

Age-related changes in the bimanual advantage and in brain oscillatory activity during tapping movements suggest a decline in processing sensory reafference

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Abstract Deficits in the processing of sensory reafferences have been suggested as accounting for age-related decline in motor coordination. Whether sensory reafferences are accurately processed can be assessed based on the bimanual advantage in tapping: because of tapping with an additional hand increases kinesthetic reafferences, bimanual tapping is characterized by a reduced inter-tap interval variability than unimanual tapping. A suppression of the bimanual advantage would thus indicate a deficit in sensory reafference. We tested whether elderly indeed show a reduced bimanual advantage by measuring unimanual (UM) and bimanual (BM) self-paced tapping performance in groups of young ($n = 29$) and old ($n = 27$) healthy adults. Electroencephalogram was recorded to assess the underlying patterns of oscillatory activity, a neurophysiological mechanism advanced to support the integration of sensory reafferences. Behaviorally, there was a significant interaction between the factors tapping condition and age group at the level of the inter-tap interval variability, driven by a lower variability in BM than

UM tapping in the young, but not in the elderly group. This result indicates that in self-paced tapping, the bimanual advantage is absent in elderly. Electrophysiological results revealed an interaction between tapping condition and age group on low beta band (14–20 Hz) activity. Beta activity varied depending on the tapping condition in the elderly but not in the young group. Source estimations localized this effect within left superior parietal and left occipital areas. We interpret our results in terms of engagement of different mechanisms in the elderly depending on the tapping mode: a ‘kinesthetic’ mechanism for UM and a ‘visual imagery’ mechanism for BM tapping movement.

Keywords EEG · Oscillation · Parietal lobe · Tapping task · Aging · Sensory reafference

Introduction

Normal aging has been repeatedly associated with a decline in sensorimotor functions (Bugnariu and Fung 2007; Berard et al. 2009; Degardin et al. 2011). Age-related deficits in motor coordination are notably illustrated by evidence that the elderly exhibit temporal impairments even in basic sensorimotor tasks consisting of synchronized tapping with two hands at an isofrequency rate (Swinnen et al. 1998; Serrien et al. 2000; Wishart et al. 2000). Although the stability of synchronization between the two hands (i.e., the relative phase) during simultaneous (in-phase) movements of both indexes is not dependent on age, the stability of the relative phase decreases in the elderly during more complex anti-phase movements (alternate movements of both indexes; Serrien et al. 2000). Similarly, age-related increases in the variability of the inter-tap interval (ITI)

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have also been reported during simple repetitive unimanual (UM) and bimanual (BM) in-phase finger tapping (Sommerhoff et al. 2011).

Converging lines of evidence suggest that the high motor instability during BM coordination in elderly might be the result of a deficit in intrinsic afferent information processing (Serrien et al. 2000). Firstly, an age-related weakening of movement-related proprioception has been reported during passive detection of motion or position occurring in the lower (Diener et al. 1984; Fitzpatrick and McCloskey 1994) or the upper limbs (Ferrell et al. 1992; Wright et al. 2011). Since kinesthetic reafferences constitute an important source of information on the produced movements, a deficit in integrating these reafferences should likely result in enhanced motor instability. Secondly, the elderly have been shown to benefit more than the young from visual feedback (Seidler-Dobrin and Stelmach 1998; Wishart et al. 2002; van Hedel and Dietz 2004), suggesting that with aging sensory reafferences compensate less reliably for a lack of other sources of feedback to stabilize motor coordination. Greater age-related differences in BM coordination have indeed been found in the performance of motor tasks based only on intrinsic information (vision and/or proprioception) than when augmented visual feedback was available (Swinnen et al. 1998). A third level of evidence supporting the fact that motor instability in the elderly might be the result of a decline in the processing of sensory reafferences comes from comparing UM and BM tapping tasks. ITIs have been shown to be less variable during synchronous BM than during UM tapping movement in young adults (Helmuth and Ivry 1996), an effect known as the 'bimanual advantage'. Because BM movements integrate twice as many effectors as UM movements, more kinesthetic reafferences are available in BM than in UM movement. This could account for the decrease in ITI variability in BM conditions (Helmuth and Ivry 1996). In addition, kinesthetic reafferences could modulate ITI variability by having an effect on the temporal coupling between the two effectors (Drewing and Aschersleben 2003), with the additional tactile and kinesthetic reafferences provided by the two hands helping to maintain the coupling stability. These assumptions are supported by the work of Drewing and Aschersleben (2003) who showed that right hand ITI variability increases when the left hand simultaneously taps into a gap (reduced tactile reafferences). Because the bimanual advantage depends on kinesthetic reafferences, the alteration of kinesthetic reafferences with aging would result in a reduction in bimanual advantage in the elderly compared to the young.

