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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:  $71 \pm 7$  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:  $29 \pm 10$  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).

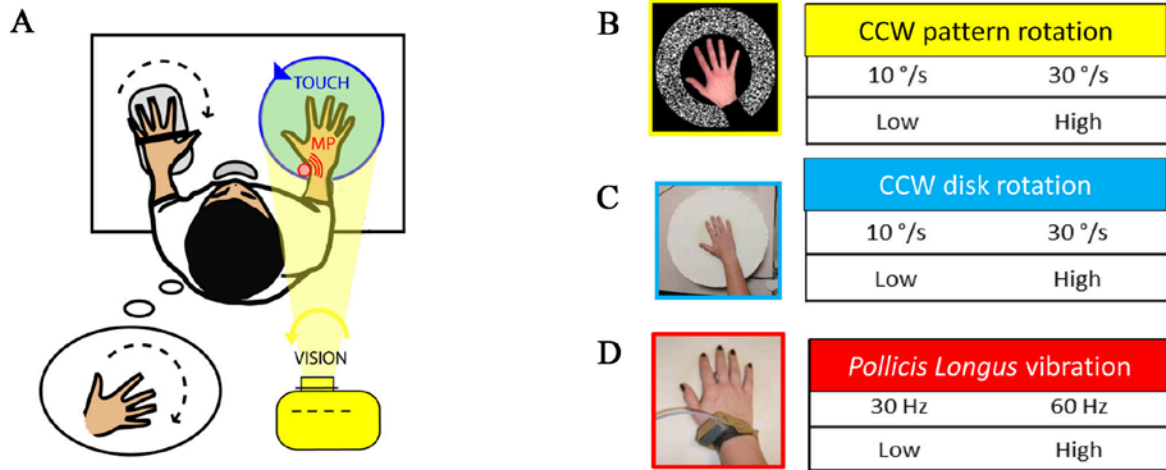
193 Visual stimulation consisted of a projection of a black and white pattern on the disk. To  
194 give the participant the feeling that the pattern was moving in the background, i.e., under his/her  
195 hand, a black mask adjusted to the size of each participant's hand was included in the video that  
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 k $\Omega$ , 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):

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

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

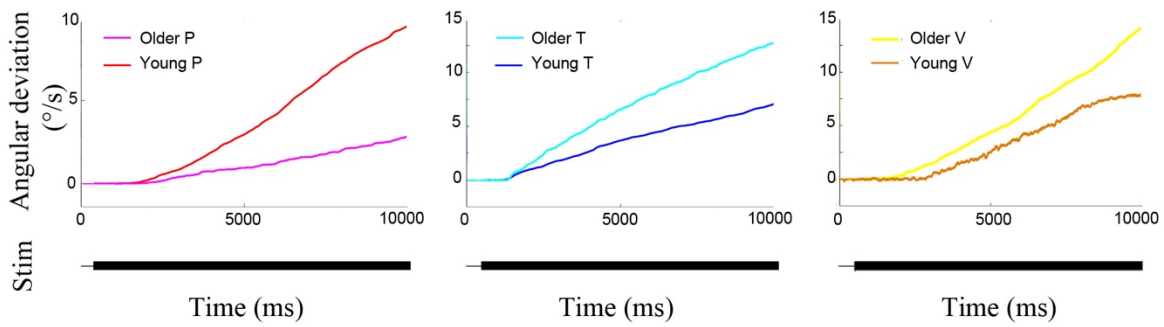
### 360 **3. Results**

#### 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  $1008 \pm 654$  ms compared to older individuals who had  
415 longer mean  $\pm$  SD latency of  $2773 \pm 1841$  ms.

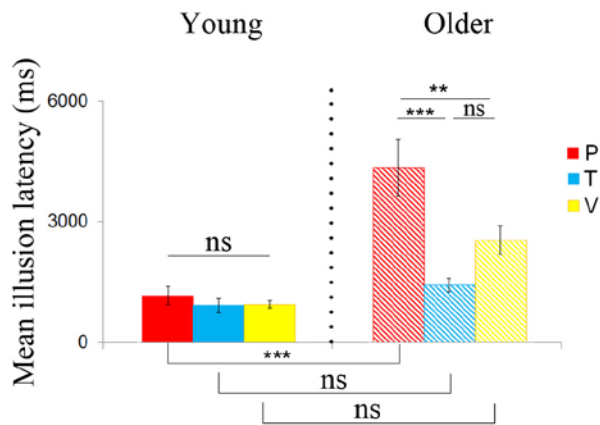
416 As shown in Figure 3, a significant interaction between age and modality was observed  
417 [ $F(2, 58) = 6.39, p = .0031, \eta^2 = 0.18$ ]. In the younger group, post hoc analysis showed that  
418 there were no significant differences regarding the latencies between any of the three stimulated  
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)

