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Age-Related Impairment of Hand Movement Perception Based on Muscle Proprioception and Touch

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Abstract—Impairment in fine hand motor dexterity is well established in older people, yet little is known, about the impaired perception of hand movement in the elderly. Only an age-related increase in movement detection threshold has been reported. Perception of hand movements relies on multiple sensory information, including touch and muscle proprioception. The present study aims to investigate to what extent aging impacts the ability to perceive hand movements accurately and whether this impairment is from a muscle touch and/or tactile origin. To disentangle proprioception and touch, we used specifically designed stimuli: a mechanical vibration applied to the wrist muscle tendon and a tactile-textured disk rotating under the participant's hand, respectively. These two stimuli elicited illusions of hand rotations in two groups of young (20–30 years) and older (65–75 years) participants. Psychophysical testing showed that velocity discrimination thresholds of tactile and proprioceptive illusions were about twice lower in the young, than the older group. Also, relatively small isometric contractions were involuntarily elicited in wrist muscles during the illusions in both groups, but this motor response was positively correlated with the discrimination performance of the young, but not the older, participants. The present results show that muscle proprioception and touch are both functionally affected in kinesthesia after 65 years old, with a more pronounced alteration for muscle proprioception. This alteration in discriminative ability is likely due to impairment in the accurate encoding of the kinematic properties of hand movements. The possible central vs peripheral origin of these perceptive–motor changes with aging is discussed.

Key words: kinesthesia, illusion, multisensory, velocity discrimination, vibration.

INTRODUCTION

The decline of all sensory systems with healthy aging is well-documented, including the somatosensory system, such as touch and muscle proprioception (Ribeiro and Oliveira, 2007; Shaffer and Harrison, 2007; see reviews by Goble et al., 2009). Healthy aging has an impact at multiple levels of sensorimotor processing, from the periphery to central integration. At the peripheral level, neurophysiological studies performed in humans and animals show alterations of structural properties and the density of both cutaneous and muscle mechanoreceptors (Iwasaki et al., 2003; Kararizou et al., 2005; Rosant et al., 2007). Peripheral and central nerve conduction is also impaired with advancing age. In the central nervous system, healthy aging is accompanied by structural changes (Hedman et al., 2012), such as the decrease in gray matter volume, with a large reduction in cortical thickness, and an increase in cerebrospinal fluid (Good et al., 2001; Resnick et al., 2003), as well as the reduction in white matter in local areas (Raz, 2005), including the corpus callosum (Ota et al., 2006; Lebel et al., 2012).

These central and peripheral structural changes observed in the elderly may result in functional impairments of self-body perceptions. Indeed, the perception of self-body positions (position sense), as well as self-body movements (kinesthetic or movement sense) relies on multiple sources including peripheral sensory inputs and centrally generated signals. It has been shown that after a transient total nerve block that removes both afferent and motor fibers from the hand, any effort to move the paralyzed hand can lead to errors in estimating the position of the hand (Gandevia et al., 2006) and illusions of hand motion (Walsh et al., 2010). These findings suggest that a centrally generated sense of effort contributes to both position and motion senses (Proske and Gandevia, 2012). Also, among the different sensory systems, touch and muscle proprioception is

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Abbreviations: ECU, extensor carpi ulnaris; GLM, general linear model; G_ZLM, generalized linear model; JND, just noticeable difference; LMM, linear mixed model; MVC, maximal voluntary contraction; T, touch; P, muscle proprioception; PL, *pollicis longus*; PSE, point of subjective equality; RMS, root mean square.

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main source contributing to kinesthesia. Microneurographic studies performed in humans have found that cutaneous receptors are sensitive to both the direction (Aimonetti et al., 2007) and velocity (Grill and Hallett, 1995) of an imposed limb movement. In addition, both primary and secondary muscle spindle afferents are known to discharge when the muscle is stretched. While primary afferents encode muscle length changes and are more involved in movement sense, the secondary afferents are more involved in position sense, by encoding length states of the muscle (Matthews, 1982; Roll and Vedel, 1982; Proske and Gandevia, 2009).

Numerous studies have been conducted to investigate age-related changes in the position sense of the lower limb. The sense of static position is commonly assessed by passively moving a joint and by asking the participant to match this imposed joint angle deviation. Although several studies have shown a decrease in joint position sense in older adults, compared to younger ones, at knee (Barrack et al., 1983; Kaplan et al., 1985; Petrella et al., 1997; Hurley et al., 1998; Tsang and Hui-Chan, 2004) and ankle (You, 2005), the results remain controversial. Some authors did not find differences, regardless of the joint level or the assessment method used (active vs passive matching tasks) for the hip (Pickard et al., 2003; Franco et al., 2015), knee (Kaplan et al., 1985; Marks, 1996), or ankle (Deshpande et al., 2003; Westlake et al., 2007; Goble et al., 2011; Boisgontier et al., 2012; Franco et al., 2015). Less attention has been paid to upper limb position sense in the elderly. In line with the controversial results found at the lower limb, some studies have shown an impairment in the detection of passive finger movements (Ferrell et al., 1992) and in elbow- or wrist-matching tasks (Adamo et al., 2007, 2009) in the elderly; by contrast, Stelmach and Sirica (1986) did not find any age-related impairment when imposing displacements at the elbow or when low amplitudes of displacements were imposed at the arm.

Unlike position sense, age-related changes in the sense of motion have been less investigated. So far, investigations have mainly considered the lower limb and have consisted of comparing the movement detection thresholds during passively imposed movements in older and young adults. Most of the studies have found a decrease in joint movement perception in the elderly at the knee (Barrack et al., 1983; Skinner et al., 1984; Xu et al., 2004) and the ankle (Verschueren et al., 2002; Xu et al., 2004; Westlake et al., 2007). Regarding the upper limb, only one study by Wright et al. (2011) reported decreased performances in older, than young, participants during the detection of passively imposed wrist movements. However, this decrease in movement detection threshold in elderly might be due to a non-specific slowing in central processing, rather than an alteration of proprioceptive acuity, *per se*. For instance, by asking the participants to estimate the shape and the trajectory of arm displacements, Wang et al. (2012) did not find any age-related differences.

One explanation can be put forward regarding the ambiguity of the literature about position and motion sense, in that both cutaneous and muscle proprioceptive afferents are concomitantly solicited during a passively imposed movement. However, the proprioceptive and cutaneous systems might not be equally affected with aging. Although older individuals show a decreased ability to detect a tactile stimulus applied on the skin surface (Desrosiers et al., 1999), the possible alteration of kinesthetic function due to age-related cutaneous deterioration has not been investigated, to our knowledge. Moreover, it has been shown that convergent redundant inputs are integrated by the central nervous system to optimize self-body movement perception in healthy adults (van Beers et al., 1999; Chancel et al., 2016). In the elderly, integrative multisensory mechanisms may be preserved, or even enhanced, as evidenced by Laurienti et al. (2006) in an audio-visual discrimination task. The latter authors found that older individuals may compensate for the sensory deficits and take greater advantage of redundant audio-visual information than younger adults, by increasing the efficiency of integrative processing.