The neurophysiological consequences of aging on the processing of kinesthetic reafferences also remain unclear. Sensory brain regions such as primary sensorimotor

cortices and the superior and posterior parietal cortices have been involved in tasks requiring the processing of kinesthetic reafferences, notably in BM (Serrien et al. 2001; Swinnen and Wenderoth 2004) and UM coordination tasks (Lacquaniti et al. 1995; Koeneke et al. 2004). Other sensory area such as the occipital lobe was also showed involved during motor imagery of a finger sequence opposition task (Guillot et al. 2009). With aging, additional activity during inter-limb coordination was found in the parietal cortex and in the cerebellum, two regions already known to be involved in high-order sensorimotor coordination during demanding tasks (Heuninckx et al. 2008). Brain oscillatory activity in the beta band has been pointed out as a mechanism supporting the maintenance of motor or cognitive states (Alegre et al. 2003; Engel and Fries 2010). In general, power modulations of brain oscillations relate to the overall level of activity in neuronal populations (see Kilavik et al. 2013). Decrease in power (desynchronization) corresponds to an activated brain state and is a correlate of excited cortical neurons (Steriade and Llinas 1988; Pfurtscheller et al. 1997; Kilavik et al. 2013). Conversely, an increase in power (synchronization) reflects decreased cortical excitability or increased inhibition of neuronal populations (Pfurtscheller et al. 1997; Kilavik et al. 2013). For example, the voluntary suppression of complex finger movements was associated with increased upper alpha power over the sensorimotor cortex compared to a rest condition (Sauseng et al. 2013). Thus, a power decrease or increase reflects changes in cerebral activation level. A decrease in beta oscillations during movement was related to the sensorimotor network (Pfurtscheller and Lopes da Silva 1999) suggesting that beta oscillations are linked to the association of sensory and motor aspects. A decrease in beta activity has been reported during finger movements (Gaetz et al. 2010) and the sequence of rhythmic movements (Alegre et al. 2003). Additionally, Keirath and collaborators (2006) showed a modulation of beta oscillation in sensorimotor regions during active and passive movements as well as during kinesthetic illusions. These findings suggest that beta oscillations within sensorimotor regions during UM and BM tapping movements might reflect the processing of kinesthetic reafferences.

To investigate the role of the beta oscillations and to examine whether kinesthetic reafferences decline with age, we compared self-paced UM and BM tapping movements in young and elderly participants. We did not provide any visual or auditory feedback on tapping movements during the task in order to ensure that the performance relied purely on kinesthetic reafferences. To identify the neural basis for the age-related effects on motor coordination, electroencephalogram was recorded during the tapping tasks.

Materials and methods

Participants

Twenty-nine young adults (14 males; aged 24 ± 2 years, mean \pm SD; range 19–29 years) and 27 elderly adults (12 males; aged 69 ± 5 years; range 60–83 years) participated in the study. The elderly participants were both active and independent, community-dwelling individuals. All participants had normal or corrected-to-normal vision and were not on any medication, and none reported a history of major medical disorders, sustained head injury, psychiatric or neurological disorders, alcohol or drug abuse. They were all right-handed (87 ± 18 , mean \pm SD. Edinburgh handedness inventory score: 100 = max right-handed and -100 = max left handed) according to a twelve-item version of the Oldfield Edinburgh handedness inventory (Oldfield 1971). All participants gave written informed consent to take part in the study. The Ethics Committee for research on humans participants (University of Lausanne) and the Faculty of Psychology and Educational Science (University of Geneva) approved all experimental procedures.

Methods

Participants were comfortably seated in front of a computer screen at a distance of about 60 cm. Two joysticks were placed inside two boxes used to attenuate auditory feedback from button-press and to avoid the possibility of visual feedback on hand movements. The joysticks were positioned 20 cm in front of each participant at a distance of 30 cm from each other. To prevent the participants from hearing the sounds from the joysticks' buttons, participants wore earplugs. Two loudspeakers delivered the tones of a metronome (low-pitched tone: 500 Hz) and the imperative signal (high-pitched tone: 4000 Hz) at an intensity of 70 dB SPL at the location where the participants were sitting (measured using an audiometer Testo 816, Testo AG, Kirchzarten). We asked to each participant if they discriminated easily the tones of the metronome. All participants confirmed that the loudness was sufficient and comfortable. Stimuli delivery and response recording were monitored by Presentation 14.4 software (Neurobehavioral System, Albany, CA).

Participants performed tapping tasks in which they were instructed to press the joysticks' buttons with their index fingers. At the beginning of each block, the frequency of the auditory metronome was set at 2 Hz for 5 s. Participants were instructed to produce symmetrical BM button presses on each beat of the metronome. After these 5 s of rhythmic auditory stimulation, the metronome was turned off and the participants had to continue self-pacing by pressing

the buttons at the same tempo as when the metronome was active (BM condition). Following a randomly varying delay (see below), a high-pitched tone was presented, prompting the participant stop the left hand tapping while continuing right hand tapping at the same pace (UM condition). The next high-pitched tone prompted the participant to switch to BM tapping again, and so on. Each UM and BM trial lasted from 4 to 7 s (i.e., from 8 to 14 manual taps). Participants performed between 10 and 12 blocks of about 60 s, consisting of 6 trials in the BM condition and 5 trials in the UM condition, for a total of 60 BM trials and 50 UM trials. The proper 10 experimental blocks were performed after 2 familiarization blocks. Participants could take short rest periods between blocks if they wished. The whole experiment lasted approximately 15 min. EEG was recorded during the whole experimental session.