435  
436

### 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:  $T_{\text{Low}}, p_{\text{corr}} = .027; T_{\text{High}}, p_{\text{corr}}$

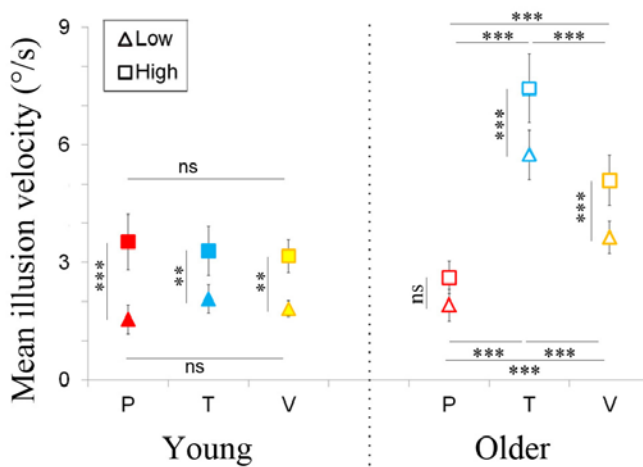
457 = .007) while the visual and proprioceptive illusions did not significantly differ on this  
 458 parameter between the two groups ( $p_{\text{corr}} > .05$ ).

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 ( $P_{\text{low}}$  vs  $P_{\text{high}}$ :  $p_{\text{corr}} = .27$ ). 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  $p_{\text{corr}} > .05$ ; \*:  $p_{\text{corr}} < .05$ ; \*\*:  $p_{\text{corr}} < .01$ ; \*\*\*:  $p_{\text{corr}} < .001$  ( $p_{\text{corr}}$  : p corrected for multiple comparisons)

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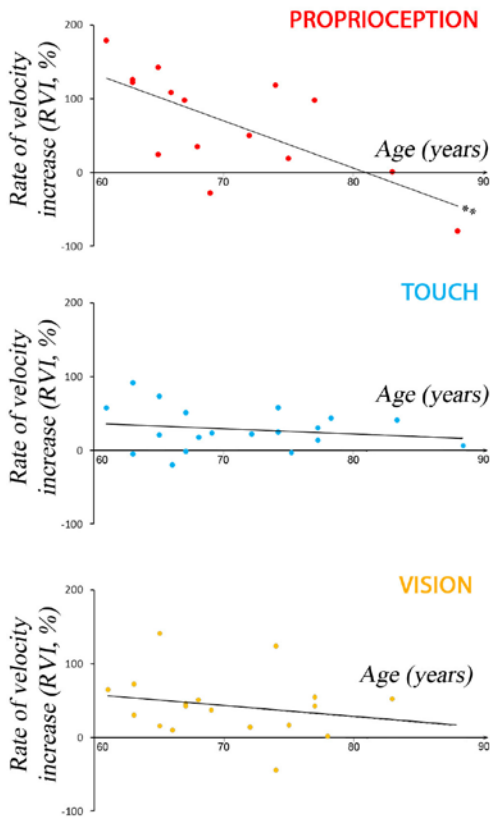
467 In order to investigate the impact of increased intensities of stimulation in both groups  
 468 independently of how fast the illusions were perceived, we computed the rate of velocity  
 469 increase (RVI). The RVI is the percentage of illusion velocity increase between the high and  
 470 low 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

509

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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,  $\eta^2$  =  
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,  $\eta^2$  = 0.17] and the intensity of the  
522 stimulation [Interaction age \* modality \* intensity : F(3, 90) = 6.07, p = .0008,  $\eta^2$  = 0.17].