Therefore, the present study attempts to determine to what extend aging impacts movement sense at the upper limb, especially the ability to accurately perceive hand movements that have been poorly studied, and whether the perceptual impairments originate from muscle proprioceptive and/or tactile sources. To disentangle muscle proprioception and touch, we used specifically designed stimuli: a mechanical vibration applied on wrist muscle tendon and a tactile-textured disk rotating under the participant's hand, respectively. Previous studies showed that these two stimulations can give rise to illusory movement sensations in participants' resting hand, with a velocity increasing with the stimulation intensity (Blanchard et al., 2011, 2013). These kinesthetic illusions are also generally accompanied by small involuntary motor responses in the muscle that would contract if the movement illusion was actually performed (Roll et al., 1980; Calvin-Figuiere et al., 1999; Blanchard et al., 2011).

Two groups of young and old (65–75 years old) participants underwent proprioceptive or tactile stimulation of various intensities to compare the velocity of movement illusions in a two-alternative forced choice task. Illusions were also assessed without a memory component by asking the participants to copy on-line with their left hand, the movement they perceived in their right hand. Electromyographic activities from wrist muscles were also recorded in both groups.

EXPERIMENTAL PROCEDURES

Participants

Twenty-five elderly volunteers aged from 65 to 75 years (5 men; mean: 70.3 ± 3.5 yrs of age) and 16 young volunteers aged from 20 to 28 years (6 men; mean: 23.3 ± 2.8 yrs of age) participated in the study. All subjects were right–handed, according to the Edinburg handedness scale (Oldfield, 1971). None of them had any history of neurological or sensorimuscular diseases, and they were not receiving medical treatment. A Mini-Mental State (MMS) score of 26 and preserved daily life autonomy were required for elderly individuals to participate in the study. The present experiment was performed on healthy human volunteers, and written, informed consent was obtained. The study was approved by the local ethics committee (CCP Marseille Sud 1 #RCB 2010-A00359-30) and performed in accordance with the Declaration of Helsinki (Fig. 1).

Stimuli

Two kinds of stimuli were applied to the right hand of each participant.

Muscle proprioceptive stimulation (P) consisted of mechanical vibration of small amplitude (0.5 mm) applied to the right *pollicis longus* (PL) tendon at five constant frequencies (ranged from 32 to 66 Hz). Previous studies have shown that vibration applied on the muscle tendon of resting young adults activates primary muscle afferents preferentially, and gives rise to an illusory movement sensation in the direction of the stretching muscle, with a velocity increasing with vibration frequency (Roll and Vedel, 1982; Calvin-Figuiere et al., 2000; Blanchard et al., 2011).

The tactile stimulation (T) consisted of a rotating disk (40 cm in diameter) covered with cotton twill (8.5 ribs/cm). This covering fabric was used because a previous microneurographic study in young adults showed that it efficiently activates cutaneous receptors, without reaching a saturation plateau within the velocity range used in the present study (Breugnot et al., 2006). Participants' right hand was stimulated by a counterclockwise rotation of the disk at five constant velocities (ranging from 5 to 30°/s). This velocity range has been chosen based on previous studies showing that the rotation of this textured disk under the resting hand of blindfolded young adults gives rise to a kinesthetic illusion of hand rotation in the opposite direction, with an illusion velocity increasing with disk velocity (Blanchard et al., 2011, 2013).

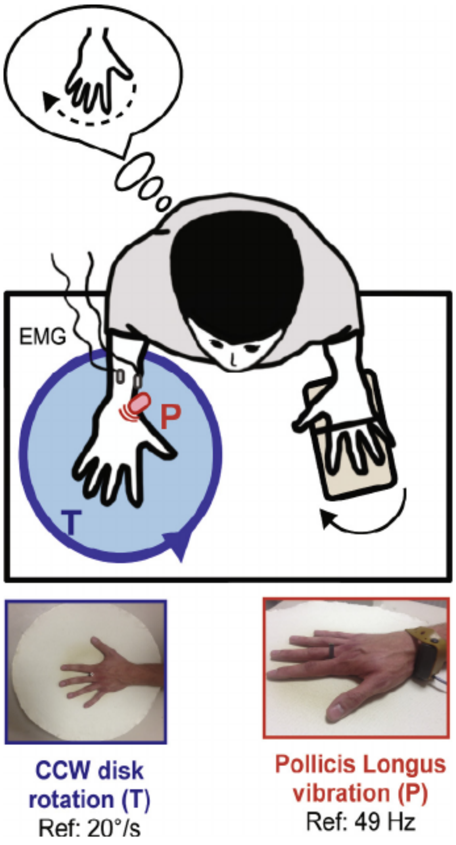

Fig. 1. Experimental set-up. Seated participants were exposed to a counterclockwise (CCW) rotation of a texture disk under their right hand or a vibratory stimulation applied on the tendon of their right pollicis longus muscle. During the stimulation delivery, they copied on-line any illusory sensation perceived in their right hand with a potentiometer held in their left hand. EMG signals from the right extensor carpi ulnaris and pollicis longus muscles were recorded.

Except for the reference vibration frequency (49 Hz) and the reference disk velocity (20°/s), which were always the same for all the participants, the other four vibration frequencies and disk velocities tested were adjusted for each subject during the training step.

The intensity levels of the stimuli were chosen based on a previous experiment, performed in young adults, showing that these ranges of stimulation intensities of the sensory modalities induced illusions of clockwise self-hand rotation efficiently (Blanchard et al., 2013). To deliver the stimulation, we used a National Instruments card (NI PCI-6229; Austin, TX) and we designed a specific software implemented in LabView (V.2011).

Participants sat comfortably and relaxed with movements of their head limited by a chin-and-chest-rest. Their forearms were mechanically constrained by resting on supports fixed to the table in front of them. The participants' left hand rested on a potentiometer and their right hand on the textured disk. The right hand of the participants was prevented from moving with the disk while it was rotating, thanks to a small stop in the center of the disk, placed between their index finger and the middle finger. The participants carried out the experiment in the dark, and they wore headphones to block the outside noise. To completely suppress visual feedback, participants also had to close their eyes at the beginning of each trial.

To assess the kinematic parameters of the illusions, we asked participants to copy in real time, with their left hand attached to a potentiometer, any movements they perceived in their stimulated right hand. At the beginning of each stimulation condition, the two hands were always parallel. Participants were asked to focus especially on the latency and velocity of the perceived movement they had to copy.

Activity of the extensor carpi ulnaris (ECU) and PL muscles of the participants' right wrist was recorded using surface electromyographic electrodes (EMG) (Delsys system – Bagnoli DE-2.1, Boston, MA, USA). These antagonist muscles are responsible for the actual rotation of the hand respectively in a clockwise and anticlockwise direction. Previous studies performed in young adults have shown that involuntary motor responses can occur during an illusory movement, induced by either a visual, tactile, or muscle proprioceptive stimulation (Calvin-Figuiere et al., 1999; Blanchard et al., 2013). The potentiometer and EMG signals were sampled at 1 kHz.

Procedure

Participants were first asked to perform twice maximal voluntary contractions (MVCs) of their right ECU and PL muscles by rotating their right hand to the left or to the right against a resistance, for 5-s duration.