Behavioral analyses

Inter-tap intervals (ITI) between each button press of the right index were calculated. Mean (ITImean) and standard deviation (ITIsd) of inter-tap intervals were computed on correct responses for each of the UM and BM tapping conditions. ITImean indexes the rhythm of the produced tempo and ITIsd its variability. Steadiness of performance was tested by the variability of the ITI in series of 8–14 taps. Series with a minimum of 4 consecutive correct taps were included in the calculation of the variability. The first tap after the switching was excluded to guarantee the steadiness of the behavior. Symmetric tapping (i.e., BM movement) was considered to be correct if the delay between the button presses of each hand did not exceed 50 ms. ITImean and ITIsd were separately submitted to a 2×2 mixed design ANOVA with age (Young; Elderly) as between-subject factor and tapping condition (UM; BM) as within-subject factor.

Electrophysiological recordings

Continuous EEG was recorded at a sampling rate of 2048 Hz through a 64-channel Biosemi ActiveTwo amplifier system (Biosemi, Amsterdam, Netherlands) referenced to the CMS-DRL ground which functions as a feedback loop driving the average potential across the montage as close as possible to amplifier zero. Eye blinks were recorded by two electrodes placed above and below the right eye, while horizontal eye movements were recorded by two supplementary electrodes placed on the exterior side of each eye. The final electrode positions were not measured in each individual subject, but a template cap was used.

Offline analyses of the EEG were performed using Car-tool software (developed by D. Brunet, Functional Brain

Mapping Laboratory, Geneva, Switzerland). Raw EEG data were first down-sampled to 1024 Hz to reduce computational load and band-pass filtered (0.34–40 Hz, Notch 50 Hz and DC removed). We used the median tap (4th tap) in a sequence of 7 consecutive taps (in UM or BM condition) to select epoch of interests. For each trial of each condition, the duration of epochs of interest was 500 ms (from 250 ms before to 250 ms after the median tap). Electrodes were visually defined as being artifacted and were then interpolated using a spherical spline interpolation (Perrin et al. 1987). On average, 5.4 % (± 2.2 , range 0–6) of the 64 electrodes were interpolated. In addition to a $\pm 100 \mu\text{V}$ peak to peak artifact rejection criterion, each epoch containing eye blinks or other noise transients were excluded. The EEG data were re-referenced to the mean voltage of all 64 channels (i.e., transformed to the common average reference). On average, the number of epochs included in the analysis was 54 ± 6 (rejection rate of 6.8 %) for the BM and of 50 ± 5 (rejection rate of 7.8 %) for the UM condition.

EEG analyses

The analyses of oscillatory activity were conducted according to previously published methods (e.g., see Arzy et al. 2010; Bernasconi et al. 2011). For each participant and condition, a fast Fourier transform approximation (FFTA; Lehmann and Michel 1990) was applied to each epoch and electrode in the following four frequency bands: low alpha (A1 = 8–10 Hz), high alpha (A2 = 10–12 Hz), low beta (B1 = 14–20 Hz), and high beta (B2 = 20–30 Hz) with a frequency resolution of 2 Hz. We subdivided the alpha and beta frequencies band to increase the frequency space resolution and to dissociate the function of each sub-frequency. Previous evidence indeed indicates that different frequency bands within the alpha frequency range reflect different cognitive processes. Lower alpha (7–9.5 Hz) has been related to attentional processes and upper alpha (9.5–12 Hz) to sensory-semantic information (Klimesch et al. 1997; Neuper and Pfurtscheller 2001). In the same vein, beta rhythms have been observed in different beta sub-frequency bands according to the part of the body involved during voluntary movements. Thereby, the largest beta activity was observed in 16–21 Hz for finger movement and 19–26 Hz during foot movement (Neuper and Pfurtscheller 1996; Pfurtscheller et al. 1997). The outputs of this analysis (i.e., FFTA power maps) were averaged across conditions for each frequency band and participant. By comparison with classical FFT power representing squared potential values, the FFTA provides the FFT for each channel and then uses the complex values of all electrodes to calculate the first principal component for each frequency point. By contrast with the FFT power map, the FFTA preserves the polarity information

and is reference-independent thereby allowing source estimations to be directly calculated in the frequency domain.