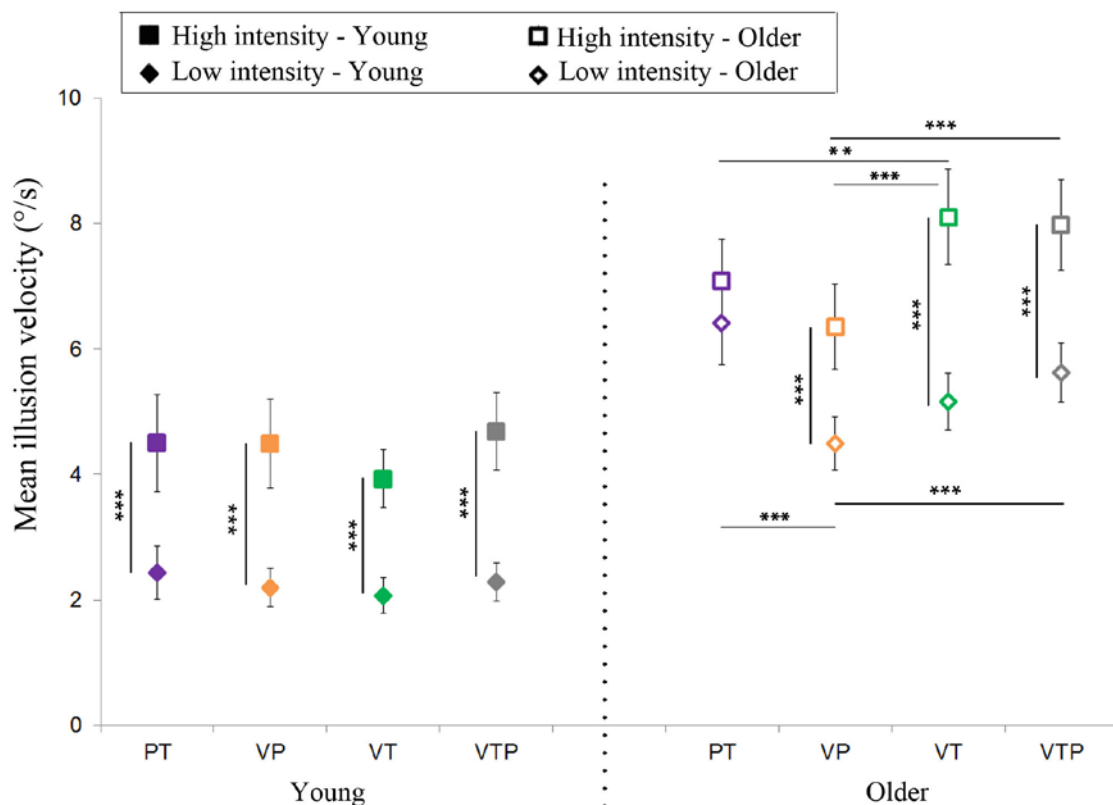
523 Post-hoc analysis (see Table 9 in supplementary data) showed that in younger adults,  
524 whatever the level of stimulation intensity, comparisons among the various multisensory  
525 conditions did not reveal any significant difference. In addition, high intensity stimulations lead  
526 systematically 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<sub>low</sub> vs PT<sub>low</sub> : p<sub>corr</sub> < .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)**

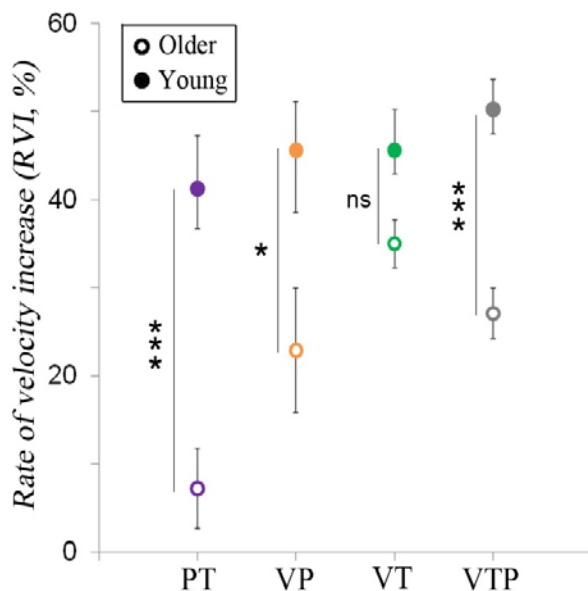


546

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.** \*:  $p_{\text{corr}} < .05$ ; \*\*:  $p_{\text{corr}} < .01$ ; \*\*\*:  $p_{\text{corr}} < .001$  ( $p_{\text{corr}}$  : 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:  $p > .05$ ; \*:  $p < .05$ ; \*\*:  $p < .01$ ; \*\*\*:  $p < .001$ .

559

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). \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\* $p < 0.001$ .

