

Presbypropria: the effects of physiological ageing on proprioceptive control

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Abstract Several changes in the human sensory systems, like presbycusis or presbyopia, are well-known to occur with physiological ageing. A similar change is likely to occur in proprioception, too, but there are strong and unexplained discrepancies in the literature. It was proposed that assessment of the attentional cost of proprioceptive control could provide information able to unify these previous studies. To this aim, 15 young adults and 15 older adults performed a position matching task in single and dual-task paradigms with different difficulty levels of the secondary task (congruent and incongruent Stroop-type tasks) to assess presumed age-related deficits in proprioceptive control. Results showed that proprioceptive control was as accurate and as consistent in older as in young adults for a single proprioceptive task. However, performing a secondary cognitive task and increasing the difficulty of this secondary task evidenced both a decreased matching performance and/or an increased attentional cost of proprioceptive control in older adults as compared to young ones. These results advocated for an impaired proprioception in physiological ageing.

Keywords Elderly · Proprioception · Joint position sense · Attention · Sensory integration · Dual task

Introduction

To provide information about the body state and features of the environment, sensory systems produce sensations that are centrally integrated into perceptions (touch, vision, hearing, taste, smell, vestibular, and proprioception). Several physiological changes occurring within the older adults' sensory systems can induce perception impairments. For instance, presbycusis, the age-related hearing impairment (Gates and Mills 2005), or presbyopia, the age-related visual impairment (Glasser and Campbell 1998), are already well known to occur in physiological ageing (Corso 1971).

From Latin *proprius* (own) and *recipere* (recept), the term *proprioception* encompasses both the senses of limb movement (kinaesthesia) and limb position (joint position sense or stataesthesia) as initially proposed by Sherrington (1900). These senses rely on the central integration of afferent and efferent signals. Among the afferent signals, the muscle spindle ones have been assigned a prominent role and appear to mediate the conscious perception of limb position and movement (Gandevia and McCloskey 1976; Goodwin et al. 1972; Matthews 1982; Proske and Gandevia 2009). Tendon organ afferents also evoke propriocep-

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tive sensation especially when the stimulus is a contractile force acting at the receptor (Houk et al. 1971). Skin stretch receptors have shown to provide information about both position and movement senses especially when the skin is adjacent to the joints (Collins et al. 2005; Edin 1992; Lowrey et al. 2010). Joint receptors also contribute to proprioception (Burke et al. 1988; Ferrell et al. 1987), but this contribution is thought to be minor (Grigg et al. 1973; Suprak 2011). Proprioception has also been evidenced to be centrally generated through efferent signals. These efferent signals have been reported under different terms [“corollary discharge” (Crapse and Sommer 2008; Sperry 1950), “efference copy” (von Holst 1954), or “sense of effort” (Gandevia et al. 2006; Smith et al. 2009; Walsh et al. 2010)], but the underlying mechanism remains the same: Information derived from the motor commands of cortical areas involved in planning (area 6, supplementary motor cortex and pre-motor cortex) and executing (area 4, primary motor cortex) a motor act is transmitted to the somato-sensory area involved in processing the resulting sensations.

Results of different age groups to threshold of movement detection (e.g. Kokmen et al. 1978; Pai et al. 1997; Thelen et al. 1998) and position-estimation protocols (e.g. Barrack et al. 1983; Barrett et al. 1991; Gilsing et al. 1995; Jordan 1978; Robbins et al. 1995), which can respectively be used to measure limb movement and limb position senses, have shown to be correlated (Skinner et al. 1984). In the present study, the performance of the proprioceptive system was tested in a *joint position matching task*. This test has widely been used over years due to its simplicity and accuracy (Goble 2010). In this test, a participant is asked to identify (i.e. to match) a reference joint angle (i.e. a position) in the absence of vision of the limb. The results in the matching task are subsequently used to compute different types of errors reflecting the participant’s proprioceptive performance. Joint position matching tasks can be conducted in several ways. The three main matching paradigms are presented in this introduction. First, in *ipsilateral* and *contralateral remembered* matching tasks (Goble et al. 2005), a subject’s limb is actively or passively displaced to the reference position and held for 2–3 s (Adamo et al. 2009; Barrack et al. 1983; Bullock-Saxton et al. 2001; Petrella et al. 1997; Skinner et al. 1984; Tsang and Hui-Chan

2004), 5 s (Deshpande et al. 2003; Goble et al. 2011; Hurley et al. 1998; Marks 1996; Marks et al. 1993; Pickard et al. 2003; Westlake et al. 2007), or 15 s (Kaplan et al. 1985) prior to being returned to its starting angle. Next, the participant is asked to identify the reference position with the same (ipsilateral) or other (contralateral) limb during an active or passive movement based on proprioceptive memory. These two methods use movement reproduction from memory and may therefore confound age-related changes in memory with possible changes in proprioceptive acuity (Toole et al. 1984). In this line, previous studies showed that recall was associated with greater resource costs than was recognition and that this effect was amplified by increasing age (Craig and McDowd 1987). Furthermore, memorising the reference position and returning the stored position of the limb could be considered as a secondary task that could lead to an additional demand of attention. The effects of a secondary task on the proprioceptive performance are discussed in the present study. Therefore, when assessing older adults’ proprioception, the *contralateral concurrent* matching (Adamo et al. 2007; Goble and Brown 2007) should be preferred to remembered conditions in order to get more specific results. In this second type of matching, a similar procedure is undertaken involving the displacement of a limb to a reference position. However, the limb is not returned to the starting position but is left at the reference one while matching is performed with the contralateral limb based on concurrent proprioceptive information coming from both limbs.

Unfortunately, previous studies on joint position sense comparing young and older adults mainly chose the remembered paradigms. Some of these studies showed greater errors in older adults’ joint position matching as compared to young ones (Adamo et al. 2007, 2009; Barrack et al. 1983; Bullock-Saxton et al. 2001; Hurley et al. 1998; Kaplan et al. 1985; Madhavan and Shields 2005; Marks et al. 1993; Petrella et al. 1997; Tsang and Hui-Chan 2004; Verschueren et al. 2002; You 2005). To explain this result, authors mentioned muscle spindles (Swash and Fox 1972; Kararizou et al. 2005; Liu et al. 2005; Rosant et al. 2007) and nervous system (Cruz-Sánchez et al. 1998; Giorgio et al. 2010) degenerations that have been evidenced to occur in ageing. They also evoked the age-related deterioration in

cognitive processing (Grady and Craik 2000), which showed a stronger interdependence with sensory/sensorimotor processes with advancing age (Li and Dinse 2002; Li and Lindenberger 2002). Other studies using the remembered matching paradigms showed no difference between young and older adults (Deshpande et al. 2003; Goble et al. 2011; Jordan 1978; Marks 1996; Pickard et al. 2003; Tsang and Hui-Chan 2004; Westlake et al. 2007) or even greater proprioceptive performances in older than in young adults (Batavia et al. 1999). To explain these results, authors suggested that the older adults' proprioceptive performance was dependent on their level of physical and functional activities as previously evidenced in the young adults (Bernauer et al. 1994). They also referred to previous studies suggesting that the proprioceptive efferent signals involved in active matchings could compensate for diminished proprioceptive afferences in older adults (Stelmach and Sirica 1986; Dick et al. 1988). Other studies used the contralateral concurrent matching to assess older adults' proprioception. Kaplan et al. (1985) showed that older adults exhibited greater absolute error than the young adults ($4^\circ \pm 1^\circ$ vs. $7^\circ \pm 1^\circ$). However, it was difficult to assign this difference to a proprioceptive deficit or to the 5° standard deviation of measurement error attributable to the clinical goniometer they used in their study. Stelmach and Sirica (1986) showed no difference between age groups in passive contralateral concurrent matching for short movements but greater absolute errors in older adults for long movements. These authors explained this discrepancy by the increasing matching error that has been evidenced to occur as a function of movement distance (Pickard et al. 2003; Stelmach et al. 1975). They also evidenced no difference between young and older adults in active contralateral concurrent matching. To explain these different results between passive and active matchings, Stelmach and Sirica (1986) suggested that, under active conditions, sensory processing centres would be prepared to receive the expected sensory consequences due to the efferent signal, whereas this would not be possible in the passive matching. However, other studies showed that the older adults' proprioceptive performance could also be affected in active contralateral concurrent paradigms (Adamo et al. 2007, 2009; Meeuwse et al. 1993). Adamo et al. (2009) explained this result by the age-related degeneration of the corpus callosum (Abe et al.