Then, all the participants underwent three experimental phases, performed the same day: familiarization, training and testing phases.

i) During the first experimental phase, participants were familiarized with the set-up and we checked whether they felt an illusion of hand movement in more than 70% of the trials, in both tactile and proprioceptive conditions. If it were not the case, they were not included in the experiment. During this familiarization test, participants were also trained to reproduce, on-line, the right hand movement illusion they perceived, with the potentiometer set under their left hand.

ii) The second phase consisted of a training session, where participants had to perform a two-alternative force choice discrimination task. Each trial consisted of a pair of proprioceptive stimuli or tactile stimuli, always including the reference stimulation randomly presented in the first or second position. During the stimulation presentation, the participants had to copy the illusion they perceived on-line with their left hand. After two consecutive stimuli, the participant had 5 s to report loudly which of these two stimuli gave rise to a faster illusion.
Intensity levels were the same for all participants in this training phase and trials were pseudo-randomized. Participants had to compare five intensities of stimulation to the reference, which corresponded with the *medium* protocol (P1 = 34 Hz; P2 = 41 Hz; P4 = 57 Hz; P5 = 64 Hz; T1 = 10°/s; T2 = 15°/s; T4 = 25°/s; T5 = 30°/s). The training session included two repetitions of the five comparisons in the two tactile and proprioceptive stimulation conditions (2 trials * 5 comparisons * 2 conditions). Each trial lasted 27.5 s (10 s for the first stimulation, 2.5 s of rest, 10 s for the second stimulation and 5 s to answer). The training phase lasted for a total of 10 min.

iii) Testing phase (Fig. 2): Depending on the individual performance during the training session, the set of five stimulation intensities was adjusted to each participant among three possibilities: if 30%, 30–70%, or 70% of verbal answers reported in the training session were right, we selected a set of five stimulation intensities to make the discrimination test easier, identical, or harder than the *medium* protocol used in the training session, respectively. To this end, in the *easy* protocol (P1 = 32 Hz; P2 = 38 Hz; P4 = 61 Hz; P5 = 66 Hz; T1 = 8°/s; T2 = 12°/s; T4 = 28°/s; T5 = 32°/s), the range of stimulation intensities with respect to the reference intensity was increased, whereas it was reduced in the *hard* protocol (P1 = 38 Hz; P2 = 45 Hz; P4 = 53 Hz; P5 = 60 Hz; T1 = 15°/s; T2 = 18°/s; T4 = 22°/s; T5 = 25°/s). Only the reference stimulation remained common in these three protocols. This individual adjustment allowed us to more accurately assess the discriminative thresholds of each participant.

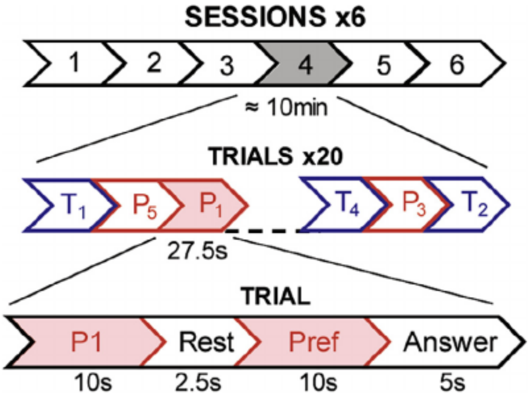

Fig. 2. Testing phase procedure. Illustration of the six experimental sessions, with each session consisting of 20 trials, including proprioceptive (P: red) or tactile stimulation (T: blue) of various intensities (P1–P5 in Hz, and T1–T5 in °/s) randomly presented. One trial was composed of two consecutive tactile stimulations or two consecutive proprioceptive stimulations, always including the reference one (Pref or Tref) randomly intermixed. All stimulation lasted for 10 s, with 2.5-s rest period between two stimulations, and 5 s to answer the question: "Which was the illusion felt faster between the two?" *Here we illustrate a trial in P condition with the first intensity of stimulation P1 compared to the reference one Pref.*

As shown in Fig. 2, the testing phase was subdivided in six sessions of 10 min each. Each testing session was similar to the training phase: the participant underwent successive pairs of proprioceptive or tactile stimuli, always including the reference stimulation. After two consecutive stimulations, the participant had 5 s to report loudly which of these two stimuli gave rise to a faster illusion. During the stimulation presentation, the participants also had to copy on-line the illusion they perceived with their left hand. In each session, a total of 20 trials were tested including two repetitions * five intensities * two conditions. During the testing phase, the potentiometer and EMG recordings were recorded continuously during each session. The full experimental testing phase lasted on average 1 h and 45 min.

Data and statistical analysis

Psychophysical, potentiometer, and EMG data were processed using MATLAB R2016a (The Mathworks, Inc., MA, USA) and statistical analyses were carried out using R programming language and environment, and in particular the "lme4" package for linear and generalized linear mixed-effects models (Bates et al., 2015). These models were fit to data by the method of maximum likelihood, providing not only estimates of the parameters (means, regression coefficients, ...) but also estimated standard errors (SE) for these estimates. For generalized linear models in which there is a dispersion parameter to estimate (Gamma or Gaussian), the Wald statistics were computed and compared to the t-distribution with n-k-1 degrees of freedom, where n is the subject number and k the number of explanatory variables (Fox, 2016). The results were considered statistically significant at $p < 0.05$.

Discrimination performances. To evaluate participants' discrimination performance in the tactile (T) and proprioceptive (P) conditions, the individual proportion of "faster than the reference" answers were fit with the Gaussian psychometric functions using the psignifit MATLAB toolbox (Wichmann and Hill, 2001). The just noticeable difference (JND) in the illusion velocity perceived by the participant was extracted from these individual psychometric curves. The JND was half the intensity difference between 25% and 75% points of the psychometric function in both P (JND_p) and T (JND_T) conditions. Therefore, a lower value of JND corresponded with a lower discrimination threshold, and a better discriminative ability.

Note that psychometric curves could not be estimated in two young and three older participants, respectively, in P and T conditions because these participants were not able to discriminate illusion velocity: for the five intensities of stimulation, they reported a faster illusion than the reference one nearly 50% of the time. We decided to give them an arbitrary JND which was the maximum intensity difference presented during the easier condition (Pref-P1 = Pref-P5 = 17 Hz or Tref-T1 = Tref-T5 = 12°/s).

We also extracted the point of subjective equality (PSE) from each individual psychometric curve, which corresponded to the stimulation intensity for which the participant perceived an illusory movement on average as fast as the illusion perceived during the reference stimulation set at 49 Hz and 20°/s for P and T conditions, respectively.

The two indexes, JND and PSE, were assimilated as positively skewed continuous variables modeled by a Gamma distribution. Thus, we used generalized linear models (G_zLMs) to compare these variables between young and older adults in P and T conditions separately (Stroup, 2013).

Potentiometer data. During all tactile and proprioceptive stimulation delivered throughout the testing phase, the participant copied on line the illusion of movement of their right hand using a potentiometer hold in their left hand. The angular deviations recorded from the potentiometer were first centered on the mean initial left hand position measured during the 100-ms recording phase preceding the start of stimulation. When the participant reported no illusion perception after stimulation, the potentiometer recordings during this stimulation were not considered for the analysis.

Two parameters were extracted from these centered angular deviations: the latency and velocity of the illusions. A threshold of +2 standard deviations (SD) above the mean pre-stimulus level was set to automatically determine the response latency (ms). The mean velocity of the illusion (°/s) was calculated between the latency of the illusion and the maximum angular deviation. Although the two variables were automatically determined, a systematic control by the experimenter was performed to check the validity of the automatic processing.