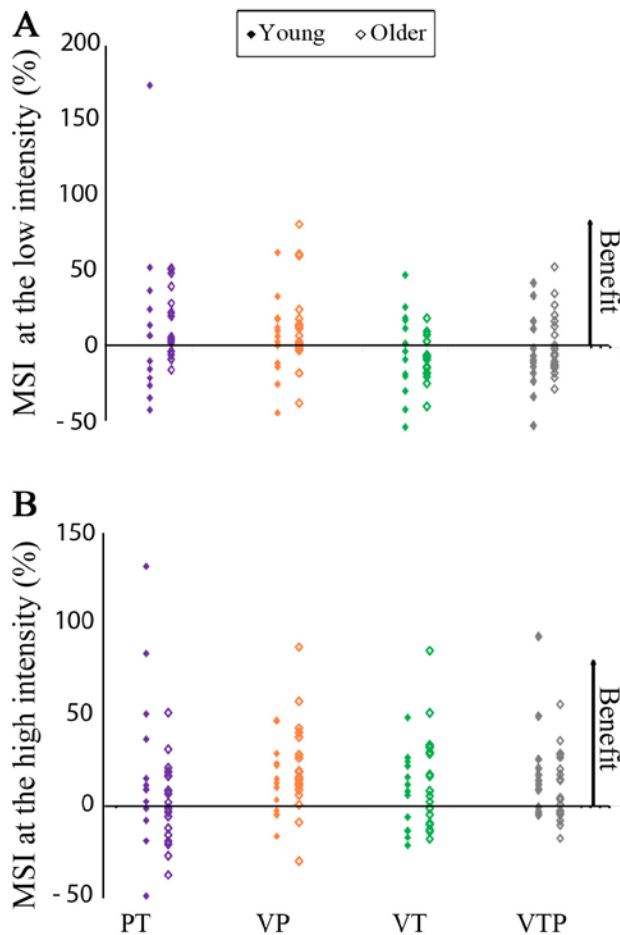
		MSI VELOCITY							
		Young			Old			Young vs. Old	
		Mean $\pm$ SD	V	<i>p</i>	Mean $\pm$ SD	V	<i>p</i>	U	<i>p</i>
Low Intensity	PT	13.62 $\pm$ 55.6	50	.39	14.07 $\pm$ 21.3	148	.016*	102	.42
	VP	6.34 $\pm$ 26.6	59	.19	12.48 $\pm$ 28.0	142	.03*	119	.88
	VT	-3.22 $\pm$ 28.5	40	.66	-7.56 $\pm$ 13.1	39	.10	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  $p_{\text{corr}} < .05$ ; \*\*:  $p_{\text{corr}} < .01$ ; \*\*\*:  $p_{\text{corr}} < .001$  ( $p_{\text{corr}}$  : 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  $p_{\text{corr}} > .05$ ; \*:  $p_{\text{corr}} < .05$ ; \*\*:  $p_{\text{corr}} < .01$ ; \*\*\*:  $p_{\text{corr}} < .001$  ( $p_{\text{corr}}$ : 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. \*:  $p_{\text{corr}} < .05$ ; \*\*:  $p_{\text{corr}} < .01$ ; \*\*\*:  $p_{\text{corr}} < .001$  ( $p_{\text{corr}}$ :  
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

848 **8. References**

- 849 Abrahamova, D., Hlavacka, F., 2008. Age-related changes of human balance during quiet stance.  
850 *Physiol Res* 57, 957–64.
- 851 Aimonetti, J.M., Roll, J.P., Hospod, V., Ribot-Ciscar, E., 2012. Ankle joint movements are encoded by  
852 both cutaneous and muscle afferents in humans. *Exp Brain Res* 221, 167–76.
- 853 Albert, F., Bergenheim, M., Ribot-Ciscar, E., Roll, J.-P., 2006. The Ia afferent feedback of a given  
854 movement evokes the illusion of the same movement when returned to the subject via  
855 muscle tendon vibration. *Experimental Brain Research* 172, 163–174. doi:10.1007/s00221-  
856 005-0325-2
- 857 Allison, L.K., Kiemel, T., Jeka, J.J., 2006. Multisensory reweighting of vision and touch is intact in  
858 healthy and fall-prone older adults. *Exp. Brain Res.* 175, 342–352.
- 859 Andersen, G.J., 2012. Aging and vision: changes in function and performance from optics to  
860 perception. *Wiley Interdiscip. Rev.-Cogn. Sci.* 3, 403–410. doi:10.1002/wcs.1167
- 861 Bates, S.L., Wolbers, T., 2014. How cognitive aging affects multisensory integration of navigational  
862 cues. *Neurobiology of Aging* 35, 2761–2769. doi:10.1016/j.neurobiolaging.2014.04.003
- 863 Blanchard, C., Roll, R., Roll, J.-P., Kavounoudias, A., 2013. Differential Contributions of Vision, Touch  
864 and Muscle Proprioception to the Coding of Hand Movements. *PLoS ONE* 8, e62475.  
865 doi:10.1371/journal.pone.0062475
- 866 Blanchard, C., Roll, R., Roll, J.-P., Kavounoudias, A., 2011. Combined contribution of tactile and  
867 proprioceptive feedback to hand movement perception. *Brain Res.* 1382, 219–229.  
868 doi:10.1016/j.brainres.2011.01.066
- 869 Borel, L., Alescio-Lautier, B., 2014. Posture and cognition in the elderly: Interaction and contribution  
870 to the rehabilitation strategies. *Neurophysiol. Clin. Neurophysiol.* 44, 95–107.  
871 doi:10.1016/j.neucli.2013.10.129
- 872 Braem, B., Honoré, J., Rousseaux, M., Saj, A., Coello, Y., 2014. Integration of visual and haptic  
873 informations in the perception of the vertical in young and old healthy adults and right brain-  
874 damaged patients. *Neurophysiol. Clin. Clin. Neurophysiol.* 44, 41–48.  
875 doi:10.1016/j.neucli.2013.10.137
- 876 Brandt, T., Dichgans, J., 1972. Circularvection, visually induced pseudocoriolis effects, optokinetic  
877 afternystagmus. A comparative study of subjective and objective optokinetic aftereffects.  
878 *Arch Klin Exp Ophthalmol* 184(1):42-57.
- 879 Breugnot, C., M.A., B., Ribot-Ciscar, E., Aimonetti, J.M., Roll, J.P., Renner, M., 2006. Mechanical  
880 Discrimination of Hairy Fabrics from Neurosensorial Criteria. *Text. Res. J.* 76, 835–46.