2002; Hopper et al. 1994) that affects interhemispheric transfer of sensorimotor information (Reuter-Lorenz and Stanczak 2000). However, by comparing ipsilateral remembered and contralateral concurrent matching tasks, Adamo et al. (2007) noticed that older adults' performance tended to be less affected as compared to young adults when continuous feedback about the reference position was available (i.e., during the contralateral matching), suggesting that utilisation of online proprioceptive feedback was only minimally impaired with ageing.

Recent studies (Heuninckx et al. 2005, 2008; Hutchinson et al. 2002; Mattay et al. 2002; Naccarato et al. 2006) showed that older adults recruited additional neural resources to reach motor performance levels comparable to those obtained in the young adults. The present study hypothesised that the same type of mechanism operated for proprioceptive control inducing an increased attentional cost. The proprioceptive control refers to the spatial and temporal characteristics of single joint movements based on the proprioceptive perception (Gandevia et al. 2002). In order to test this hypothesis, this study used a dual-task paradigm implying to divide attention between the two tasks (Braun 1998). Attention is defined as a cognitive mechanism dealing with the limited processing capacity of the brain (Pashler 1998). Dividing attention have shown to lead to a limitation in the recruitment of sensory cortices involved in the single tasks (Loose et al. 2003; Rémy et al. 2010), and the best performances were related to the ability to recruit these sensory cortices (Johnson and Zatorre 2006). If older adults have to recruit greater neural resources than the young ones to reach the same performance, the required attentional cost for performing this task should be greater, too. With the addition of a concurrent secondary task, the system should be expected to reach a limit on the available attentional resources resulting in an alteration of the performance (Reuter-Lorenz and Lustig 2005). In the present study, participants were therefore instructed to perform a dual task, which required performing a primary task (i.e. an ankle matching task) as well as possible and at the same level with and without the execution of a secondary task (i.e. a Stroop-type task). The secondary task also had to be performed as well as possible without affecting the performance in the primary task. The extent to which performance in the secondary task declined was used to assess the increasing attentional demand imposed by the primary task.

This study was an attempt to investigate to which extent there was an age-related proprioceptive deficit. To this aim, participants performed a contralateral concurrent ankle matching task in single- and dual-task paradigms. It was hypothesised that (1) proprioceptive performance was not different between young and older adults in a single matching task, but (2) performing a secondary task and increasing the difficulty of this secondary task resulted in a degraded proprioceptive performance and/or an increased attentional cost for processing the proprioceptive task.

Materials and methods

Participants

Fifteen older adults (age, 77.2 ± 7.3 years; weight, 57.0 ± 10.5 kg; height, 161.8 ± 10.5 cm; mean \pm SD) and fifteen young adults (age, 27.9 ± 2.9 years; weight, 68.1 ± 10.6 kg; height, 174.2 ± 10.5 cm) without history of neurological disease, diabetes or lower limb injuries, participated in the study. To ensure that this study assessed physiological ageing, participants had to validate different criteria to be involved in the experiment. They all had a normal pre-testing examination to exclude peripheral vascular disease and peripheral neuropathy. In both age groups, participants lived independently in their own accommodation and reported no history of fall in the past year. A fall was defined as an event resulting in a person inadvertently coming to rest on the ground or another lower level. Older adults exhibiting a score to the Mini-Mental State Examination (MMSE) inferior to 24 were excluded (Folstein et al. 1975). The MMSE was used to assess cognitive function because poor cognition might have influenced their ability to follow instructions (Adamo et al. 2009; Deshpande et al. 2003; Petrella et al. 1997; Tsang and Hui-Chan 2004). The older adults average MMSE score was 28.4 ± 0.4 . Self-reports of activities of daily living indicated that all participants were engaged in light housekeeping, volunteered, social and recreational activities in addition to most driving their own motor vehicles (Adamo et al. 2007). Leg dominance was an inclusion criterion. To identify the dominant leg, participants were asked their preference for kicking a ball towards a target (Peters 1988). All participants indicated their right leg as their dominant leg. All participants gave written informed consent, and their

rights were protected as required by the Helsinki declaration (1964) and the local ethics committee.

Experimental set-up

Ankle joint position sense was measured with an apparatus and a set-up described previously (Forestier et al. 2002; Vuillerme et al. 2007) and illustrated in Fig. 1. Participants were comfortably seated barefoot with the feet secured on two rotating footplates with Velcro straps. To ensure that the feet did not shift on the footplate during the matching, the posteroinferior aspect of the heel was initially positioned on a 2-mm line relief, which was perpendicular to the longitudinal axis of the footplates. During trials, one experimenter

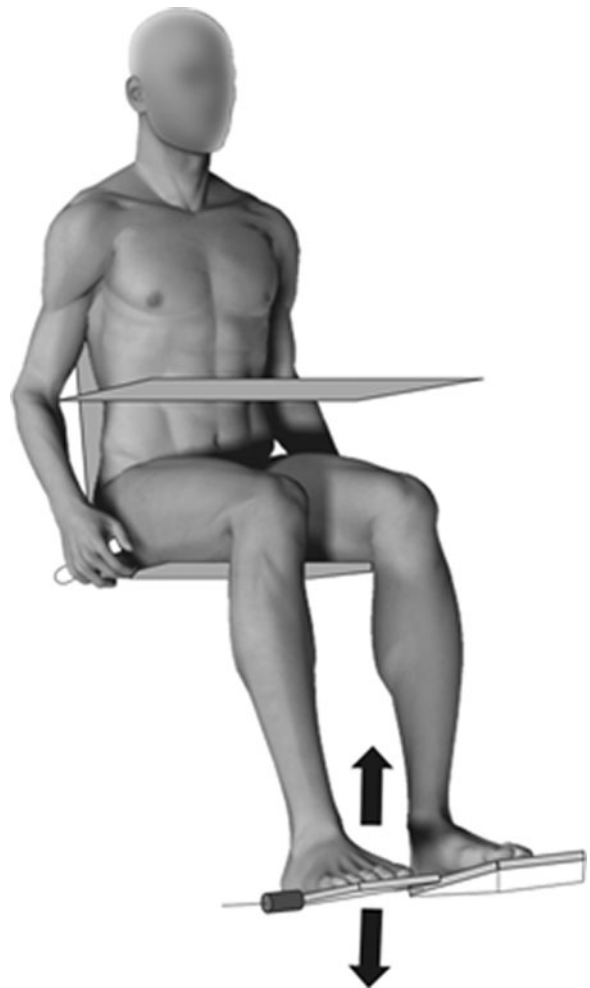


Fig. 1 Set-up for the contralateral concurrent matching task. *Black arrows* indicate the possible motion of the matching foot

checked that the heel did not move from this relief. A panel was placed above participants' legs to ensure the absence of ankle visual feedback. The lower extremities position was standardised and maintained for all conditions with the thigh horizontal and the knee joints bent at approximately 70° of flexion. Movements were restricted to the ankle in the sagittal plane. The axis of rotation of the footplates was vertically aligned with the axis of plantarflexion–dorsiflexion of the ankles. Precision linear potentiometers attached on both footplates provided analogue voltage signals, which were converted to angular displacements proportional to the angle of the ankles. At the beginning of each experiment, potentiometer output for both footplates were checked and, when calibrated, gave an angle resolution of 0.01° . Participants held a switch in the dominant hand to record the matching. Signals from the potentiometers and the switch were sampled at 100 Hz (12 bit A/D conversion), then processed and stored within the Labview 5.1 data acquisition system. To ensure that participants remained relaxed during and after positioning of their reference ankle, one physical therapist experimenter continuously checked visually the absence of muscle contraction in the reference ankle and provided feedback to the participants when they were not relaxed. When there was a doubt about a state of muscle contraction, the physical therapist palpated the concerned muscle for confirmation.