Of note, movement-related beta changes have been previously characterized by a decrease followed by an increase in power. Precisely, a premovement desynchronization phase (ERD) about 1 s before the movement followed with a post-movement synchronization phase (ERS or beta rebound) has been reported. The ERD phase has been advanced to correspond to the preparation and the execution of the movement, while the ERS phase has been associated either to sensory reafferences, to the return of the motor cortex to a ‘rest’ state or to the closure of the motor process (see Pfurtscheller et al. 1996; Derambure et al. 1999; Alegre et al. 2003, 2004). Because we have selected a 500-ms period, our analyses might have missed potential power modulations during this interval. However, the previously reported fast beta changes were mainly described during discrete hand/foot movements during time intervals of 8 s or more (Pfurtscheller et al. 1996; Derambure et al. 1999; Pfurtscheller and Lopes da Silva 1999; Pfurtscheller 2001; Alegre et al. 2003) but were not observed for each movement in a sequence of two consecutive movements (Alegre et al. 2004). Post-movement ERS was indeed not observed after the first movement but only at the end of the sequence of movements. In our study, we focused on a 500-ms period in the middle of a long sequence of movement. Hence, based on previous literature, beta ERD could be expected to be stable around each tap of continuous tapping movement as in the current study.

In each frequency band, modulations of frequency power for all conditions and groups were assessed using the global power spectra (GPS) by averaging the absolute value of the frequency power of all electrodes. The main advantage of using the GPS is that it does not require the (arbitrary) selection of electrodes of interest, which could induce experimenter’s biases, and allows having more data-driven analysis. GPS in each frequency band were then submitted to a 2×2 mixed design ANOVA with age (Young; Elderly) as between-subject factor and tapping condition (UM; BM) as within-subject factor. This first analysis served to determine the frequency bands in which significant modulation manifested. Source estimations were then calculated and statistically compared across conditions for the frequency bands showing significant GPS modulations.

The sources of oscillatory activity were estimated by applying a distributed linear inverse solution based on the local autoregressive average (LAURA; Grave de Peralta Menendez et al. 2001, 2004). LAURA selects the source configuration that better mimics the biophysical behavior of electric fields (i.e., activity at one point depends on the activity at neighboring points according to electromagnetic law). The accuracy of the estimation of sources from a 64-scalp electrode was shown sufficient

to determine the deep source activity in the brain (Michel et al. 2004). The solution space was based on a realistic head model and included 4,996 nodes selected from a $3 \times 3 \times 3$ mm grid equally distributed within the gray matter of the Montreal Neurological Institute’s average brain. Several validation and clinical studies demonstrated the accuracy of distributed source localization, mostly by investigating epileptic patients (see Michel and Murray 2012 for review). We applied statistical parametric mapping analyses to the source estimation and thus even if the estimated activity in brain regions was of unrealistic size, statistical analysis revealed whether differences between experimental conditions were reliable. One ANOVA was conducted at each of the 4,996 solution points. Correction for multiple comparisons was implemented by considering as significant only the clusters of at least 14 contiguous nodes. This spatial criterion was determined using the AlphaSim program (available at <http://afni.nimh.nih.gov>). The 10,000 Monte Carlo permutations were performed using the 4,996 nodes of our lead field matrix and revealed a false-positive probability <0.001 for observing a cluster of 14 nodes. We interpreted only the most pronounced effects by choosing to focus on the maxima: solution point with the minimal p value within each cluster. For the frequency bands of interest, source estimations were calculated for each participant and each condition and then submitted to 2×2 , age group \times tapping condition ANOVA.

The normality of the distributions of the behavioral and EEG data was assessed using a Kolmogorov–Smirnov test, which did not reach our $p < 0.05$ significance criterion (all p values >0.2) except in the alpha frequency band. Tukey HSD test was used as post hoc analyses when necessary.

Results

Behavior

Analyses of the mean inter-tap interval (ITI_{mean}) revealed no significant main effects or interaction of the factors age and tapping condition (all p values >0.05 ; Table 1). Analyses of the inter-tap interval variability (ITI_{sd}) revealed a tendency on the age factor with a larger rhythm variability

in old than young participants ($F(1,54) = 3.33, p = 0.07$) and a significant age \times tapping condition interaction ($F(1,54) = 4.94, p = 0.03$). Tukey HSD post hoc test revealed a greater variability of tapping rhythm in UM than BM in the young group only ($p < 0.05$; Fig. 1).

EEG

Analyses of the oscillatory activity, as indexed by the global power spectra (GPS), revealed a main effect of tapping condition in both low and high beta bands (B1 and B2), with lower power in BM than UM in both age groups ($F(1,54) = 6.18, p < 0.01$ and $F(1,54) = 1.81, p < 0.01$, for B1 and B2, respectively). In B1 (14–20 Hz), there was a significant interaction between age and tapping condition ($F(1,54) = 4.67, p < 0.05$), driven by a lower power in BM than UM in the elderly (Tukey HSD test, $p < 0.05$; Fig. 2). We found no other significant GPS differences. We conducted multiple Pearson linear correlations between inter-tap variability (ITI_{sd}) and frequency power values (GPS) in low and high beta band in each age group (young; old) and condition (UM; BM). No significant correlations were observed.

