
620 the illusion velocity in the older adults compared with the younger adults (attested by lower
621 RVI values in the older than the younger group). Because this was not observed for the tactile
622 and visual stimulation for which the response latencies did not differ between older and younger
623 participants, alterations in the perceptual responses observed in the present study cannot be
624 fully explained by a nonspecific effect such as a general slowdown of central processing in the
625 elderly nor by a deterioration of the motor system leading to difficulties in actively reproducing
626 with their left hands what they perceive of their right hands. In addition, we ensured in the pre-
627 testing session that older individuals included in this study were able to copy with their left
628 hand a movement passively imposed on their right hand within the range of the younger
629 participants' performances that were included in the present study; i.e., the latencies and

630 velocities of the copied movements should not exceed the mean performance of the younger
631 group from more than two standard deviations).

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

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

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

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

679 Finally, the relative greater decline in muscle proprioception may also be related to a
680 generally more frequent lack of physical activity in the elderly. Indeed, we did not precisely
681 assess the daily physical activity of our participants, either for the older or the younger ones.
682 The informal interview that we had with every participant before the experiment confirmed that
683 they had really different daily occupations (volunteering in association, regular hiking,
684 gardening, sewing, amateur musician...) and came from different lines of work. Some of the
685 elderly were very active while others had little physical exercise a day. This disparity between
686 our participants reduced the possibility of a systematic bias. In addition, elderly participants in
687 the present study did not exhibit manual motor deficits when they reproduced a passively
688 imposed rotation using their contralateral hand as evidenced by the pre-testing session.
689 Nevertheless, the hypothesis of an aging-related reduced engagement in physical activity
690 cannot be fully ruled out, and this issue should be further investigate in follow-up works.

691

692 *4.2 Preservation of multisensory integration processing in elderly*

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

719 During a sensorimotor task such as maintaining upright balance, stance perturbation
720 provoked by a privation of one of the vestibular, proprioceptive or visual systems is generally
721 found to be more severe in the elderly who respond with larger body excursions than younger
722 adults (Abrahamova and Hlavacka, 2008; Peterka and Black, 1990; Quoniam et al., 1995;
723 Speers et al., 2002; Whipple et al., 1993). This instability remains greater in elderly when two
724 sensory systems are simultaneously deprived (Horak et al., 1989; Whipple et al., 1993).

725 However, it is not clear from deprivation experiments whether impairments in postural control
726 result from a degradation of the remaining sensory systems or from a decline in their central
727 integrative processing. The postural consequences induced by multisensory stimulation rather
728 than deprivation have been poorly studied. By applying variable concomitant visual and tactile
729 stimulation in upright standing subjects, Allisson et al. (2006) showed that older participants
730 performed as well as younger participants in adapting the relative weight of one sensory cue
731 with respect to another, i.e., elderly demonstrated an intact inter-sensory reweighting to vision
732 and touch for postural control. This previous study brings into question the general assumption
733 that elderly would have more difficulty in quickly adapting the weighting of the different
734 sensory information to sudden environmental changes ('sensory reweighting adaptation')
735 resulting in greater imbalance and risk of fall in elderly (Horak et al., 1989; Teasdale and
736 Simoneau, 2001).

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

752 With regard to the neuronal basis of multisensory integration in the elderly, there is
753 physiological evidence of compensatory mechanisms at the brain level. Despite the alteration
754 of central structures, such as the reduction of grey (Good et al., 2001; Resnick et al., 2003) and
755 white matter (Lebel et al., 2012) in the brain of the elderly, functional neuroplastic changes
756 occur, and this modulation of brain activity can be correlated with cognitive and sensorimotor
757 decline in older adults. The most general view is that older adults might first compensate for

758 weak cognitive and sensorimotor deficits by increasing related brain network activity (Cabeza
759 et al., 2002; Ward and Frackowiak, 2003) and by extending activations into the ipsilateral
760 hemisphere (Ward, 2006; Kalisch et al. 2009; Brodoehl et al 2013). As an example, during a
761 peripheral tactile stimulation, older adults display an enlarged activation in the contralateral
762 primary somatosensory cortex (SI) and a lesser deactivation of the homologous ipsilateral
763 region (Lenz et al., 2012). A general reduction of inhibitory phenomenon in the brain of elderly
764 is supposed to facilitate such hemispheric asymmetrical reduction in particular between cortical
765 sensorimotor regions (Cabeza et al., 2002; Lenz et al., 2012). In addition to recruit more brain
766 areas, older people seem to have a loss of specialization of specific brain circuits. At the neural
767 level, it is attested by a reduction in stimulus selectivity as evidenced in older monkeys by a
768 degradation of visual orientation and direction selectivity in the visual cortex (Schmolesky et
769 al., 2000). Although the exact neural bases are still debated, the authors seem to converge
770 towards the idea that multisensory integration is maximized in the elderly, which is an
771 advantage when the information is relevant, but a disadvantage when it is not relevant or simply
772 noise.

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

780

781 **3. Conflict of interest**

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

784

785 **4. Author contributions**

786 Conceived and designed the work: AK, MG, OF. Acquired and analyzed the data: MC, CL,
787 CB. Wrote the paper: AK and MC. All authors revised the work for important intellectual

788 content. All of the authors have read and approved the final version of the manuscript. All
789 authors agree to be accountable for the content of the work.

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794

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798

799 **7. Figure captions**

800

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

808

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

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

818 **Figure 3:** Mean illusion latencies (\pm SEM) for younger (solid fill) and older (striped fill)
819 participants in response to muscle proprioceptive (P, red), tactile (T, blue) and visual (V,
820 yellow) stimuli for the two stimulation intensities confounded. ns: non-significant $p_{\text{corr}} > .05$; *:
821 $p_{\text{corr}} < .05$; **: $p_{\text{corr}} < .01$; ***: $p_{\text{corr}} < .001$ (p_{corr} : p corrected for multiple comparisons)

822

823 **Figure 4:** Mean illusion velocity (\pm SEM) perceived by the younger (solid fill) and older (solid
824 line) participants in response to muscle proprioceptive (P, red), tactile (T, blue) and visual (V,
825 yellow) stimulations at low (triangle symbol) and high (square symbol) intensities. ns: non-
826 significant $p_{\text{corr}} > .05$; *: $p_{\text{corr}} < .05$; **: $p_{\text{corr}} < .01$; ***: $p_{\text{corr}} < .001$ (p_{corr} : p corrected for multiple
827 comparisons)

828 **Figure 5:** Correlations between individual RVI values and Age within the older group for the
829 proprioceptive (higher panel), the tactile (middle panel), and the visual stimulation (lower
830 panel). Note that the negative correlation was significant only for the proprioceptive condition
831 ($p = .004$).

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

836 **Figure 7:** Rate of illusion velocity increase (\pm SEM) between the low and the high level of
837 stimulation intensity in the four multisensory conditions observed in the younger (full dots) and
838 older (empty dots) groups.

839 PT: proprio-tactile (purple), VP: visuo-proprioceptive (orange), VT : visuo-tactile (green), and
840 VTP: visuo-proprio-tactile (grey) conditions. ns: $p > .05$; *: $p < .05$; **: $p < .01$; ***: $p < .001$.

841

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

847

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