Task and procedures

Matching task

To perform the contralateral concurrent matching task, participants were asked to relax their legs. The initial feet position was $40^\circ \pm 0.1^\circ$ under horizontal. Next, one experimenter positioned the reference foot on a fixed support at $10^\circ \pm 0.1^\circ$ above horizontal, corresponding approximately to a 10° plantarflexion target position (Madhavan and Shields 2005; Verschueren et al. 2002; Westlake et al. 2007). This positioning was made at a rate of approximately 5°/s (Meeuwssen et al. 1993; Pickard et al. 2003; Westlake et al. 2007). Participants were instructed to maintain this foot relaxed throughout the duration of the 10 trials. Immediately following the positioning of the reference limb, a verbal “ready” command alerted the subject to the start of the trial. Following a 2-s delay and the verbal command “go”, the participants'

task was to actively re-produce this target position with the matching foot at a self-selected movement speed (Meeuwssen et al. 1993). Participants were instructed to indicate that they had achieved a subjective satisfactory matching by pressing the switch that registered the performance. After each trial, the matching foot returned to the initial position, whereas the reference foot remained on the support for the 10 trials of the considered condition. The target foot and the matching foot were the non-dominant and dominant foot, respectively. Since we had no specific hypothesis regarding the differential effects of ageing on the dominant and non-dominant hemisphere systems, we focused on the matching task that was presumed to be more difficult, i.e. the matching task performed with the dominant limb. This type of matching has shown to induce the largest matching errors, suggesting that the non dominant hemisphere system is specialised for the processing of position-related proprioceptive feedback (Adamo et al. 2009; Goble et al. 2009; Leonard and Milner 1995; Naito et al. 2005).

Cognitive task

The cognitive task was inspired from a computerised version of the verbal Stroop test in which participants were instructed to name the colour of 7 cm high \times 17 cm wide colour words that appeared on a 46-cm screen as quickly and as accurately as possible. This “Stroop-type” task was selected because (1) it allowed investigating different levels of cognitive difficulty and (2) processing of this task was based on automatic reading, which does not interfere with the proprioceptive matching task. Two levels of difficulty of the cognitive task were investigated. In the easy cognitive task (congruent condition), participants were asked to name the colour of colour words written in the same (congruent) colour. In the difficult cognitive task (incongruent condition), participants were asked to name the colour of colour words written in a different (incongruent) colour. Due to automatic reading and in comparison to neutral words, the facilitation provided by the congruent colour word generally leads to faster responses and fewer errors, whereas the distraction provided by the incongruent colour word generally leads to slower responses and higher errors (Stroop 1935). The presentation of the Stroop stimuli started on the “go” signal simultaneously with the matching task.

The words were always presented one by one on the screen, and the following word was immediately presented once participants had named the colour of the displayed colour word. Words running proceeded until the switch that registered the matching task result was pressed. The displayed words for the Stroop tests were the words “green”, “red”, “blue” and “yellow”. To write these words, the corresponding colours were used congruently or incongruently depending on the cognitive condition (Fig. 2a, b).

Procedures

The matching task was the primary task and was performed in the single- and dual-task conditions. In the *matching single-task* condition, participants performed the matching task while fixating a point located at the centre of a white 46-cm screen that was placed in front of them. In the *dual-task* condition, participants performed the matching task concurrently with the congruent or incongruent Stroop tasks, which were used to determine the attentional demand related to the proprioceptive control. The order of presentation of the three conditions was randomised across participants, and there was a short rest interval (3 min) between each condition (Stelmach and Sirica 1986). The participants were instructed to perform the matching task in the best possible manner and at the same level with and without the Stroop task. The Stroop task had to be performed as well as possible. The congruent and incongruent Stroop tasks were also performed alone to get the baseline in the cognitive performance. Since the number of named colour words in the dual-task condition was dependent on the time needed to

perform the matching task, the *cognitive single-tasks* were performed in a second step. To allow comparison between the cognitive single- and dual-task conditions, for each trial of the cognitive single tasks, participants had to name as many colours of colour words as in the corresponding trial of the dual-task condition. To make sure that participants named the colours and did not read the words in the congruent condition, they were instructed that there may have incongruent colour words in the “congruent” lists.

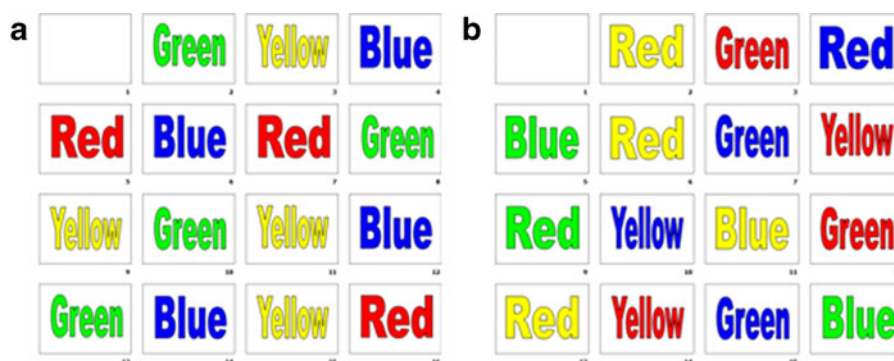
Before each condition, participants received specific instructions on how to perform the experimental tasks and then performed three trials of familiarisation. For each condition, 10 trials were performed for a total of 50 trials (10 matching single-task trials; 10 congruent and 10 incongruent dual-task trials both with the matching task; and 10 cognitive congruent and 10 cognitive incongruent single-task trials). No performance feedback was provided to participants.

Dependent variables

Matching performance

Four dependent variables were used to assess the matching performance: (1) the total variability also called total error, (2) the variable error, (3) the constant error and (4) the matching time (Schmidt and Lee 2005). In the literature, the absolute error (AE) and the total error (TE) are two statistically closed dependant variables, which are used to measure the overall performance combining accuracy and variability. However, the mathematical properties of AE have been shown to be a complex combination of accuracy and variability that makes it difficult to determine the relative contribution of each component

Fig. 2 Instances of word lists for the congruent (a) and incongruent (b) Stroop-type tests



(Schutz and Roy 1973). Since TE is always an exact combination of the variability and accuracy (namely, $TE^2 = \text{variable error}^2 + \text{constant error}^2$), TE was preferred to AE in the present study (Henry 1975). Its formula is $\sqrt{\Sigma(x_i - T)^2/n}$, where x_i is the score on trial i , T is the target ($10^\circ \pm 0.1^\circ$ above horizontal) and n is the number of trials the participant performed ($n=10$). In psychophysics experiments, different parameters are used to summarise behaviour. The *difference threshold* is defined as the magnitude of stimulus difference needed to make two stimuli just discriminable (Gescheider 1997, Kingdom and Prins 2010). This difference threshold delineate an uncertainty zone wherein the subject cannot discriminate between positions beyond chance and is computed as a measure of variability of adjustment, also referred to as *variable error* (VE) (Kingdom and Prins 2010; Luce 1959). VE is a measure of the spread about participant's own average and its formula is $\sqrt{\Sigma(x_i - M)^2/n}$, where M is the participant's average score. The *point of subjective equality* is the point where the subject can no longer discriminate the matched position as being different from the reference position. Therefore, it represents the position that has become the subject's own reference. The difference between the point of subjective equality and the real reference is called *constant error* (CE) or bias. CE is a measure of accuracy and its formula is $\Sigma(x_i - T)/n$. This variable represents the amount and direction of deviation relative to the target and reflects systematic effects of factors, unrelated to the difference threshold (Gescheider 1997). Negative CE indicated that the matching position was short of the reference position, whereas positive CE indicated that the matching foot went beyond the reference position. The matching time was defined as the mean time elapsed between the instruction "go" and the moment the participant pressed the switch to record the match.

Cognitive performance

For the two cognitive tasks, (1) the colour naming latency (*cognitive index of speed*), i.e. the time needed to perform the matching divided by the number of named colour words, and (2) the percentage of errors in colour naming (*cognitive index of accuracy*), i.e. the number of errors divided

by the total number of named colour words, were calculated.

Results

Data obtained were averaged across the 10 trials. All data were summarised by mean \pm SEM unless otherwise specified. A Kolmogorov–Smirnov test of equality of variances first showed that the distributions used for the analysis did not depart from normality ($P > 0.05$).

Matching performance

For the analysis of the matching performance, two age groups (young adults vs. older adults) \times three tasks (matching single task vs. congruent dual task vs. incongruent dual task) analyses of variance (ANOVAs) with repeated measures on the last factor were applied to the three types of matching errors (TE, VE and CE) and the matching time. For all ANOVAs, post hoc pairwise testing (Tukey's honestly significant difference) was used whenever necessary, and the level of significance was set at $P < 0.05$. The purpose of these ANOVAs was to determine to which extent the proprioceptive performance in a matching task was influenced by an added concurrent cognitive task.