For the five intensities tested, we first calculated the individual means of illusion latency and illusion velocity. Then, to remove possible inter-subject variabilities due to hand movement reproduction, we calculated a relative index between the mean illusion latency or velocity for a given intensity tested (I_{test}) and the illusion latency or velocity reported by the participant during the corresponding reference stimulation (I_{ref}):

$$\textit{Relative velocity}\ (\%) = \frac{\textit{Velocity}(I_{\text{test}}) - \textit{Velocity}(I_{\text{ref}})}{\textit{Velocity}(I_{\text{ref}})} \times 100$$

$$\textit{Relative latency}\ (\%) = \frac{\textit{Latency}(I_{\text{test}}) - \textit{Latency}(I_{\text{ref}})}{\textit{Latency}(I_{\text{ref}})} \times 100$$

Thus, a positive value of these relative indexes indicated an increase in these parameters compared to those observed during the reference stimulation whereas a negative value would indicate a decrease. To test the effect of the stimulation intensity on illusion latency and velocity, we performed linear mixed models (LMMs) on these two relative indexes in both P and T conditions, separately (West et al., 2015). LMMs are models that account for the variability within and between subjects, by means of fixed (group and intensity) and random effects (subject) respectively. These models allowed us to take into account the heterogeneity of the subject's observations due to the fact that vibration frequencies and disk velocities tested were adjusted for each participant in the sense that for each participant we recorded their relative velocity or latency twelve times for the different five stimulation intensities. In order to compare groups despite the three protocols (easy, medium and hard) used in term of participants, intensity fixed factor was coded as a continuous variable.

EMG data. Electromyographic signals of the ECU and PL muscles of the right wrist of all participants were preamplified (×1000), band-pass filtered (forth order, 20–500 Hz) and sampled at 1 kHz. The raw recordings were first centered on the mean motor activity calculated 750 ms before the stimulation onset, notch filtered (forth order, 50 Hz) and rectified.

To quantify individual EMG responses of the ECU and PL muscles during the maximal voluntary contraction test (MVC), the root mean squared (RMS) values were calculated over the 5-s duration of the contractions. We selected the highest MVC value between the two performed by the participant for each muscle as a reference to estimate the relative amplitude of EMG responses during all the stimulation conditions. Mean individual EMG responses were calculated as the mean RMS value of ECU and PL activities recorded during the five tactile and proprioceptive intensities tested and were expressed as a percentage of the maximum voluntary contraction (%MVC).

We processed the same statistical analyses than that carried out for potentiometric data. The influence of intensity of stimulation on the EMG responses (%MVC) was tested using LMMs for both the ECU and PL muscles, separately.

Since no effect of intensity level was found, the individual EMG responses of the ECU and PL muscles were averaged across all intensities of stimulation. In both tactile and proprioceptive conditions, we used general linear models (GLMs) to compare the mean motor response (in %MVC) over all intensities in PL and ECU between young and older adults.

We also tested whether ECU activity and performances' measures (JND) co-varied in each group and each condition. Because JND was assimilated as a positively skewed continuous variable with a Gamma distribution we used GzLMs to process a linear regression between JND and ECU activity. The group and condition factors were included in the model to compare regression coefficients between the two groups (young versus old) and/or between the two conditions (P versus T).

RESULTS

A total of 17 older and 16 young participants satisfied the inclusive criteria of having more than 70% of illusory sensations of clockwise rotations of their right hand, during both proprioceptive and tactile stimulation (eight old participants were not included in the experimental test after the familiarization session). Fig. 3 shows typical angular deviations and wrist muscle responses (ECU and PL) recorded for two representative young and older participants in response to proprioceptive (Fig. 3A) or tactile (Fig. 3B) stimuli.

Discrimination thresholds

The level of difficulty of the discrimination test was adjusted to each participant depending on their performances during the previous training session. Most of the young participants (P: 14/16; T: 11/16), and only two older participants, underwent the *hard* protocol. By contrast, older participants mostly took part in the *medium* protocol (P: 12/17, T: 12/17). Three old participants and no young participants underwent the *easy* protocol in both P and T conditions.

During the experimental session, participants were asked to compare the velocities of two illusions induced by pairs of stimulation consisting in either two proprioceptive (P) or two tactile (T) stimuli, which always included the reference one (P reference = 49 Hz, T reference = 20°/s). For both the proprioceptive and tactile conditions, participants' answers were collected to compute individual psychometric functions illustrating the proportion of illusions perceived faster than the reference one. Fig. 4 shows four typical individual psychometric curves, for two representative young and old participants in P (Fig. 4A) and T (Fig. 4B) conditions. It should be noted that the curves of the older participants were less steep than the curves of the young participants, reflecting a higher discriminative thresholds (JND) for the older participants in both conditions. Generalized linear model analysis (G_zLM) performed on the two conditions extended this individual result at the group level, and revealed that JND values in both P and T conditions were significantly higher in the older group, than in the younger one (Fig. 4C, D, Table 1). The discriminative thresholds of the older group ($JND_P = 10.57 \pm 5.8$ Hz, $JND_T = 7.49 \pm 3.4$°/s) were around two times higher and more variable than those of the young group ($JND_P = 4.24 \pm 3.5$ Hz; $JND_T = 4.26 \pm 3.6$°/s), reflecting lower discriminative abilities in the elderly for both proprioceptive and tactile conditions. Regarding the PSE, no significant differences were found between groups in both the proprioceptive and tactile conditions (Table 1).

Kinematic parameters of the illusions

During all stimulations, the participants had to copy on line any perception of movement of their right hand using a potentiometer hold in their left hand. The latency and the velocity of the illusions perceived by all the participants were extracted from the angular deviation recorded during this matching copy.

Fig. 5A, B shows individual mean latency across conditions as a function of stimulation intensity. Linear regression curves were fitted for each group, which showed the effect of intensity of stimulation on the illusion latency. For both groups, the negative slope reflected the finding that the higher the stimulation, the earlier the illusions, in both conditions (Table 2). In P and T condition, respectively, the younger participants' latency decreased by 1.79% per Hz or 1.45 per °/s whereas it decreased only by 0.60% per Hz or 0.39% per °/s in the older group, reflecting a weaker influence of the stimulation intensity on the illusion latency in elderly. This decrease was significant in the P condition for both groups and in the T condition only for the younger group. In addition, group comparisons reached a significant level only in the proprioceptive condition, i.e., increasing the intensity of the proprioceptive stimulation led to a higher latency decrease in young compared to older adults ($p = 0.0048$).

Individual illusion velocities, as a function of intensity of stimulation tested, are illustrated in Fig. 5C, D. The influence of stimulation intensity on the illusion velocity was tested statistically by fitting linear curves, in both proprioceptive and tactile conditions. The positive slope indicated that illusion velocities increased linearly with the stimulus intensity in both groups and for the two sensory conditions (Table 2). In the younger group, velocity increased by 2.93% per Hz or 2.02 per °/s whereas it slowly increased by 0.70% per Hz or 0.64% per °/s in the older group, for P and T conditions, respectively. However, this increase was significant in both conditions only for the younger group. Moreover, group comparisons reached a significant level in both conditions, i.e., by increasing the tactile or proprioceptive stimulation intensity, the illusion velocity increased more in the young group than in the older one.