881 Brodoehl, S., Klingner, C., Stieglitz, K., Witte, O.W., 2013. Age-related changes in the somatosensory  
882 processing of tactile stimulation—An fMRI study. *Behavioural Brain Research* 238, 259–264.  
883 doi: 10.1016/j.bbr.2012.10.038

884 Brodoehl, S., Klingner, C., Witte, O.W., 2016. Age-dependent modulation of the somatosensory  
885 network upon eye closure. *Behavioural Brain Research* 298, 52–56.  
886 doi:10.1016/j.bbr.2015.10.035

887 Cabeza, R., Anderson, N.D., Locantore, J.K., McIntosh, A.R., 2002. Aging gracefully: compensatory  
888 brain activity in high-performing older adults. *Neuroimage* 17, 1394–402.

889 Chancel, M., Blanchard, C., Guerraz, M., Montagnini, A., Kavounoudias, A., 2016a. Optimal visuo-  
890 tactile integration for velocity discrimination of self-hand movements. *J. Neurophysiol.*  
891 jn.00883.2015. doi:10.1152/jn.00883.2015

892 Chancel, M., Brun, C., Kavounoudias, A., Guerraz, M., 2016b. The kinesthetic mirror illusion: How  
893 much does the mirror matter? *Exp. Brain Res.* 234, 1459–1468. doi:10.1007/s00221-015-  
894 4549-5

895 Collins, D.F., Refshauge, K.M., Gandevia, S.C., 2000. Sensory integration in the perception of  
896 movements at the human metacarpophalangeal joint. *J. Physiol.* 529, 505–515.

897 Cordo, P.J., Horn, J.L., Kunster, D., Cherry, A., Bratt, A., Gurfinkel, V., 2011. Contributions of skin and  
898 muscle afferent input to movement sense in the human hand. *J Neurophysiol* 105, 1879–88.

899 de Boer-Schellekens, L., Vroomen, J., 2014. Multisensory integration compensates loss of sensitivity  
900 of visual temporal order in the elderly. *Exp. Brain Res.* 232, 253–262. doi:10.1007/s00221-  
901 013-3736-5

902 de Dieuleveult, A.L., Siemonsma, P.C., van Erp, J.B.F., Brouwer, A.-M., 2017. Effects of Aging in  
903 Multisensory Integration: A Systematic Review. *Frontiers in Aging Neuroscience* 9.  
904 doi:10.3389/fnagi.2017.00080

905 Desrosiers, J., Hébert, R., Bravo, G., Rochette, A., 1999. Age-related changes in upper extremity  
906 performance of elderly people: a longitudinal study. *Exp. Gerontol.* 34, 393–405.

907 Diaconescu, A.O., Hasher, L., McIntosh, A.R., 2013. Visual dominance and multisensory integration  
908 changes with age. *NeuroImage* 65, 152–166. doi:10.1016/j.neuroimage.2012.09.057

909 Diederich, A., Colonius, H., Schomburg, A., 2008. Assessing age-related multisensory enhancement  
910 with the time-window-of-integration model. *Neuropsychologia* 46, 2556–2562.