As illustrated in Fig. 3a, analysis of TE showed significant main effects of age group ($F_{1,14} = 8.92$, $P = 0.009$) and task ($F_{2,28} = 19.56$, $P < 0.001$). The interaction of group \times task was also significant ($F_{2,28} = 4.45$, $P = 0.021$). The decomposition of the interaction into its simple main effects showed that the older adults exhibited a greater TE than the young adults in the congruent (3.6 ± 0.5 vs. $7.9^\circ \pm 1.1^\circ$; $P < 0.001$) and incongruent (4.9 ± 0.6 vs. $8.2^\circ \pm 1.0^\circ$; $P = 0.010$) dual tasks. No difference was evidenced for the matching single task between the two age groups (3.0 ± 0.2 vs. $3.8^\circ \pm 0.5^\circ$; $P = 0.954$).

As illustrated in Fig. 3b, analysis of VE showed no significant main effect of age group ($F_{1,14} = 2.28$, $P = 0.153$) but a significant main effect of task ($F_{2,28} = 6.65$, $P = 0.004$). The interaction of group \times task was not significant ($F_{2,28} = 0.07$, $P = 0.933$).

As illustrated in Fig. 3c, analysis of CE showed no significant main effect of age group ($F_{1,14} = 4.15$, $P = 0.061$) but a significant main effect of task ($F_{2,28} = 4.54$, $P = 0.020$). The interaction of group \times task was also

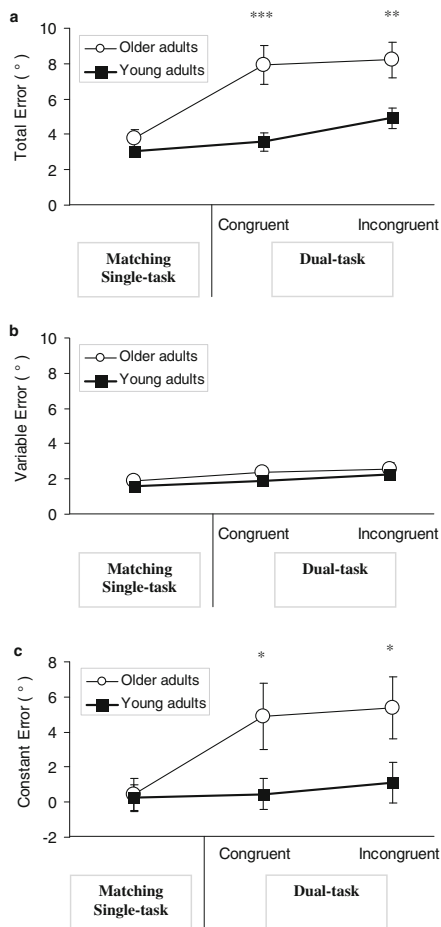


Fig. 3 Total error (a), variable error (b) and constant error (c) for the matching task in degrees (mean±SEM) as a function of age group (young adults, older adults) and task (matching single task, congruent dual task, incongruent dual task). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

significant ($F_{2,28}=3.62$, $P=0.040$). The decomposition of the interaction into its simple main effects showed that the older adults exhibited an increased CE as compared to the young adults in the congruent (0.5 ± 0.9 vs. $4.9 \pm 1.9^\circ$; $P=0.011$) and incongruent (1.1 ± 1.2 vs. $5.4 \pm 1.8^\circ$; $P=0.016$) dual tasks. No difference was evidenced for the matching single task between the two age groups (0.2 ± 0.7 vs. $0.4 \pm 1.0^\circ$; $P > 0.999$).

As illustrated in Fig. 4, analysis of matching time showed significant main effects of age group ($F_{1,14}=9.02$, $P=0.009$) and task ($F_{2,28}=16.29$, $P < 0.001$). The interaction of group×task was also significant ($F_{2,28}=3.84$, $P=0.034$). The decomposition of the interaction into its simple main effects showed that the older adults needed more time to match than the young adults in the

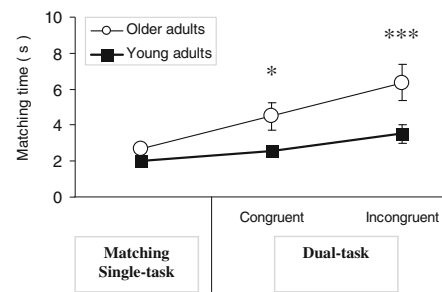


Fig. 4 Matching time in seconds (mean±SEM) as a function of age group (young adults, older adults) and task (matching single task; congruent dual task; incongruent dual task). * $P < .05$; *** $P < .001$

congruent (2.54 ± 0.31 vs. 4.49 ± 0.75 s; $P=0.022$) and incongruent (3.51 ± 0.53 vs. 6.37 ± 1.01 s; $P < 0.001$) dual tasks. No difference was evidenced for the matching single task between the two age groups (2.03 ± 0.22 vs. 2.67 ± 0.22 s; $P=0.870$).

Cognitive performance

For analysis of the cognitive performance, a two age groups (young adults vs. older adults)×two tasks (cognitive single task vs. dual task)×two conditions (congruent vs. incongruent) ANOVA with repeated measures on the two last factors was applied to the cognitive index of speed. Since there were no errors in colour naming for the congruent conditions (single and dual tasks), a two groups (young adults vs. older adults)×two tasks (incongruent single task vs. incongruent dual task) ANOVA with repeated measures on the last factor was applied to the cognitive index of accuracy in the incongruent conditions.

As illustrated in Fig. 5, analysis of the cognitive index of speed revealed main effects of age group ($F_{1,14}=73.78$, $P < 0.001$), task ($F_{1,14}=53.06$, $P < 0.001$) and condition ($F_{1,14}=108.54$, $P < 0.001$). Crucially, there was also a three-way interaction of group×task×condition ($F_{1,14}=4.85$, $P=0.045$). The decomposition of the interaction into its simple main effects showed that the colour naming latency was similar between the two age groups in the congruent single task (735 ± 23 vs. 709 ± 12 ms; $P > 0.999$), whereas it was significantly greater for older than for young adults in the incongruent single task (921 ± 28 vs. $1,282 \pm 73$ ms; $P=0.011$) and in the congruent (842 ± 34 vs. $1,367 \pm 101$ ms; $P < 0.001$) and incongruent ($1,190 \pm 46$ vs. $1,739 \pm 82$ ms; $P < 0.001$) dual tasks.

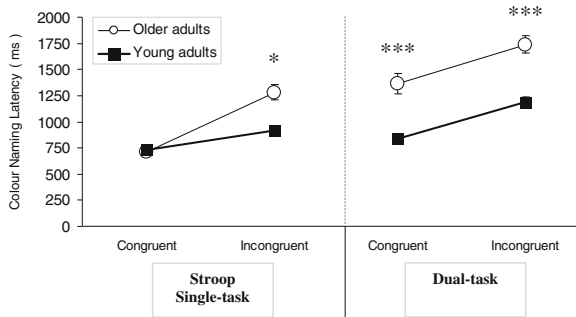


Fig. 5 Colour naming latency in milliseconds (mean±SEM) as a function of age group (young adults, older adults), task (cognitive single task, dual task) and condition (congruent; incongruent). * $P<0.05$; *** $P<0.001$

As illustrated in Fig. 6, analysis of the cognitive index of accuracy showed main effects of age group ($F_{1,14}=8.52$, $P=0.011$), task ($F_{1,14}=19.40$, $P<0.001$) and an interaction of group×task ($F_{1,14}=8.58$, $P=0.011$). The decomposition of the interaction into its simple main effects showed no differences in the incongruent single task (1.8 ± 0.7 vs. $5.1\pm 2.1\%$; $P=0.269$) but a greater percentage of colour naming errors for the older than for the young adults in the incongruent dual task (3.4 ± 1.1 vs. $13.8\pm 2.9\%$; $P<0.001$).

Discussion

In this study, 15 young adults and 15 older adults performed an ankle joint position matching task in single- and dual-task paradigms to assess age-related presumed deficits in proprioceptive control.

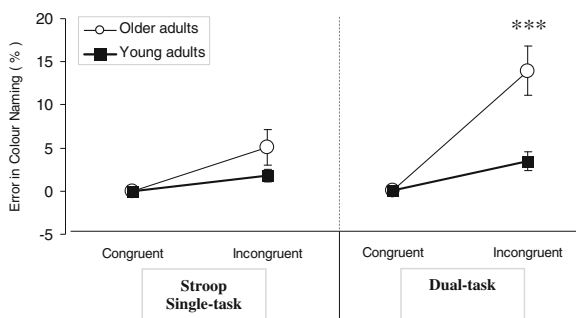


Fig. 6 Percentage of errors for the colour naming (mean±SEM) as a function of age group (young adults, older adults), task (cognitive single task, dual task) and condition (congruent, incongruent). *** $P<0.001$

Effects of age on proprioception in a matching single task

In the *matching single-task*, no differences for the four matching dependent variables (TE, VE, CE and matching time) were observed between age groups (*hypothesis 1*).