In addition to analyses performed on angular deviation expressed in percentage of the response obtained in the reference condition, a complementary analysis was carried out on absolute values of displacement reproduced by the participants during the only two

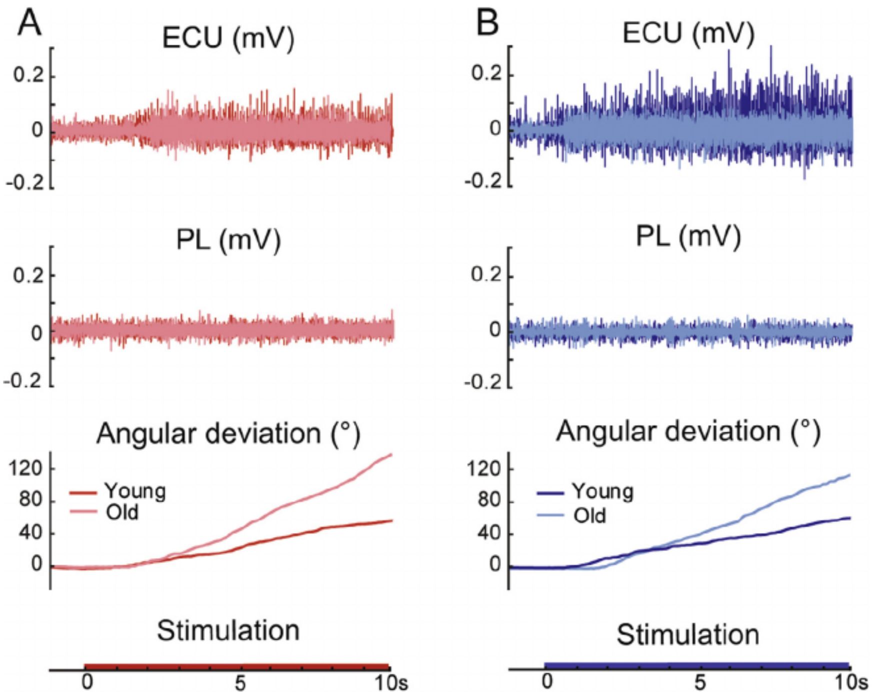

Fig. 3. Typical individual responses of one older and one young participant during a proprioceptive (A, red) and a tactile (B, blue) stimulation condition. From top to bottom: 1st and 2nd traces are raw EMG activity (mV) recorded in the extensor carpi ulnaris (ECU) and in the pollicis longus (PL) muscles of the stimulated right hand during the proprioceptive or tactile stimulation; the bottom 3rd traces are clockwise angular deviations (°) copied by the two participants to reproduce the illusion they perceived in their right hand using their left hand. Reference intensity of stimulation was: vibration frequency at 49 Hz (A) and counterclockwise disk rotation at 20°/s (B).

conditions common to all participants: the two tactile and proprioceptive reference conditions. For the proprioceptive reference condition (49 Hz), young participants reproduced significantly earlier movements than older participants (Young 2301 ms ± 1674 vs Old 3351 ms ± 1489, $t(df = 31) = 2.04$, $p = 0.025$) and tended to reproduce faster movements without reaching a significant threshold (Young 7.46°/s ± 3.5 vs Old 5.69°/s ± 3.9, $t(df = 31) = 1.55$, $p = 0.065$). By contrast, for the tactile reference condition (20°/s), reproduced illusory movements did not significantly differ between the two groups, considering the mean velocity (Young 5.62°/s ± 2.7 vs Old 5.98°/s ± 4.8, $t(df = 31) = 0.14$, $p = 0.45$) and the mean latency (Young 2841 ms ± 1833 vs Old 3118 ms ± 1669, $t(df = 31) = 0.43$, $p = 0.66$) of the movements.

EMG responses

During both proprioceptive and tactile stimulations, EMG activity was recorded from the PL and the ECU muscles of each participant. No noticeable PL activity was observed in both groups, over both conditions. In contrast, EMG recordings showed a small involuntary activity in the ECU, corresponding on average to 12–17% of the maximal voluntary contraction (MVC) individually tested. For both proprioceptive and tactile conditions, no significant differences were found between the amplitudes of the motor responses observed in the young and older groups (Table 3).

Using $\mathrm{G_zLMs}$, we also tested statistically the non-linear influence of ECU activity (%MVC) on the discriminative ability (JND) in both proprioceptive and tactile conditions (Fig. 6). Interestingly, the fitting curves have significant negative slope in the younger group, reflecting that better was the discriminative ability, higher was the motor response in both proprioceptive and tactile conditions (Table 4). In the older group, the slopes of the fitting curves were not significant and differed significantly from the younger ones in both conditions.

DISCUSSION

The present study aimed to compare age-related changes in hand movement discriminative ability from two sensory inputs: muscle proprioception and touch. To this end we compared psychophysical results of a younger (mean: 23.3 years old) and an older (mean 70.3 years old) group, in a discriminative illusory hand movement velocity task, using proprioceptive or tactile stimulation. The present findings showed that the velocity discrimination of illusory hand movements declined with age, regardless of the sensory source stimulated. However, degradation of kinesthetic perceptions seemed more pronounced in muscle proprioception than in touch. In addition, our results revealed age-relative differences in involuntary motor responses elicited by both proprioceptive and tactile stimulation.

Kinesthetic impairment of the hand in elderly

Most previous research concerning the effects of age on self-body perceptions has focused on the lower limbs, and controversial results have been reported regarding static position sense (Boisgontier et al., 2012). In addition, little is known about the ability of older individuals to perceive self-body movements, except for a reduction in motion detection. This has been found at the wrist level (Wright et al., 2011) and in lower limbs, specifically the knee (Barrack et al., 1983; Skinner et al., 1984; Xu et al., 2004) and the ankle (Xu et al., 2004; Westlake et al., 2007). However, these previous studies used passively imposed movements and cannot dissociate to what extend these perceptual impairments were due to more cutaneous or muscle proprioceptive declines. The present study provides evidence that movement perception of the hand, based on these two sensory inputs, was significantly impaired in healthy older adults. Indeed, a third of the older participants could not take part in the present study because they did not feel any illusion sensation dur-