ANOVAs on the source estimations were computed from the FFTA topographies of the B2 and B1 band. For B2, there was a main effect of tapping condition in the right cingulate cortex (cingulate gyrus, limbic lobe. BA 24; $F(1,54) = 25.66, p < 0.01$), with a lower activity in BM than UM (Fig. 3a, right panel). For B1, there was a main effect of tapping condition within the right premotor cortex with a decrease in power during BM than UM (sub-gyral frontal lobe. BA 6; $F(1,54) = 33.64, p < 0.01$; Fig. 3a, left panel). There was also a significant age \times tapping condition interaction for B1 within two clusters. The maxima of the first cluster were localized within the left occipital lobe (Middle occipital gyrus, BA 19) and showed a lower power in the elderly during BM than UM condition ($F(1,54) = 12.28, p < 0.01$; Fig. 3b, left panel). The maxima of the second cluster were localized within the left superior parietal lobule (post-central gyrus, BA 5; $F(1,54) = 11.47, p < 0.01$; Fig. 3b, right panel) and showed a lower power in the elderly during UM than BM condition ($p < 0.05$). Power tended to decrease during BM than UM ($p = 0.07$) within the left superior parietal lobule in the young group (Fig. 3b, right panel).

Discussion

We investigated the effect of aging on the behavioral and electrophysiological responses during self-paced unimanual and bimanual tapping movements. Behaviorally, we found a bimanual advantage in the young, but not in the

Table 1 Inter-tap interval (ITI) mean and variability in the bimanual and unimanual tapping condition for the young and the elderly groups

ITI mean \pm SD (ms)	Bimanual	Unimanual
Young	484.30 \pm 12.98	483.44 \pm 14.24
Elderly	485.33 \pm 17.29	483.90 \pm 16.54

Fig. 1 Inter-tap interval variability in the bimanual and unimanual tapping condition for the young and the elderly groups * $p < 0.05$; # $p = 0.06$, HSD Tukey test

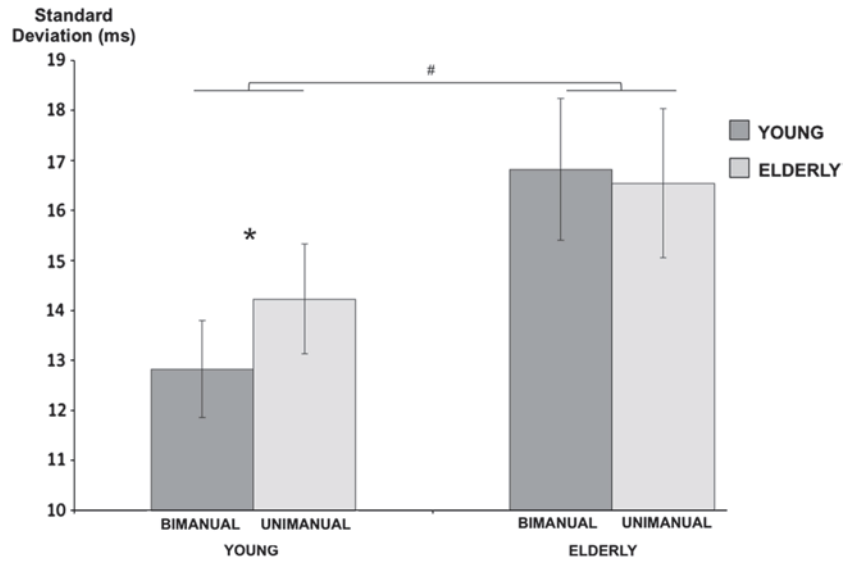
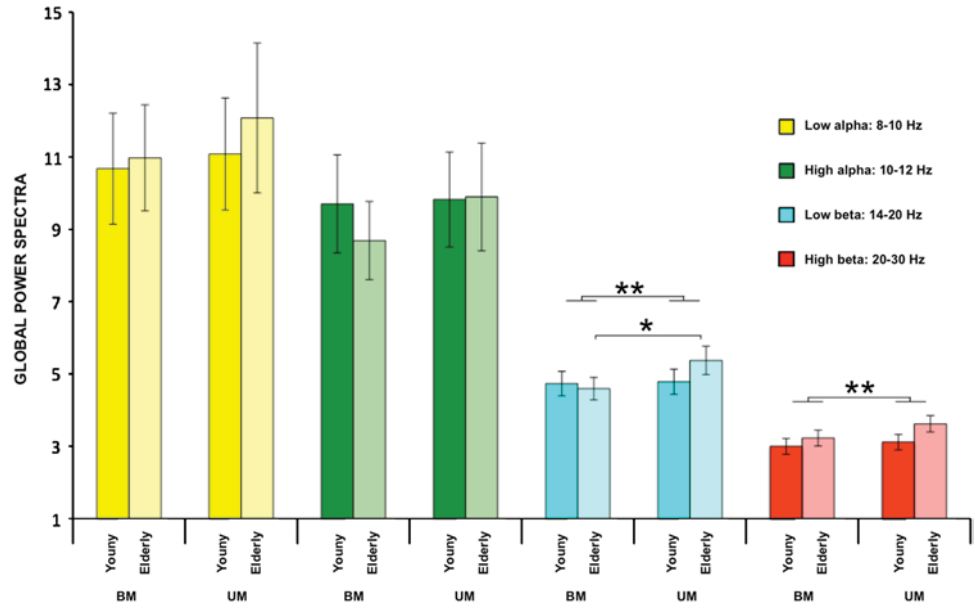


Fig. 2 Global power spectra across frequency bands for the young and the elderly groups in the bimanual (BM) and unimanual (UM) tapping condition. * $p < 0.05$; ** $p < 0.01$, HSD Tukey test



elderly. Electrophysiologically, in the elderly group, the EEG analyses showed a lower oscillatory activity in the 14–20 Hz beta band during bimanual compared to unimanual tapping movements. Source estimations revealed that this interaction followed from modulations in beta activity in the left occipital and left superior parietal areas. Since the experimental conditions were not compared to a baseline, the results were interpreted as a difference between the conditions and age group during the tapping task, independently on whether the global oscillatory activity changed compared to when participants were not tapping.