The absence of significant age-related difference for TE supported the study of Stelmach and Sirica (1986), which used the AE-dependent variable to assess overall proprioceptive performance. These authors showed no age-related deficit in a contralateral concurrent matching task when both the reference and the matching limbs were active. To explain this result, they suggested that the proprioceptive efferent signal available in active movements could offset any drop in proprioceptive function by heightening the encoding of that information with expected sensory consequences. The present results suggested that availability of the proprioceptive efferent signal from the matching limb only would be sufficient to compensate for the presumed proprioceptive-afferent deficit. However, other studies using the same matching paradigm as the present one evidenced that older adults exhibited greater AE than young ones (Adamo et al. 2007, 2009; Meeuwssen et al. 1993). The discrepancy observed with the present results could be explained by the difference in time spent in the reference position. In the present study, the reference foot was maintained in the target position for 10 trials, whereas it was maintained for one trial in the abovementioned studies (Adamo et al. 2007, 2009; Meeuwssen et al. 1993). Previous investigations have demonstrated that proprioception was quite stable in the absence of vision (Brown et al. 2003a,b; Desmurget et al. 2000) and could even be enhanced by holding the limb in a static position for an extended period of time without visual calibration (Goble et al. 2010). The present results suggested that when the reference limb was presented during a sufficient period of time, older adults' overall proprioceptive performance was not different from the young adults' one, in an active contralateral concurrent single task, at least. As outlined by Goble et al. (2010), a longer time of reference limb presentation affords individuals an increased opportunity to develop neural representations of the reference limb position to be matched. This added processing time is likely of critical importance when compensating for inherent noise within peripheral proprioceptive signals in young adults (van Beers et

al. 2002a) as well as muscle spindles and nervous system degenerations in older adults.

The breakdown of the overall performance variable (TE) into VE and CE provided additional information related to the proprioceptive acuity and factors' effects. The VE refers to the difference threshold, which measures the participant's ability to discriminate two stimuli and reflects the proprioceptive acuity (Gescheider 1997). In the present study, the results in VE showed that older adults were as consistent as young adults in a single-task context, which suggested that proprioceptive acuity was not altered with ageing. These results in VE corroborate the study of Stelmach and Sirica (1986) but not that of Meeuwssen et al. (1993), which evidenced for the first trials a greater variability in older adults than in young ones when performing a contralateral concurrent matching. However, this latter study evidenced an interaction of age by trial blocks showing that there was no more difference of variability between young and older adults after the second block of three trials. Goble et al. (2010) showed that when the reference was provided for a longer period of time, VE significantly decreased in young adults. In the present study, the long target presentation time (i.e., constantly maintaining the reference position) could have optimised the variability of the proprioceptive performance in older adults.

The CE or bias is the difference between the point of subjective equality and the real reference and reflects systematic effects of experimental factors and is unrelated to a different proprioceptive threshold (Gescheider 1997). In the present study, the results in CE showed that older adults were as accurate as the young adults. These results corroborated the study of Meeuwssen et al. (1993) and suggested that matching accuracy was not different between young and older populations, at least in a single matching task.

The matching time was measured to control that older adults did not increase the limb presentation period of time to compensate for a possible decrease of proprioceptive performance. Results showed that older adults did not take longer time to match and therefore did not increase the time of presentation of the reference limb.

However, the absence of difference for the four matching dependent variables (TE, VE, CE and matching time) between young and older adults was not sufficient to conclude whether the proprioceptive control was altered in the older population as compared to the young one or not. Indeed, this

absence of difference in an easy proprioceptive task did not exclude changes in the attentional cost of the proprioceptive control. As evidenced for motor performance, older adults may recruit additional neural resources to reach proprioceptive performance levels comparable to those obtained in the young adults (Heuninckx et al. 2005, 2008; Hutchinson et al. 2002; Mattay et al. 2002; Naccarato et al. 2006). To unmask a presumed proprioceptive deficit, the difficulty of the task had to be increased.

Effects of a dual-task paradigm on proprioception

Interestingly, in the *dual-task* paradigm, older adults decreased their overall proprioceptive performance as compared to young ones as evidenced by TE. This result suggested that despite the experimenter instructions, participants were not able to perform the matching task at the same level with and without the Stroop task. The breakdown of TE into VE and CE showed that this decreased in the overall proprioceptive performance was not related to VE but to CE. The absence of difference in VE between the single- and dual-task paradigms suggested that proprioceptive acuity remained the same among conditions. This result was expected because the matching task was the primary task, and participants were therefore instructed to perform this task at the same level with and without the secondary task. However, older adults tend to produce responses that went beyond the reference position as evidenced by the positive values of CE. This decreased performance in CE between the single- and the dual-task paradigms evidenced in older adults suggested that they were not able to fully compensate for the increased attentional demand imposed by the dual-task paradigms. The increased matching time observed in older adults for dual-tasks suggested that the strategy they used to try to compensate for the increased attentional demand was to increase the time of presentation of the reference limb. As mentioned above, a longer time of reference limb presentation affords individuals an increased opportunity to develop neural representations of the reference limb position to be matched.

Simultaneously with TE, the cognitive performance decreased in older adults but not in young ones with a longer colour naming latency in the *congruent dual-task* than in the *congruent cognitive single-task* condition (*hypothesis 2*). In other words, dividing attention between the two tasks had a more

deleterious effect for older than young adults. This result could be related to a necessity for older adults to recruit greater cortical resources to reach performance levels comparable to those obtained by young adults. When the amount of attention required to perform the cognitive task increased in the *dual-task* condition (*congruent vs. incongruent*), older and young adults managed to maintain their matching performance, but both groups increased their colour naming latency. In addition, older adults increased their percentage of errors for the colour naming (*hypothesis 2*). Taken together, these results advocated for an impaired proprioception in physiological ageing. As the prefix *presby* comes from Greek *presbus* (old) and as proprioception appeared to be physiologically different between young and older adults, the word “*presbypropria*” could be appropriate to name the alterations of older adults’ proprioception.

Studies examining the relationship between attention and the control of posture or/and gait is a rapidly expanding area but is relatively new (see Woollacott and Shumway-Cook 2002 for a review). These studies demonstrated that postural control appeared to be more attentionally demanding in older than in young adults and performance of a secondary task that was attentionally demanding appeared to have a more deleterious effect on postural control in older adults than in young ones. However, when assessing the effect of ageing on the attentional cost of proprioception in a posture or gait task, the attentional cost for processing vestibular information cannot be ruled out from the reflexion. Vestibular sense has shown to be altered with ageing (Rosenhall 1973). Therefore, when the vestibular sense and proprioception are assessed simultaneously, the results may confound age-related changes due to the vestibular sense with those due to proprioception itself. To our knowledge, no previous study singled the limb proprioception out from the vestibular sense and examined the age-related changes in the attentional requirements of limb proprioception in a dual-task paradigm. Two complementary hypotheses (peripheral and central) can explain the impaired proprioception observed in older adults.

From a peripheral point of view, age-related changes in muscle (Kararizou et al. 2005; Liu et al. 2005; Rosant et al. 2007; Swash and Fox 1972), joint (Aydoğ et al. 2006; Morisawa 1998; Salo and Tatton 1993) and skin (Bolton et al. 1966; Cauna and

Mannan 1958) receptors are well documented. These changes lead to a decreased quality and intensity of the sensory inputs coming from these proprioceptive receptors (Levin and Benton 1973; Miwa et al. 1995). Such an alteration of the proprioceptive inputs at the peripheral level would result in an increase of the attentional cost required to process these inputs at the central level. Furthermore, this alteration of proprioceptive inputs could affect older adults’ body schema. Indeed, body schema, the internal representation of the body’s current position (Berlucchi and Aglioti 2010; Head and Holmes 1911), is built on the basis of multisensory inputs including proprioceptive receptors (Maravita et al. 2003). Alteration of the information provided by the proprioceptive receptors to the somato-sensory cortical area could alter in turn the older adults’ body schema. To develop adapted muscular responses for performing the matching task, the internal model for action must be based on an appropriate body schema (Morasso et al. 1999). Therefore, alteration of the body schema would affect the efficiency of the internal model, which is discussed in the central hypothesis.