911 Dorfman, L.J., Bosley, T.M., 1979. Age-related changes in peripheral and central nerve conduction in  
912 man. *Neurology* 29, 38–44.

913 Eikema, D.J.A., Forrester, L.W., Whittall, J., 2014. Manipulating the stride length/stride velocity  
914 relationship of walking using a treadmill and rhythmic auditory cueing in non-disabled older

915 individuals. A short-term feasibility study. *Gait & Posture* 40, 712–714.  
 916 doi:10.1016/j.gaitpost.2014.06.003  
 917 Fetsch, C.R., Turner, A.H., DeAngelis, G.C., Angelaki, D.E., 2009. Dynamic Reweighting of Visual and  
 918 Vestibular Cues during Self-Motion Perception. *J. Neurosci.* 29, 15601–15612.  
 919 doi:10.1523/JNEUROSCI.2574-09.2009  
 920 Freiherr, J., Lundström, J.N., Habel, U., Reetz, K., 2013. Multisensory integration mechanisms during  
 921 aging. *Frontiers in Human Neuroscience* 7. doi:10.3389/fnhum.2013.00863  
 922 Goble, D.J., Coxon, J.P., Wenderoth, N., Van Impe, A., Swinnen, S.P., 2009. Proprioceptive sensibility  
 923 in the elderly: degeneration, functional consequences and plastic-adaptive processes.  
 924 *Neurosci Biobehav Rev* 33, 271–8.  
 925 Good, C.D., Johnsrude, I.S., Ashburner, J., Henson, R.N., Friston, K.J., Frackowiak, R.S., 2001. A voxel-  
 926 based morphometric study of ageing in 465 normal adult human brains. *Neuroimage* 14, 21–  
 927 36.  
 928 Goodwin, G.M., McCloskey, D.I., Matthews, P.B., 1972. Proprioceptive illusions induced by muscle  
 929 vibration: contribution by muscle spindles to perception? *Science* 175, 1382–1384.  
 930 Guerraz, M., Bronstein, A.M., 2008. Mechanisms underlying visually induced body sway.  
 931 *Neuroscience Letters* 443, 12–16. doi:10.1016/j.neulet.2008.07.053  
 932 Guerraz, M., Provost, S., Narison, R., Brugnon, A., Virolle, S., Bresciani, J.-P., 2012. Integration of  
 933 visual and proprioceptive afferents in kinesthesia. *Neuroscience* 223, 258–268.  
 934 doi:10.1016/j.neuroscience.2012.07.059  
 935 Haibach, P., Slobounov, S., Newell, K., 2009. Egomotion and vection in young and elderly adults.  
 936 *Gerontology* 55, 637–643. doi:10.1159/000235816  
 937 Hay, L., Bard, C., Fleury, M., & Teasdale, N., 1996. Availability of visual and proprioceptive afferent  
 938 messages and postural control in elderly adults. *Experimental Brain Research* 108(1), 129–  
 939 139.  
 940 Horak, F.B., Shupert, C.L., Mirka, A., 1989. Components of postural dyscontrol in the elderly: a  
 941 review. *Neurobiol Aging* 10, 727–38.  
 942 Hugenschmidt, C.E., Mozolic, J.L., Laurienti, P.J., 2009. Suppression of multisensory integration by  
 943 modality-specific attention in aging: *NeuroReport* 20, 349–353.  
 944 doi:10.1097/WNR.0b013e328323ab07  
 945 Kalisch, T., Ragert, P., Schwenkreis, P., Dinse, H.R., Tegenthoff, M., 2009. Impaired Tactile Acuity in  
 946 Old Age Is Accompanied by Enlarged Hand Representations in Somatosensory Cortex.  
 947 *Cerebral Cortex* 19, 1530–1538. doi:10.1093/cercor/bhn190  
 948 Kararizou, E., Manta, P., Kalfakis, N., Vassilopoulos, D., 2005. Morphometric study of the human  
 949 muscle spindle. *Anal Quant Cytol Histol* 27, 1–4.

950 Karmali, F., Whitman, G.T., Lewis, R.F., 2018. Bayesian optimal adaptation explains age-related  
951 human sensorimotor changes. *Journal of Neurophysiology* 119, 509–520. doi:  
952 10.1152/jn.00710.2017

953 Kavounoudias, A., 2017. Sensation of Movement : a Multimodal Perception in: *Movement sensation*,  
954 *Thor Grünbaum and Mark Schram Christensen Eds*, Routledge, Psychology Press ed, New-  
955 York, pp. 87-109.