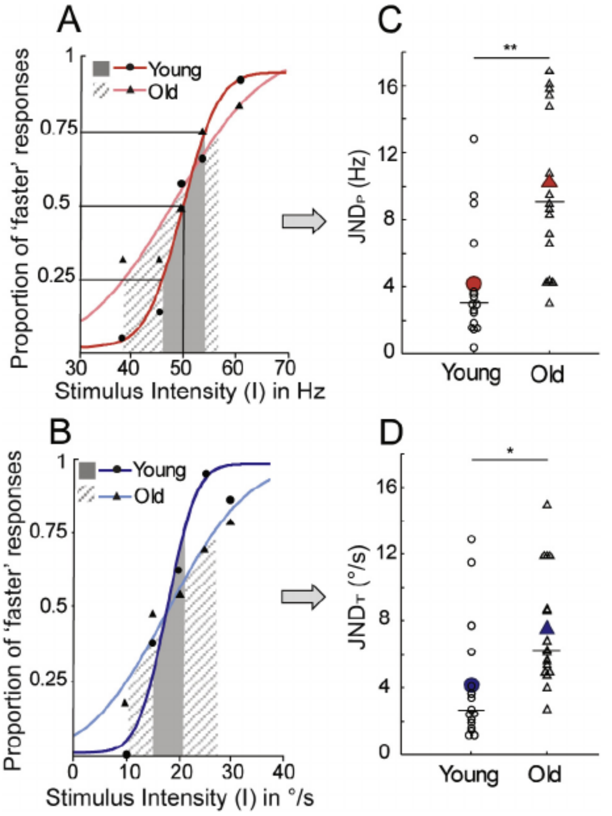

Fig. 4. Comparison of velocity discrimination thresholds between older and young participants in the proprioceptive (P, red) and tactile (T, blue) conditions. A, B: Typical individual psychometric curves from one older (fine line) and one young (thick line) participant. Each curve reflects the percentage of illusion velocity perceived faster than the reference one. Symbols are the mean values for each participant obtained at the five stimulation intensities tested for the older (triangle symbols) and young (dot symbols) participants. The intensity of stimulation corresponding to 50% correct responses is the point of subjective equality (PSE). The just noticeable difference (JND) corresponds to half the intensity difference between 25% and 75% points of the psychometric function. C & D: Individual and mean JND for the younger (dot symbols) and older (triangle symbols) participants in response to proprioceptive (C) or tactile (D) stimulation. Full symbols are the mean of group, empty gray symbols are individual values and the bars are the median of the groups. $^{*}p < 0.05$; $^{**}p < 0.01$.

ing the familiarizing session, in contrast to younger adults who were all able to perceive proprioceptive and tactile-induced illusions (in at least in more than 70% of the trials). In the older participants able to perceive illusory movements, their ability to discriminate hand movement velocity was reduced, as attested by the higher discriminative thresholds found in the older group compared to the younger group in both the proprioceptive and tactile conditions. This decline in kinesthetic discrimination might be explained by an impairment in encoding hand movement velocities. In fact, we found that increasing the intensity of tactile or proprioceptive stimulation resulted in a lesser increase in illusion velocities in the older, as compared to the young participants. Nevertheless, comparisons between groups revealed that proprioceptive responses appeared more affected than tactile one as increasing the intensity of stimulation led to a lower decrease in illusion latency in older compared to younger adults, but only for the proprioceptive condition.

The question arises about the possible peripheral and/or central origins of the age-related decline in kinesthesia evidenced in the present study. The deterioration of cutaneous and muscle spindle receptors with aging (Ribeiro and Oliveira, 2007; Shaffer and Harrison, 2007) might be responsible for a poorer encoding of movement kinematic parameters, resulting in a lower velocity discrimination in elderly. In particular, several studies performed in animals and human have reported structural age-related changes of muscle spindles including a decrease in intrafusal muscle fibers number, an increase in spindle capsule thickness and a loss of the annulospiral configuration of primary endings, together with a decrease in axonal conduction velocity and a reduction in the number of fibers in peripheral nerves (Kararizou et al., 2005; Liu et al., 2005; Kim et al., 2007). These structural changes are supposed to explain the decrease in the dynamic response of muscle spindle primary endings reported in aged rats (Kim et al., 2007). Extended to humans, an alteration in dynamic sensitivity of muscle spindles may result in a specific impairment in movement sense. In the same line, density and properties of cutaneous mechanoreceptors have been found degraded with aging (Iwasaki et al., 2003). Therefore, peripheral degradation of the somatosensory system could explain the difficulty in inducing proprioceptive or tactile illusions in one third of the older participants. However, using a vibration stimulation applied on the arm muscles of young and old participants, Quoniam et al. (1995) explored the sensitivity of muscle receptors and the integrity of proprioceptive reflex pathways in elderly (60–86 years old). Interestingly, the latter authors did not find any differences in the tonic vibration reflexes elicited in young and old participants, suggesting that the efficiency of spinal sensorimotor pathways as evidenced by joint muscle vibration seems unaffected in elderly. In the same line,

Table 1. Summary of the mean variable ± standard error (SE) and statistics of the Group fixed effects (Young vs. Old) in generalized linear models G_zLMs for the discrimination thresholds (JND) and point of subjective equality (PSE) in both proprioceptive (P) and tactile (T) conditions. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

Variable	MEAN ± SE				
	Young ($n = 16$)	Old ($n = 17$)	Slope ± SE	t (df = 31)	p
$\mathrm{JND_P}$	4.24 ± 3.5 Hz	10.57 ± 5.8 Hz	0.13 ± 0.04	3.24	0.0028^{**}
$\mathrm{JND_T}$	4.26 ± 3.6°/s	7.49 ± 3.4°/s	0.10 ± 0.04	2.23	0.032^{*}
$\mathrm{PSE_P}$	49.39 ± 1.8 Hz	50.26 ± 4.3 Hz	< 0.001	0.96	0.35
$\mathrm{PSE_T}$	20.46 ± 2.5°/s	20.52 ± 1.8°/s	< 0.001	0.078	0.94

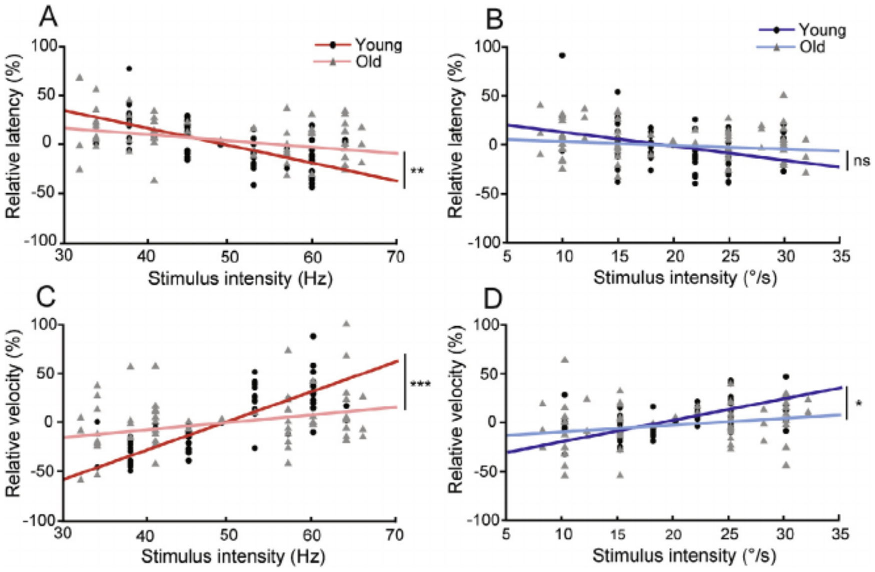

Fig. 5. Effect of the intensity of stimulation on the latency and the velocity of the illusions across groups (older: fine line, young: thick line) in the proprioceptive (A–C) and tactile (B–D) conditions. Lines are linear regression curve fitting of relative latency (A, B) or velocity (C, D) as a function of stimulation intensity. (A, B) Illusion latencies are expressed as the relative illusion latency, with respect to the latency of the illusion evoked by the reference stimulation. (C–D) Illusion velocities are expressed as the relative illusion velocity with respect to the illusion velocity evoked by the reference stimulation. Symbols are individual mean illusion latencies or velocities at different stimulation intensities for young (full dot symbols) and older (full triangle symbols) participants. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Verschueren et al. (2002) reported that applying a vibration on the tibialis anterior muscle of participants, while a passive movement was imposed at their foot, resulted in larger errors in ankle angle deviation assessment in older, than young participants. On the contrary, one would have expected smaller errors observed in the elderly if the impact of the vibration was reduced due to the peripheral deterioration of the muscle mechanoreceptors. These two studies thus support the hypothesis that the decrease in proprioceptive discrimination observed in the present study may not be fully explained by a decrease in the efficiency of the stimulation, with respect to muscle spindle and afferent fibers deterioration with aging. Although peripheral degradation of the proprioceptive system must have indubitably an impact on kinesthetic function in older people, mechanical vibration as used in the present study may be sufficiently efficient to massively recruit muscle spindle afferents in older as in young participants. Regarding the kinesthetic impairment from a tactile origin, the effect of the stimulation intensity on the present illusion latencies did not significantly differ between young and older participants. This result suggests that, as for the proprioceptive results, the perceptual differences observed in tactually induced illusions may not be fully explained by peripheral deterioration of the cutaneous sensory system.