From a central point of view, age-related changes in the cerebral cortex with cell loss (Giorgio et al. 2010) and damage to the myelin and nerve fibres (Peters 2002) may result in a decrease of the central processing capacity (Teasdale et al. 1991). This decrease could alter integration of sensory inputs (muscles, joints and skin), which has been shown to require a given amount of attention (Redfern et al. 2001) that could be increased with ageing. The fact that information from the proprioceptive system arises from multiple sensory organs has also to be highlighted. Indeed, proprioception relies on information from receptors including muscle length transducers (muscle spindles) (Goodwin et al. 1972), muscle tension receptors (Golgi tendon organs) (Houk et al. 1971), cutaneous (Edin 1992) and joint receptors (Ferrell et al. 1987). In the present approach to proprioceptive control, we could not identify the specific contribution of each sensory receptor encoding proprioceptive information. Thus, we only considered the final outcome of the individual sensors, which is used to provide estimates of ankle positioning. However, inputs from the different proprioceptive receptors are differently weighted in order to compute this estimate. Central weighting of sensory inputs has been used to explain how the integration of multiple

sensory cues is performed to face the unpredictability of the environment and the measurement error associated with sensory encoding (Knill and Pouget 2004). This model has been validated in a number of different psychophysical paradigms, across sensory modalities (e.g. van Beers et al. 2002b), and also within the same sensory system (e.g. Hillis et al. 2004) as for instance across the different types of receptors of the proprioceptive system (Mugge et al. 2009). Since sensory weighting has shown to be less efficient in older adults as compared to young ones (Speers et al. 2002; Stephen et al. 2010), additional attentional resources may be required when the performance in a proprioceptive task has to be maintained in older adults. Finally, neurophysiological studies evidenced neurons, which have the characteristic of discharging both during the perception of an action and the production of the same action (Umiltà et al. 2001). The coexistence of motor and sensory properties in the same neuron suggests that the motor cortex not only executes actions but also participates to the internal construction of their representation by matching perception and execution of motor actions (Gallese et al. 1996). Recent findings suggested a specific decline of action representation in the ageing brain with internal models of action that become imprecise with advance in age (Personnier et al. 2008). Due to this decline, the internal model of action updating in older adults probably required additional central resources. In other words, it can be reasonably assumed that a combination of both peripheral and central factors led to the impairment of proprioceptive control observed in older adults.

It is well known that the CNS has a limited capacity and limited attentional resources. The present study supported previous results suggesting that older adults did not reach these limits in a single proprioceptive task paradigm since these studies showed no proprioceptive deficit in older adults with respect to younger ones (Batavia et al. 1999; Deshpande et al. 2003; Goble et al. 2011; Jordan 1978; Marks 1996; Pickard et al. 2003; Stelmach and Sirica 1986; Tsang and Hui-Chan 2004; Westlake et al. 2007). Conversely, other studies showed a proprioceptive deficit in older adults, in a single task (Adamo et al. 2007, 2009; Barrack et al. 1983; Bullock-Saxton et al. 2001; Hurley et al. 1998; Kaplan et al. 1985; Madhavan and Shields 2005; Marks et al. 1993; Meeuwssen et al. 1993; Petrella et al. 1997; Stelmach and Sirica 1986; Tsang and Hui-Chan

2004; Verschueren et al. 2002; You 2005). Put together, these results suggested that older adults are generally closer than the young adults to the cognitive limits of the CNS when performing a single matching task. In addition, it can be reasonably assumed that the proprioceptive signal is also altered with age. When the proprioceptive task is not too complex and/or when the cognitive capacities are sufficient, the performance of older adults can be unaffected, as for example in the single proprioceptive matching task of the present study. However, when the task becomes too complex and/or when the olders' cognitive system is overloaded, the proprioceptive performance can be degraded, and/or the attentional cost for processing the task can increase, as for example in the dual task of the present study.

In summary, the present study demonstrated that proprioception was as accurate and as consistent in older and young adults for a single proprioceptive task, only. However, performing a secondary cognitive task and increasing the difficulty of this secondary task evidenced both a decrease of the matching performance and an increased attentional cost of proprioceptive control in older adults as compared to young ones. These results advocated for an impaired proprioception in physiological ageing (i.e. presbypropria). However, it remains unclear whether the increased attentional demand in older adults is (1) strictly related to degraded proprioceptive signals, (2) strictly related to an alteration of the central mechanisms processing the proprioceptive signals or (3) a combination of these factors.

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References

- Abe O, Aoki S, Hayashi N, Yamada H, Kunimatsu A, Mori H, Yoshikawa T, Okubo T, Ohtomo K (2002) Normal aging in the central nervous system: quantitative MR diffusion-tensor analysis. *Neurobiol Aging* 23:433–441
- Adamo DE, Martin BJ, Brown SH (2007) Age-related differences in upper limb proprioceptive acuity. *Percept Mot Skills* 104:1297–1309

- Adamo DE, Alexander NB, Brown SH (2009) The influence of age and physical activity on upper limb proprioceptive ability. *J Aging Phys Act* 17:272–293
- Aydoğ ST, Korkusuz P, Doral MN, Tetik O, Demirel HA (2006) Decrease in the numbers of mechanoreceptors in rabbit ACL: the effects of ageing. *Knee Surg Sports Traumatol Arthrosc* 14:325–329
- Barrack R, Skinner H, Cook S, Haddad RJ (1983) Effect of articular disease and total knee arthroplasty on knee joint-position sense. *J Neurophysiol* 50:684–687
- Barrett DS, Cobb AG, Bentley G (1991) Joint proprioception in normal, osteoarthritic and replaced knees. *J Bone Joint Surg Br* 73:53–56
- Batavia M, Gianutsos JG, Ling W, Nelson AJ (1999) The effects of circumferential wrist pressure on reproduction accuracy of wrist placement in healthy young and elderly adults. *J Gerontol A Biol Sci Med Sci* 54:M177–M183
- Berlucchi G, Aglioti SM (2010) The body in the brain revisited. *Exp Brain Res* 200:25–35
- Bernaer EM, Walby WF, Ertl AC, Dempster PT, Bond M, Greenleaf JE (1994) Knee-joint proprioception during 30-day 6 degrees head-down bed rest with isotonic and isokinetic exercise training. *Aviat Space Environ Med* 65:1110–1115
- Bolton CF, Winkelmann RK, Dyck PJ (1966) A quantitative study of Meissner's corpuscles in man. *Neurology* 16:1–9
- Braun J (1998) Divided attention: narrowing the gap between brain and behaviour. In: Parasuraman R (ed) *The attentive brain*. MIT Press, Cambridge, pp 327–351
- Brown LE, Rosenbaum DA, Sainburg RL (2003a) Limb position drift: implications for control of posture and movement. *J Neurophysiol* 90:3105–3118
- Brown LE, Rosenbaum DA, Sainburg RL (2003b) Movement speed effects on limb position drift. *Exp Brain Res* 153:266–274
- Bullock-Saxton JE, Wong WJ, Hogan N (2001) The influence of age on weight-bearing joint reposition sense of the knee. *Exp Brain Res* 136:400–406
- Burke D, Gandevia SC, Macefield G (1988) Responses to passive movement of receptors in joint, skin and muscle of the human hand. *J Physiol* 402:347–361
- Cauna N, Mannan G (1958) The structure of human digital pacinian corpuscles (corpuscula lamellosa) and its functional significance. *J Anat* 92:1–20
- Collins DF, Refshauge KM, Todd G, Gandevia SC (2005) Cutaneous receptors contribute to kinesthesia at the index finger, elbow, and knee. *J Neurophysiol* 94:1699–1706
- Corso JF (1971) Sensory processes and age effects in normal adults. *J Gerontol* 26:90–105
- Craik FI, McDowd JM (1987) Age differences in recall and recognition. *J Exp Psychol Learn Mem Cogn* 13:474–479
- Crapse TB, Sommer MA (2008) Corollary discharge across the animal kingdom. *Nat Rev Neurosci* 9:587–600
- Cruz-Sánchez FF, Moral A, Tolosa E, de Bellerocche J, Rossi ML (1998) Evaluation of neuronal loss, astrogliosis and abnormalities of cytoskeletal components of large motor neurons in the human anterior horn in aging. *J Neural Transm* 105:689–701
- Deshpande N, Connelly DM, Culham EG, Costigan PA (2003) Reliability and validity of ankle proprioceptive measures. *Arch Phys Med Rehabil* 84:P883–P889
- Desmurget M, Vindras P, Gréa H, Viviani P, Grafton ST (2000) Proprioception does not quickly drift during visual occlusion. *Exp Brain Res* 134:363–377
- Dick MB, Kean ML, Sands D (1988) The preselection effect on the recall facilitation of motor movements in Alzheimer-type dementia. *J Gerontol* 43:P127–P135
- Edin BB (1992) Quantitative analysis of static strain sensitivity in human mechanoreceptors from hairy skin. *J Neurophysiol* 67:1105–1113
- Ferrell WR, Gandevia SC, McCloskey DI (1987) The role of joint receptors in human kinaesthesia when intramuscular receptors cannot contribute. *J Physiol* 386:63–71
- Folstein MF, Folstein SE, McHugh PR (1975) Mini-mental state. A practical method for grading the cognitive state of patients for the clinician. *J Psychiatr Res* 12:189–198
- Forestier N, Teasdale N, Nougier V (2002) Alteration of the position sense at the ankle induced by muscular fatigue in humans. *Med Sci Sports Exerc* 34:117–122
- Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. *Brain* 119:593–609
- Gandevia SC, McCloskey DI (1976) Joint sense, muscle sense, and their combination as position sense, measured at the distal interphalangeal joint of the middle finger. *J Physiol* 260:387–407
- Gandevia SC, Refshauge KM, Collins DF (2002) Proprioception: peripheral inputs and perceptual interactions. *Adv Exp Med Biol* 508:61–68
- Gandevia SC, Smith JL, Crawford M, Proske U, Taylor JL (2006) Motor commands contribute to human position sense. *J Physiol* 571:703–710
- Gates GA, Mills JH (2005) Presbycusis. *Lancet* 366:1111–1120
- Gescheider GA (1997) *Psychophysics: the fundamentals*. Lawrence Erlbaum Associates, Mahwah
- Gilings MG, Van den Bosch CG, Lee SG, Ashton-Miller JA, Alexander NB, Schultz AB, Ericson WA (1995) Association of age with the threshold for detecting ankle inversion and eversion in upright stance. *Age Ageing* 24:58–66
- Giorgio A, Santelli L, Tomassini V, Bosnell R, Smith S, De Stefano N, Johansen-Berg H (2010) Age-related changes in grey and white matter structure throughout adulthood. *Neuroimage* 51:943–951
- Glasser A, Campbell MC (1998) Presbyopia and the optical changes in the human crystalline lens with age. *Vision Res* 38:209–229
- Goble DJ (2010) Proprioceptive acuity assessment via joint position matching: from basic science to general practice. *Phys Ther* 90:1176–1184
- Goble DJ, Brown SH (2007) Task-dependent asymmetries in the utilization of proprioceptive feedback for goal-directed movement. *Exp Brain Res* 180:693–704
- Goble DJ, Lewis CA, Hurvitz EA, Brown SH (2005) Development of upper limb proprioceptive accuracy in children and adolescents. *Hum Mov Sci* 24:155–170
- Goble DJ, Hurvitz EA, Brown SH (2009) Deficits in the ability to use proprioceptive feedback in children with hemiplegic cerebral palsy. *Int J Rehabil Res* 32:267–269