The behavioral results did not reveal any effect of age on the mean inter-tap intervals (ITI) and a marginally significant age-related increase in the ITI variability in both

tapping conditions, although the result did not reach the conventional 0.05 p -value level. Impacts of age on the variability of motor coordination, but not on its average accuracy, are typically reported in motor control studies (Galganski et al. 1993; Wishart et al. 2000; Bangert et al. 2010; Summers et al. 2010; Sommervoll et al. 2011). Our results do not show any increase in variability in the elderly during self-paced tapping.

In addition, we observed a decrease in the ITI variability during bimanual but not unimanual tapping in the young group. This bimanual advantage supports previous evidence showing a decrease in tapping variability when both hands are used (Helmuth and Ivry 1996; Drewing and Aschersleben 2003; Bangert et al. 2010). Furthermore, our

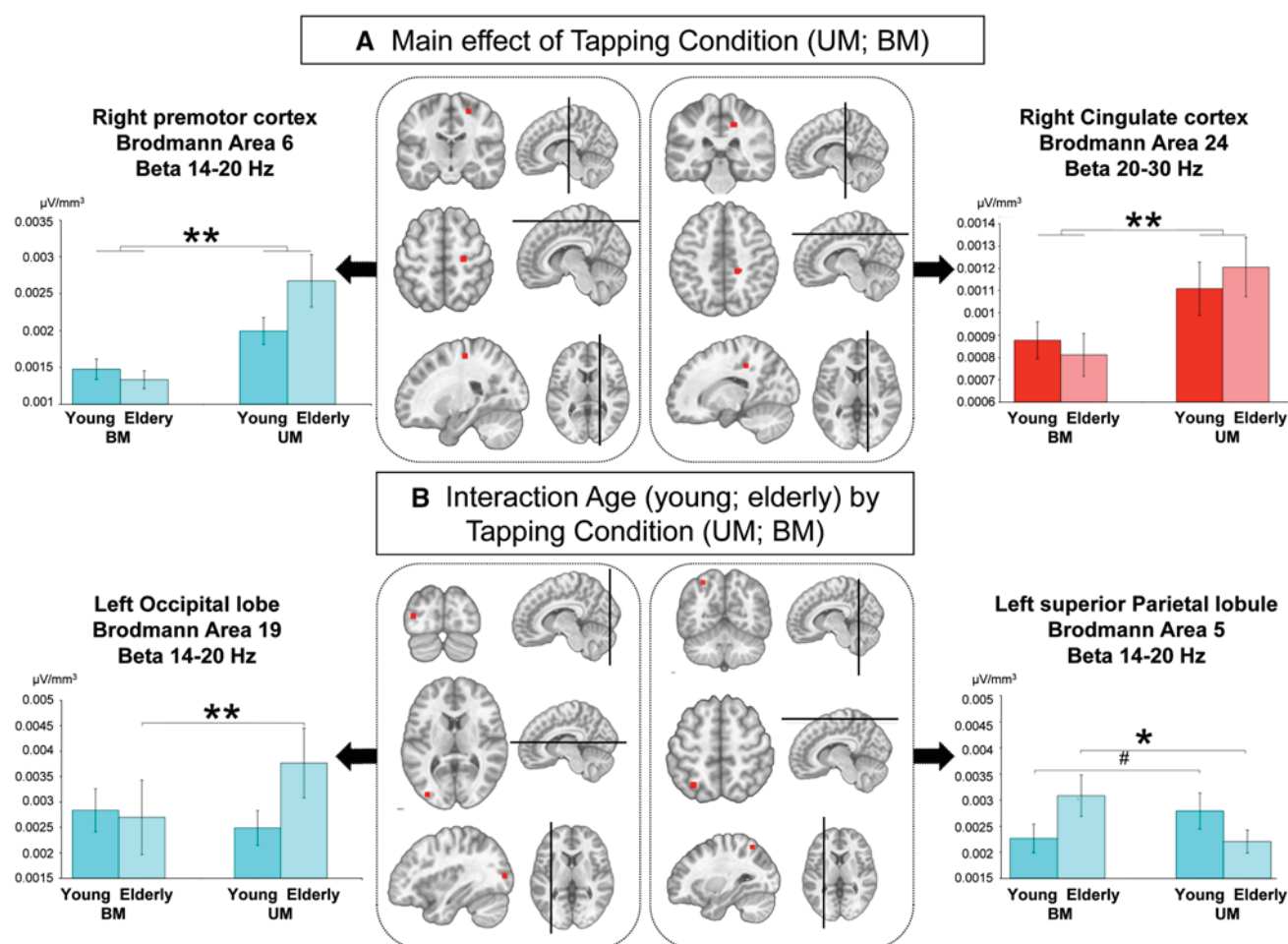


Fig. 3 a The two-by-two age \times condition ANOVA on the electrical source estimations of the beta generators revealed a main effect of Tapping condition within the right premotor cortex (sub-gyral frontal lobe, BA 6; 14–20 Hz) and the right cingulate cortex (cingulate gyrus, limbic lobe, BA 24; 20–30 Hz). b There was a significant age \times Tapping condition interaction in the left occipital lobe (mid-

dle occipital gyrus, BA 19; 14–20 Hz) and the left superior parietal lobule (postcentral gyrus, BA 5; 14–20 Hz). Red points correspond to the minimal p values. The bar graphs depict the mean activity of the beta generators at the locus of the minimal p value. $*p < 0.05$, $**p < 0.01$, $\#p = 0.07$ HSD Tukey test

results confirm the hypothesis of similar ITI variability in bimanual tapping as in unimanual tapping in the elderly group. We suppose that the absence of bimanual advantage in the elderly indicates a decline in sensory reafferences. During self-paced unimanual and bimanual tapping movements performed under sole kinesthetic reafference control (considered to be a more difficult setting for movement), the elderly did not benefit from the additional hand in inter-tapping stabilization that is observed in young adults (Helmuth and Ivry 1996; Drewing and Aschersleben 2003). Supporting this hypothesis, when visual feedback is present, bimanual advantage is maintained in the elderly (Bangert et al. 2010; see also Sasaki et al. 2011) providing evidence that guided-paced movements are easier to perform than self-paced movements. Two suppositions support the concept of bimanual advantage. The first involves separate timing mechanisms associated with

each effector. In bimanual movement, the outputs of these timing mechanisms are averaged (Helmuth and Ivry 1996; Drewing and Aschersleben 2003). As we consider that action timing is based on its sensory reafferences (Aschersleben and Prinz 1995) and that our experimental settings excluded any visual or auditory feedback, we hypothesize that the variability of the ITI was mainly dependent on kinesthetic reafferences. Our results support the second supposition assuming the role of sensory reafferences in temporal coupling (Drewing and Aschersleben 2003), in which bimanual movement is enhanced as a result of the second hand's additional kinesthetic reafferences (Aschersleben and Prinz 1995). Age-related bimanual tapping variability could therefore be interpreted as a consequence of inefficient processing of movement-related kinesthetic information. Supporting this hypothesis, it is known that tactile and proprioceptive information is impaired with the process