956 Kuehn, E., Perez-Lopez, M.B., Diersch, N., Döhler, J., Wolbers, T., Riemer, M., 2018. Embodiment in  
957 the aging mind. *Neuroscience & Biobehavioral Reviews* 86, 207–225.  
958 doi:10.1016/j.neubiorev.2017.11.016

959 Laurienti, P.J., Burdette, J.H., Maldjian, J.A., Wallace, M.T., 2006. Enhanced multisensory integration  
960 in older adults. *Neurobiol. Aging* 27, 1155–1163. doi:10.1016/j.neurobiolaging.2005.05.024

961 Lebel, C., Gee, M., Camicioli, R., Wieler, M., Martin, W., Beaulieu, C., 2012. Diffusion tensor imaging  
962 of white matter tract evolution over the lifespan. *NeuroImage* 60, 340–352.  
963 doi:10.1016/j.neuroimage.2011.11.094

964 Lenz, M., Tegenthoff, M., Kohlhaas, K., Stude, P., Hoffken, O., Gatica Tossi, M.A., Kalisch, T., Dinse,  
965 H.R., 2012. Increased Excitability of Somatosensory Cortex in Aged Humans is Associated  
966 with Impaired Tactile Acuity. *Journal of Neuroscience* 32, 1811–1816.  
967 doi:10.1523/JNEUROSCI.2722-11.2012

968 Mahoney, J.R., Verghese, J., Dumas, K., Wang, C., Holtzer, R., 2012. The effect of multisensory cues  
969 on attention in aging. *Brain Res.* 1472, 63–73. doi:10.1016/j.brainres.2012.07.014

970 Mozolic, J.L., Hugenschmidt, C.E., Peiffer, A.M., Laurienti P.J., 2012. Multisensory Integration and Aging.  
971 In: *The Neural Bases of Multisensory Processes Murray MM and Wallace MT, eds*. Boca Raton  
972 (FL): CRC Press/Taylor & Francis; 2012. Chapter 20.

973 Owsley, C., 2011. Aging and vision. *Vision Res.* 51, 1610–1622. doi:10.1016/j.visres.2010.10.020

974 Owsley, C., Sekuler, R., Siemsen, D., 1983. Contrast sensitivity throughout adulthood. *Vis. Res* 23,  
975 689–99.

976 Peiffer, A.M., Mozolic, J.L., Hugenschmidt, C.E., Laurienti, P.J., 2007. Age-related multisensory  
977 enhancement in a simple audiovisual detection task. *Neuroreport* 18, 1077–1081.

978 Peterka, R.J., Black, F.O., 1990. Age-related changes in human posture control: sensory organization  
979 tests. *J. Vestib. Res. Equilib. Orientat.* 1, 73–85.

980 Peters, R.M., Blouin, J.-S., Dalton, B.H., Inglis, J.T., 2016. Older adults demonstrate superior vestibular  
981 perception for virtual rotations. *Exp. Gerontol.* 82, 50–57. doi:10.1016/j.exger.2016.05.014

982 Poliakoff, E., Ashworth, S., Lowe, C., Spence, C., 2006. Vision and touch in ageing: Crossmodal  
983 selective attention and visuotactile spatial interactions. *Neuropsychologia* 44, 507–517.

984 Prsa, M., Gale, S., Blanke, O., 2012. Self-motion leads to mandatory cue fusion across sensory  
985 modalities. *J. Neurophysiol.* 108, 2282–2291. doi:10.1152/jn.00439.2012

986 Quoniam, C., Hay, L., Roll, J.P., Harlay, F., 1995. Age effects on reflex and postural responses to  
987 propriomuscular inputs generated by tendon vibration. *J Gerontol Biol Sci Med Sci* 50, B155-  
988 65.

989 Resnick, S.M., Pham, D.L., Kraut, M.A., Zonderman, A.B., Davatzikos, C., 2003. Longitudinal magnetic  
990 resonance imaging studies of older adults: a shrinking brain. *J. Neurosci. Off. J. Soc. Neurosci.*  
991 23, 3295–3301.

992 Reuschel, J., Drewing, K., Henriques, D.Y.P., Rösler, F., Fiehler, K., 2009. Optimal integration of visual  
993 and proprioceptive movement information for the perception of trajectory geometry. *Exp.*  
994 *Brain Res.* 201, 853–862. doi:10.1007/s00221-009-2099-4

995 Ribeiro, F., Oliveira, J., 2007. Aging effects on joint proprioception: the role of physical activity in  
996 proprioception preservation. *Eur. Rev. Aging Phys. Act.* 4, 71–76.

997 Roll, J.P., Vedel, J.P., 1982. Kinesthetic role of muscle afferents in man, studied by tendon vibration  
998 and microneurography. *Exp. Brain Res.* 47, 177–190.