- Goble DJ, Noble BC, Brown SH (2010) Where was my arm again? Memory-based matching of proprioceptive targets is enhanced by increased target presentation time. *Neurosci Lett* 481:54–58
- Goble DJ, Coxon JP, Van Impe A, Geurts M, Van Hecke W, Sunaert S, Wenderoth N, Swinnen SP (2011) The neural basis of central proprioceptive processing in older versus younger adults: an important sensory role for right putamen. *Hum Brain Mapp*. doi:10.1002/hbm.21257
- Goodwin GM, McCloskey DI, Matthews PB (1972) Proprioceptive illusions induced by muscle vibration: contribution by muscle spindles to perception? *Science* 175:1382–1384
- Grady CL, Craik FI (2000) Changes in memory processing with age. *Curr Opin Neurobiol* 10:224–231
- Grigg P, Finerman GA, Riley LH (1973) Joint-position sense after total hip replacement. *J Bone Joint Surg Am* 55:1016–1025
- Head H, Holmes G (1911) Sensory disturbances from cerebral lesion. *Brain* 34:102–254
- Henry FM (1975) Absolute error vs “E” in target accuracy. *J Mot Behav* 7:227–228
- Heuninckx S, Wenderoth N, Debaere F, Peeters R, Swinnen SP (2005) Neural basis of aging: the penetration of cognition into action control. *J Neurosci* 25:6787–6796
- Heuninckx S, Wenderoth N, Swinnen SP (2008) Systems neuroplasticity in the aging brain: recruiting additional neural resources for successful motor performance in elderly persons. *J Neurosci* 28:91–99
- Hillis JM, Watt SJ, Landy MS, Banks MS (2004) Slant from texture and disparity cues: optimal cue combination. *J Vis* 4:967–992
- Hopper KD, Patel S, Cann TS, Wilcox T, Schaeffer JM (1994) The relationship of age, gender, handedness, and sidedness to the size of the corpus callosum. *Acad Radiol* 1:243–248
- Houk JC, Singer JJ, Henneman E (1971) Adequate stimulus for tendon organs with observations on mechanics of ankle joint. *J Neurophysiol* 34:1051–1065
- Hurley M, Rees J, Newham D (1998) Quadriceps function, proprioceptive acuity and functional performance in healthy young, middle-aged and elderly subjects. *Age Ageing* 27:55–62
- Hutchinson S, Kobayashi M, Horkan CM, Pascual-Leone A, Alexander MP, Schlaug G (2002) Age-related differences in movement representation. *Neuroimage* 17:1720–1728
- Johnson JA, Zatorre RJ (2006) Neural substrates for dividing and focusing attention between simultaneous auditory and visual events. *Neuroimage* 31:1673–1681
- Jordan T (1978) Age differences in visual and kinesthetic short-term memory. *Percept Mot Skills* 46:667–674
- Kaplan F, Nixon J, Reitz M, Rindfleisch L, Tucker J (1985) Age-related changes in proprioception and sensation of joint position. *Acta Orthop Scand* 56:72–74
- Kararizou E, Manta P, Kalfakis N, Vassilopoulos D (2005) Morphometric study of the human muscle spindle. *Anal Quant Cytol Histol* 27:1–4
- Kingdom FAA, Prins N (2010) *Psychophysics: a practical introduction*. Academic Press, London
- Knill DC, Pouget A (2004) The Bayesian brain: the role of uncertainty in neural coding and computation. *Trends Neurosci* 27:712–719
- Kokmen E, Bossemeyer RW Jr, Williams WJ (1978) Quantitative evaluation of joint motion sensation in an aging population. *J Gerontol* 33:62–67
- Leonard G, Milner B (1995) Recall of self-generated arm movements by patients with unilateral cortical excisions. *Neuropsychologia* 33:611–622
- Levin HS, Benton AL (1973) Age effects in proprioceptive feedback performance. *Geront Clin* 15:161–169
- Li SC, Dinse HR (2002) Aging of the brain, sensorimotor, and cognitive processes. *Neurosci Biobehav Rev* 26:729–732
- Li KZ, Lindenberger U (2002) Relations between aging sensory/sensorimotor and cognitive functions. *Neurosci Biobehav Rev* 26:777–783
- Liu JX, Eriksson PO, Thornell LE, Pedrosa-Domellof F (2005) Fiber content and myosin heavy chain composition of muscle spindles in aged human biceps brachii. *J Histochem Cytochem* 53:445–454
- Loose R, Kaufmann C, Auer DP, Lange KW (2003) Human prefrontal and sensory cortical activity during divided attention tasks. *Hum Brain Mapp* 18:249–259
- Lowrey CR, Strzalkowski ND, Bent LR (2010) Skin sensory information from the dorsum of the foot and ankle is necessary for kinesthesia at the ankle joint. *Neurosci Lett* 485:6–10
- Luce RD (1959) *Individual choice behaviour: a theoretical analysis*. Wiley, New York
- Madhavan S, Shields RK (2005) Influence of age on dynamic position sense: evidence using a sequential movement task. *Exp Brain Res* 164:18–28
- Maravita A, Spence C, Driver J (2003) Multisensory integration and the body schema: close to hand and within reach. *Curr Biol* 13:R531–R539
- Marks R (1996) Further evidence of impaired position sense in knee osteoarthritis. *Physiother Res Int* 1:127–136
- Marks R, Quinney HA, Wessel J (1993) Proprioceptive sensibility in women with normal and osteoarthritic knee joints. *Clin Rheumatol* 12:170–175
- Mattay VS, Fera F, Tessitore A, Harii AR, Das S, Callicott JH, Weinberger DR (2002) Neurophysiological correlates of age-related changes in human motor function. *Neurology* 58:630–635
- Matthews PB (1982) Where does Sherrington's "muscular sense" originate? Muscles, joints, corollary discharges? *Annu Rev Neurosci* 5:189–218
- Meeuwse HJ, Sawicki TM, Stelmach GE (1993) Improved foot position sense as a result of repetitions in older adults. *J Gerontol* 48:P137–P141
- Miwa T, Miwa Y, Kanda K (1995) Dynamic and static sensitivities of muscle spindle primary endings in aged rats to ramp stretch. *Neurosci Lett* 201:179–182
- Morasso PG, Baratto L, Capra R, Spada G (1999) Internal models in the control of posture. *Neural Netw* 12:1173–1180
- Morisawa Y (1998) Morphological study of mechanoreceptors on the coracoacromial ligament. *J Orthop Sci* 3:102–110
- Mugge W, Schuurmans J, Schouten AC, van der Helm FC (2009) Sensory weighting of force and position feedback in human motor control tasks. *J Neurosci* 29:5476–5482