of aging (Diener et al. 1984; Ferrell et al. 1992; Fitzpatrick and McCloskey 1994; Wright et al. 2011). Similarly, elderly subjects have been shown to experience more difficulties while performing cycling bimanual movements when they have to rely exclusively on their intrinsic sources of sensory information (Swinnen et al. 1998).

Our EEG results revealed a marginally significant decrease in beta power in the left superior parietal lobule (BA 5, posterior parietal cortex: PPC) in the young group during the bimanual as opposed to the unimanual tapping condition. This region is known to play a major role in the integration of sensorimotor information (Serrien et al. 2001; Wenderoth et al. 2005) and more specifically in kinesthetic processing (Debaere et al. 2003) while carrying out motor activity. This tendency for a decrease in beta activity in the parietal lobule supports the hypothesis that kinesthetic reafferences account for bimanual advantage.

In contrast and as a probable consequence of the age-related decline of kinesthetic reafferences (Diener et al. 1984; Ferrell et al. 1992; Madhavan and Shields 2005; Shaffer and Harrison 2007; Goble et al. 2009; Wright et al. 2011), there was a significant increase in beta power in the left superior parietal lobule in the elderly when both hands were used as opposed to the right hand alone. This result suggests that the motor system does not favor a tactile kinesthetic mechanism in order to control bimanual tapping movements that in turn might explain the absence of reduced bimanual variability in the elderly. In addition, the kinesthetic mechanism seems to be involved only during unimanual tapping. In line with previous interpretations (Muller et al. 2003; Kilavik et al. 2013), we associate the decreases in beta power during movement production with the amount of sensorimotor processing rather than with purely motor processes.

Another hypothesis concerning the role ascribed to the PPC during sensorimotor tapping concerns its anticipatory motor control function (see Blakemore and Sirigu 2003; Krause et al. 2012). The principle is that the PPC compares the actual feedback-related response with the anticipated movement of the stimulus at each movement and sends the information about the error of matching to the cerebellum. Hence, the PPC would play a role in adjusting the internal model in order to improve the synchronization for the subsequent taps. Using unimanual synchronization tapping task (with visual and auditory externally cues), Krause and collaborators (2012) reported a major role of the left PPC for anticipatory motor control over its multisensory integration function. The design of our study which do not manipulate pacing modalities do not allow to interpret our data set in light of the anticipatory motor function of the PPC. Further research would be necessary to investigate the role of the PPC in anticipatory motor control with aging.