999 Schmolesky, M.T., Wang, Y., Pu, M., Leventhal, A.G., 2000. Degradation of stimulus selectivity of  
1000 visual cortical cells in senescent rhesus monkeys. *Nature neuroscience* 3, 384.

1001 Serbruyns, L., Leunissen, I., Huysmans, T., Cuypers, K., Meesen, R.L., van Ruitenbeek, P., Sijbers, J.,  
1002 Swinnen, S.P., 2015. Subcortical volumetric changes across the adult lifespan: subregional  
1003 thalamic atrophy accounts for age-related sensorimotor performance declines. *Cortex J.*  
1004 *Devoted Study Nerv. Syst. Behav.* 65, 128–138. doi:10.1016/j.cortex.2015.01.003

1005 Setti, A., Finnigan, S., Sobolewski, R., McLaren, L., Robertson, I.H., Reilly, R.B., Anne Kenny, R., Newell,  
1006 F.N., 2011. Audiovisual temporal discrimination is less efficient with aging: an event-related  
1007 potential study. *NeuroReport* 22, 554–558. doi:10.1097/WNR.0b013e328348c731

1008 Shaffer, S.W., Harrison, A.L., 2007. Aging of the somatosensory system: a translational perspective.  
1009 *Phys. Ther.* 87, 193–207.

1010 Sherback, M., Valero-Cuevas, F.J., D’Andrea, R., 2010. Slower Visuomotor Corrections with  
1011 Unchanged Latency are Consistent with Optimal Adaptation to Increased Endogenous Noise  
1012 in the Elderly. *PLoS Computational Biology* 6, e1000708. doi:10.1371/journal.pcbi.1000708

1013 Speers, R.A., Kuo, A.D., Horak, F.B., 2002. Contributions of altered sensation and feedback responses  
1014 to changes in coordination of postural control due to aging. *Gait Posture* 16, 20–30.  
1015 doi:10.1016/S0966-6362(02)00003-6

1016 Stein, B.E., Stanford, T.R., Ramachandran, R., Perrault, T.J., Rowland, B.A., 2009. Challenges in  
1017 quantifying multisensory integration: alternative criteria, models, and inverse effectiveness.  
1018 *Exp. Brain Res.* 198, 113–126. doi:10.1007/s00221-009-1880-8

1019 Swash, M., Fox, K.P., 1972. The effect of age on human skeletal muscle. Studies of the morphology  
1020 and innervation of muscle spindles. *J Neurol Sci* 16, 417–32.

1021 Tardy-Gervet, M.F., Gilhodes, J.C., Roll, J.P., 1986. Interactions between visual and muscular  
1022 information in illusions of limb movement. *Behav Brain Res* 20, 161–74.

1023 Tardy-Gervet, M.F., Gilhodes, J.C., Roll, J.P., 1984. Perceptual and motor effects elicited by a moving  
1024 visual stimulus below the forearm: an example of segmentary vection. *Behav Brain Res* 11,  
1025 171–84.

1026 Teasdale, N., Simoneau, M., 2001. Attentional demands for postural control: the effects of aging and  
1027 sensory reintegration. *Gait Posture* 14, 203–210. doi:10.1016/S0966-6362(01)00134-5

1028 van Beers, R.J., Wolpert, D.M., Haggard, P., 2002. When Feeling Is More Important Than Seeing in  
1029 Sensorimotor Adaptation. *Curr. Biol.* 12, 834–837. doi:10.1016/S0960-9822(02)00836-9

1030 Vidal, M., Bühlhoff, H.H., 2010. Storing upright turns: how visual and vestibular cues interact during  
1031 the encoding and recalling process. *Exp. Brain Res.* 200, 37–49. doi:10.1007/s00221-009-  
1032 1980-5

1033 Ward, N.S., 2006. Compensatory mechanisms in the aging motor system. *Ageing Res Rev* 5, 239–54.

1034 Ward, N.S., Frackowiak, R.S., 2003. Age-related changes in the neural correlates of motor  
1035 performance. *Brain* 126, 873–88.

1036 Warren, W.H., Blackwell, A.W., Morris, M.W., 1989. Age differences in perceiving the direction of  
1037 self-motion from optical flow. *J. Gerontol.* 44, P147-153.

1038 Whipple, R., Wolfson, L., Derby, C., Singh, D., Tobin, J., 1993. 10 Altered Sensory Function and  
1039 Balance in Older Persons. *J. Gerontol.* 48, 71–76. doi:10.1093/geronj/48.Special\_Issue.71  
1040