- Naccarato M, Calautti C, Jones PS, Day DJ, Carpenter TA, Baron JC (2006) Does healthy aging affect the hemispheric activation balance during paced index-to-thumb opposition task? An fMRI study. *Neuroimage* 32:1250–1256
- Naito E, Roland PE, Grefkes C, Choi HJ, Eickhoff S, Geyer S, Zilles K, Ehrsson HH (2005) Dominance of the right hemisphere and role of area 2 in human kinesthesia. *J Neurophysiol* 93:1020–1034
- Pai YC, Rymer WZ, Chang RW, Sharma L (1997) Effect of age and osteoarthritis on knee proprioception. *Arthritis Rheum* 40:2260–2265
- Pashler HE (1998) *The psychology of attention*. MIT Press, Cambridge
- Personnier P, Paizis C, Ballay Y, Papaxanthis C (2008) Mentally represented motor actions in normal aging II. The influence of the gravito-inertial context on the duration of overt and covert arm movements. *Behav Brain Res* 186:273–283
- Peters M (1988) Footedness: asymmetries in foot preference and skill and neuropsychological assessment of foot movement. *Psychol Bull* 103:179–192
- Peters A (2002) The effects of normal aging on myelin and nerve fibers: a review. *J Neurocytol* 31:581–593
- Petrella R, Lattanzio P, Nelson M (1997) Effect of age and activity on knee joint proprioception. *Am J Phys Med Rehabil* 76:235–241
- Pickard CM, Sullivan PE, Allison GT, Singer KP (2003) Is there a difference in hip joint position sense between young and older groups? *J Gerontol A Biol Sci Med Sci* 58:631–635
- Proske U, Gandevia SC (2009) The kinaesthetic senses. *J Physiol* 587:4139–4146
- Redfern MS, Jennings JR, Martin C, Furman JM (2001) Attention influences sensory integration for postural control in older adults. *Gait Posture* 14:211–216
- Rémy F, Wenderoth N, Lipkens K, Swinnen SP (2010) Dual-task interference during initial learning of a new motor task results from competition for the same brain areas. *Neuropsychologia* 48:2517–2527
- Reuter-Lorenz PA, Lustig C (2005) Brain aging: reorganizing discoveries about the aging mind. *Curr Opin Neurobiol* 15:245–251
- Reuter-Lorenz PA, Stanczak L (2000) Differential effects of aging on the functions of the corpus callosum. *Dev Neuropsychol* 18:113–137
- Robbins S, Waked E, McClaran J (1995) Proprioception and stability: foot position awareness as a function of age and footwear. *Age Ageing* 24:67–72
- Rosant C, Nagel MD, Pérot C (2007) Aging affects passive stiffness and spindle function of the rat soleus muscle. *Exp Gerontol* 42:301–308
- Rosenhall U (1973) Degenerative patterns in the aging human vestibular neuro-epithelia. *Acta Otolaryngol* 76:208–220
- Salo PT, Tatton WG (1993) Age-related loss of knee joint afferents in mice. *J Neurosci Res* 35:664–677
- Schmidt RA, Lee TD (2005) Motor control and learning: A behavioral emphasis. *Human Kinetics, Champaign*
- Schutz RW, Roy EA (1973) Absolute error: the devil in disguise. *J Mot Behav* 5:141–153
- Sherrington CS (1900) The muscular sense. In: Schäfer EA (ed) *Textbook of physiology*. Pentland, Edinburgh/London, pp 1002–1025
- Skinner HB, Barrack RL, Cook SD (1984) Age-related decline in proprioception. *Clin Orthop Relat Res* 184:208–211
- Smith JL, Crawford M, Proske U, Taylor JL, Gandevia SC (2009) Signals of motor command bias joint position sense in the presence of feedback from proprioceptors. *J Appl Physiol* 106:950–958
- Speers RA, Kuo AD, Horak FB (2002) Contributions of altered sensation and feedback responses to changes in coordination of postural control due to aging. *Gait Posture* 16:20–30
- Sperry RW (1950) Neural basis of the spontaneous optokinetic response produced by visual inversion. *J Comp Physiol Psychol* 43:482–489
- Stelmach GE, Sirica A (1986) Aging and proprioception. *Age* 9:99–103
- Stelmach GE, Kelso JA, Wallace SA (1975) Preselection in short-term motor memory. *J Exp Psychol Hum Learn* 1:745–755
- Stephen JM, Knoefel JE, Adair J, Hart B, Aine CJ (2010) Aging-related changes in auditory and visual integration measured with MEG. *Neurosci Lett* 484:76–80
- Stroop JR (1935) Studies of interference in serial verbal reactions. *J Exp Psychol* 18:643–662
- Suprak DN (2011) Shoulder joint position sense is not enhanced at end range in an unconstrained task. *Hum Mov Sci* 30:424–435
- Swash M, Fox KP (1972) The effect of age on human skeletal muscle: studies of the morphology and innervation of muscle spindles. *J Neurol Sci* 16:417–432
- Teasdale N, Stelmach GE, Breunig A (1991) Postural sway characteristics of the elderly under normal and altered visual and support surface conditions. *J Gerontol* 46: B238–B244
- Thelen DG, Brockmiller C, Ashton-Miller JA, Schultz AB, Alexander NB (1998) Thresholds for sensing foot dorsi- and plantarflexion during upright stance: effects of age and velocity. *J Gerontol A Biol Sci Med Sci* 53:M33–M38
- Toole T, Pyne A, McTarsney PA (1984) Age differences in memory for movement. *Exp Aging Res* 10:205–210
- Tsang W, Hui-Chan C (2004) Effects of exercise on joint sense and balance in elderly men: Tai Chi versus golf. *Med Sci Sports Exerc* 36:658–667
- Umiltà MA, Kohler E, Gallese V, Fogassi L, Fadiga L, Keysers C, Rizzolatti G (2001) I know what are you doing: a neurophysiological study. *Neuron* 31:155–165
- van Beers RJ, Baraduc P, Wolpert DM (2002a) Role of uncertainty in sensorimotor control. *Philos Trans R Soc Lond B Biol Sci* 357:1137–1145
- van Beers RJ, Wolpert DM, Haggard P (2002b) When feeling is more important than seeing in sensorimotor adaptation. *Curr Biol* 12:834–837
- Verschueren SM, Brumagne S, Swinnen SP, Cordo PJ (2002) The effect of aging on dynamic position sense at the ankle. *Behav Brain Res* 136:593–603
- von Holst E (1954) Relations between the central nervous system and the peripheral organs. *Br J Anim Behav* 2:89–94
- Vuillerme N, Boisgontier M, Chenu O, Demongeot J, Payan Y (2007) Tongue-placed tactile biofeedback suppresses the

- deleterious effects of muscle fatigue on joint position sense at the ankle. *Exp Brain Res* 183:235–240
- Walsh LD, Gandevia SC, Taylor JL (2010) Illusory movements of a phantom hand grade with the duration and magnitude of motor commands. *J Physiol* 588:1269–1280
- Westlake K, Wu Y, Culham E (2007) Sensory-specific balance training in older adults: effect on position, movement, and velocity sense at the ankle. *Phys Ther* 87:560–568
- Woollacott M, Shumway-Cook A (2002) Attention and the control of posture and gait: a review of an emerging area of research. *Gait Posture* 16:1–14
- You S (2005) Joint position sense in elderly fallers: a preliminary investigation of the validity and reliability of the SENSERite measure. *Arch Phys Med Rehabil* 86:346–352