Table 2. Summary of the Intensity fixed effects within and between Groups in linear mixed models (LMMs) for the relative latency (%) and the relative velocity (%) of the illusions elicited in both proprioceptive (P) and tactile (T) conditions. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

Variable	$\text{Condition}_{\text{Group}}$	Slope ± SE	t (df = 29)	*p*
Relative latency	P_{Young}	−1.79 ± 0.3	−6.06	$< 0.001^{***}$
	P_{Old}	−0.60 ± 0.2	−2.34	0.028^{*}
	P_{Young} vs. P_{Old}	−1. 18 ± 0.4	−3.04	0.0048^{**}
	T_{Young}	−1.45 ± 0.6	−2.60	0.014^{*}
	T_{Old}	−0.39 ± 0.5	−0.84	0.41
	T_{Young} vs. T_{Old}	−1.05 ± 0.7	−1.45	0.17
Relative velocity	P_{Young}	2.93 ± 0.4	6.94	$< 0.001^{***}$
	P_{Old}	0.70 ± 0.4	1.81	0.081
	P_{Young} vs. P_{Old}	2.23 ± 0.6	3.88	$< 0.001^{***}$
	T_{Young}	2.02 ± 0.5	4.19	$< 0.001^{***}$
	T_{Old}	0.64 ± 0.4	1.65	0.12
	T_{Young} vs. T_{Old}	1.38 ± 0.6	2.24	0.034^{*}

Table 3. Summary of the mean root mean square EMG activity (mean RMS ± SE) and Group fixed effects (Young vs. Old) in general linear models for Extensor Carpi Ulnaris (ECU) and Pollicis Longus (PL) muscles in both proprioceptive (P) and tactile (T) conditions. MVC: maximal voluntary contraction; SE: standard error

Variable	Mean RMS ± SE (in% MVC)		Young vs. old		
	Young	Old	Slope (±SE)	t (df = 31)	*p*
ECU_P	12.05 ± 9.1	17.84 ± 25.0	0.022 ± 0.02	1.05	0.30
ECU_T	13.72 ± 9.7	17.38 ± 15.5	0.015 ± 0.04	0.83	0.41
PL_P	0.87 ± 1.0	3.80 ± 8.9	0.88 ± 0.5	1.62	0.11
PL_T	0.86 ± 0.9	2.64 ± 2.7	0.78 ± 0.3	2.02	0.052

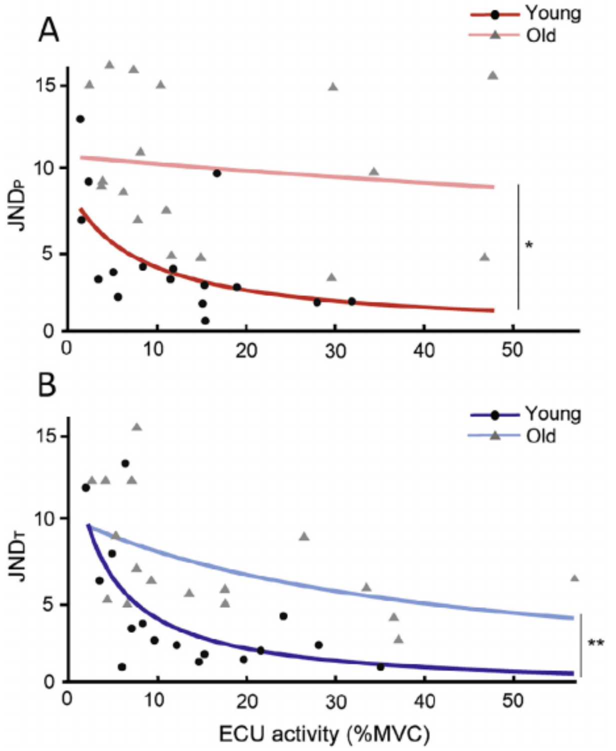

Fig. 6. Velocity discrimination thresholds (JND) with respect to amplitudes of involuntary motor responses in both young and older participants for proprioceptive (A, red) and tactile (B, blue) conditions. Traces are non linear regression curve fitting of JND as a function of EMG activity (%MVC) across groups (older: fine line, young: thick line). The extensor carpi ulnaris (ECU) activity is the individual mean EMG activity which was calculated as the mean root mean square (rms) value of ECU EMG recordings during the five stimulation intensities tested, in both proprioceptive (A) and tactile (B) conditions. rmsECU activity is expressed as a percentage of the maximum voluntary contraction (%MVC) tested for each participant. Symbols correspond to individual JND as a function of EMG activity values for young (full dot symbols) and older (full triangle symbols) participants. Note that significant differences were found between the two groups for both proprioceptive and tactile conditions. $^{*}p < 0.05$; $^{**}p < 0.01$.

Table 4. Summary of the ECU activity fixed effects within and between Groups in generalized linear models G$_Z$LMs for the discriminative thresholds (JND) in both proprioceptive (P) and tactile (T) conditions. ECU: extensor carpi ulnaris muscle $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

Condition$_{Group}$	Slope ± SE	t (df = 29)	*p*
P$_{Young}$	−0.014 ± 0.006	2.51	0.017*
P$_{Old}$	< 0.001	0.37	0.71
P$_{Young}$ vs. P$_{Old}$	0.014 ± 0.06	2.40	0.023*
T$_{Young}$	0.017 ± 0.004	3.78	< 0.001***
T$_{Old}$	0.0024 ± 0.001	1.74	0.092
T$_{Young}$ vs. T$_{Old}$	0.015 ± 0.005	3.11	0.004**

Alternatively, the lower ability of the elderly to discriminate movement velocity of their hand may have a central origin. Anatomical and functional alterations of the brain have been largely reported in aging. In particular, Goble et al. (2012) showed age-dependent changes in sub-cortical brain activation during mechanical vibration applied on the ankle muscle tendon. In addition, applying a superficial tactile stimulation on the elderly human hand resulted in an enlarged regional activation in the contralateral primary somatosensory cortex (SI) (Kalisch et al., 2009; Brodoehl et al., 2013) and a lesser deactivation of the homologous ipsilateral region (Lenz et al., 2012; Gröschel et al., 2013). This expansion of the body representation within the contralateral SI correlated with a decline in a two-point discrimination performance in the elderly (Kalisch et al., 2009). In the same line, impaired tactile acuity correlated with enhanced cortical excitability due to a reduction in cortical inhibition (Lenz et al., 2012). These findings are consistent with the decrease in neural specificity, or the reduced difference of the neural responses, between different conditions, as described in the visual system (Grady et al., 1994; Park et al., 2004). Such reduction in stimulus selectivity was also reported in animal electrophysiological recordings, showing a degradation of visual orientation and direction selectivity in the visual cortex of old monkeys (Schmolesky et al., 2000). Together, a change in the balance between the excitatory and inhibitory cortical mechanisms, and a reduction in stimulus selectivity response, might cause difficulty in the precise encoding of kinematic parameters of hand movements based on tactile and/or muscle proprioceptive information. This may result in a decreased ability to discriminate the velocity of hand movements, as found in the present study. However, future neuroimaging studies should be conducted to further validate this hypothesis.

Sensorimotor impairment of the hand in the elderly

During illusory sensations of movement, various studies have reported concomitant, involuntary, tonic activity in the muscle that would have been involved in the corresponding actual movement. In particular, using proprioceptive, tactile or visual stimulation, Blanchard et al. (2013) reported similar EMG activity in the extensor carpi ulnaris muscle group during clockwise illusory hand rotations, showing that equivalent perceptive and associated motor effects can be elicited by any kind of sensory stimulation. Consistently, the present results show that as in young adults, the elderly displayed involuntary motor activities with similar amplitudes in the extensor carpi ulnaris muscle during either a vibration of the PL muscle or a counterclockwise rotation of the tactile disk.

Since involuntary motor responses occurred during the stimulation-induced illusions, it is first questionable to what extend this motor response in turn activated both the cutaneous and muscle afferents. However, the motor responses associated with the illusions were relatively small involuntary isometric contractions that have not produced any actual hand movement. Also, the stimulated participants' hands were physically limited by the abutment at the center of the disk. Therefore, these motor responses should not have a significant impact on cutaneous afferents. In addition, physiological studies have demonstrated that if a voluntary isometric contraction activates muscle proprioceptive afferents likely through the fusimotor drive (alpha-gamma co-activation, Edin and Vallbo, 1990), this is less likely to occur for involuntary muscle contractions as in the present experiment (Duclos et al., 2004). Overall, even if this motor influence cannot be totally ruled out, it should be insufficient to account for the perceptual illusions reported here and for the differences observed between younger and older participants.

Previous studies provided arguments in favor of a high level origin of these motor responses rather than a spinal reflex origin. Indeed, such motor responses can be generated not only by somatosensory stimulation, but also visual stimulation (Blanchard et al., 2013). In addition, illusions and motor responses evoked by vibrating wrist muscles were perturbed by a direct transcranial magnetic stimulation over the sensorimotor cortex (Romaiguere et al., 2005). Neuroimaging studies have further shown that movement sensation induced by a vibratory stimulation is associated with brain activation of not only sensory- but also motor-related brain areas (Naito et al., 1999; Romaiguere et al., 2003; Duclos et al., 2007). The same sensorimotor network was also activated during a tactually induced illusion of hand rotation using the same rotating disk as the one used in the present study (Kavounoudias et al., 2008). This indicates that whether they have a tactile or a proprioceptive origin, kinesthetic illusions and the associated motor responses share a common sensorimotor activation within the brain.

The present results show that as for young healthy subjects, the perception of movement generated appropriate corresponding motor activity in the elderly, stressing that perceiving a movement illusion cannot be based on pure sensory activity, but implies also motor-related activity, regardless of the modality that gave rise to the sensation of movement.

However, based on our previous study (Blanchard et al., 2013), it should have been expected that EMG responses would have increased with stimulus intensities, at least in young participants. This discrepancy might be explained by the fact that the positive correlation found in this latter study was observed when a wider range of stimulation intensity (tactile disk: from 5°/s to 40°/s; vibration frequency: from 30 to 80 Hz) was applied, whereas in the present study we used the smallest possible range of intensity stimulation to accurately determine each participant's discrimination threshold. Therefore, it appears that the relatively small modulation of motor responses ranged on average from 12% to 17% of the maximal voluntary contraction in the present study was not enough to reveal a significant linear increase in muscle responses within such a low intensity range.

Because we postulate that kinesthetic illusions result in a perceptual-to-motor loop activation, a question arises as to what extent the general activation of the sensorimotor network was correlated with the discriminative ability of the subjects, at least in the young group. For this reason, we averaged all individual EMG responses for the different intensity levels. In line with our hypothesis, we observed that the stronger EMG responses among young participants, the better their discrimination performance, for both tactile and proprioceptive modalities. It could be assumed that precise discrimination would require fine modulation of the sensorimotor network around a minimum activation level. In contrast with young participants, the ability of older participants to discriminate the velocity of the tactile or proprioceptive illusions was not correlated to the amplitude of their motor responses. These findings suggest that the alteration of body movement perception, with aging, might not solely be due to pure sensory decline, but also the central alteration of the motor system.

It is well known that older adults generally perform movements more slowly than younger adults and have impaired motor coordination, fine dexterity and muscle strength (see review Bowden and McNulty, 2013). Therefore, the present findings observed in the reproduction task may have resulted from impairment in motor dexterity of the left hand in elderly people rather than from an alteration of kinesthetic sensation. However, if it was the case, one should have expected that motor dysfunction would have the same impact in any left-hand movement reproduction, which does not support the present result that proprioceptive reproduction seems more affected than tactile one in the older group. Indeed, difference between the latency of the illusion reproduction was found in the proprioceptive condition but not in the tactile condition. Moreover, movement reproduction during the tactile reference condition did not differ significantly between the two groups, showing that older participants could perform as well as younger ones in at least one experimental condition. Although it cannot be totally ruled out that motor impairment in elderly may have influenced the reproduction task, this cannot explain the main differences observed in the present experiment, which may be mainly due to more perceptive deficits rather than a pure impairment in motor execution. Nevertheless, the accurate perception of self-movements requires activation within both sensory and motor brain areas. Several functional magnetic resonance imaging (fMRI) studies consistently reported that to perform similar motor activities as those performed by young adults, older individuals show an overall increase in the magnitude of motor brain activations, compared to young adults, and an increase in the recruitment of brain regions ipsilateral to the side of movement (Mattay et al., 2002; Heuninckx et al., 2008; Ward et al., 2008; Noble et al., 2011). About the reduced laterality observed in the motor cortex, it can be explained by a decrease in the interhemispheric inhibition in the motor cortex of the elderly, rather than a greater recruitment of the ipsilateral motor cortex, as shown in fMRI (Ward et al., 2008) and TMS studies (Talelli et al., 2008). One might hypothesize that these over-activations and/or changes in the interhemispheric balance of motor brain regions may also occur during induced illusory movement, preventing the elderly from having the fine modulation required to distinguish the kinematic parameters of different limb movements accurately.

We conclude that the perception of hand movements is altered in the elderly, with a decrease in their ability to detect such movements, but also to precisely encode their velocity. Using specific stimulation, our study demonstrates that kinesthetic deterioration with aging seems to occur through the degradation of both the muscle proprioception and cutaneous systems, with a more pronounced alteration of muscle proprioception. Although the present results and those from the literature support a likely central origin of this functional deficit, this hypothesis remains to be further investigated in neuroimaging studies to examine age-related changes in brain activations during self-body movement perception.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

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