A last aspect to consider is the link between working memory and internal representation of rhythms. It was shown that the internal time representations rely on attentional and working memory systems primarily localized within prefrontal and parietal areas (e.g., Lewis and Miall 2003; Serrien and Brown 2004). In our study, these systems might have played a role since the participants had to maintain a previously learned beat during the tapping. Because working memory tends to decrease with aging (Craik and Byrd 1982), tapping performance across our group of interest might have been influenced by such unspecific factors. We would note, however, that tapping movement is a simple coordination task performed relatively automatically, and automatic timing mechanisms remain intact in normal aging (Wishart et al. 2000; Summers et al. 2010).

In the elderly, the lower beta power in the left occipital lobe (BA 19) during bimanual tapping signifies that this region is more activated when the two hands are engaged. Changes in power are evidently related to motor cortical activation/inhibition since power modulations in alpha and beta frequency bands are inversely correlated with the fMRI-BOLD signal during a bimanual motor task (Ritter et al. 2009). We postulate that this specific activation within the left occipital lobe in the older participants might rely on a visual imagery mechanism to control bimanual movements. This hypothesis is reinforced by several neuroimaging studies. Using MEG, recent research showed a decreased of alpha and beta power over occipital area during mental rotation task (van Wijk et al. 2013) and mental stimulation of movement (de Lange et al. 2008). In a motor imagery study, multiple occipital areas (BA 17, 18 and 19) have been shown activated during visual imagery of a finger sequence opposition task (Guillot et al. 2009). Interestingly, in the same study, the left and right superior parietal lobules (BA 5) were not activated during visual imagery, but they were during kinesthetic imagery of the same sequence. In addition, when older participants were required to perform the imagery task of stepping over an obstacle, the fMRI results emphasized an extensive network of cortical areas involved in visuomotor transformation, including visual association areas (BA 19), that were activated more in older than in younger participants (Wai et al. 2012). A recent study showed in a deafferented patient a decrease in the quality of sensory reafference and an increased in the quality of visual imagery during a mental rotation task (ter Horst et al. 2012). Moreover, a reduction in beta power has been shown during imagery of manual movement (McFarland et al. 2000; Nakagawa et al. 2011). Our observation supports the theory that older participants rely on visual imagery in order to compensate for the poor quality of kinesthetic reafferences when performing bimanual tapping.

Age-related decline is characterized by two distinct mechanisms combining behavioral and neurophysiological observations. Both mechanisms being associated with an age-related increase in cerebral activation (i.e., brain oscillation power decrease): Compensation is accompanied by a similar behavioral performance level between age groups (Cabeza 2002; Mattay et al. 2002; Reuter-Lorenz and Lustig 2005; Heuninckx et al. 2008), whereas dedifferentiation is associated with a poorer performance level in older than younger subjects (Li and Lindenberger 1999). In our study, the general decrease in GPS in low beta band during the BM condition compared to the UM condition, together with the absence of bimanual advantage in older subjects, would be compatible with a dedifferentiation mechanism. However, since no correlation was established between behavioral and electrophysiological data, this hypothesis cannot be formally confirmed.

Two other beta generators were identified as distinguishing two tapping conditions irrespective of age. The right premotor cortex (rPMC; BA 6; low beta band) and the right cingulate cortex (BA 24; high beta band) showed a decrease in beta activity during bimanual as opposed to unimanual tapping movements in both age groups. The involvement of areas in the right hemisphere could arise from the supplementary movement performed by the left hand during the bimanual condition compared to the unimanual condition. Previous studies on motor control have shown a left hemispheric dominance during bimanual movements and the preferential involvement of contralateral brain areas during unimanual movements (Jancke et al. 1998; Serrien et al. 2003; Serrien and Brown 2004; Serrien 2008). The lower right hemispheric activity during the right hand movement might follow from transcallosal inhibitory inputs from the left hemisphere (Beaule et al. 2012). In our study, the left hemisphere might be involved during both conditions, whereas the right hemisphere might be involved during bimanual condition only. The fact our finding corroborates well-established effects can be considered as a positive control that our methodological approach was appropriate and reliable for the investigation of our theoretical questions.

Conclusions

We have provided supplementary evidence on the age-related changes in electrocortical oscillations during self-paced unimanual and bimanual tapping performed under tactile and proprioceptive reafferences condition. Electrical source estimations of oscillatory activity identified two main regions involved in age-related differences in beta oscillation during manual tapping. In the elderly, decreased beta oscillatory power was observed in the left

superior parietal lobule during unimanual movement and in the left occipital lobe during bimanual movement. We interpret these results as reflecting the involvement of a kinesthetic and a visual imagery mechanism, respectively. The elderly would switch between these two mechanisms that control each tapping condition using a visuomotor imagery control during bimanual movements and a kinesthetic control during unimanual movements. In addition, the present data suggest that a decline in kinesthetic processing accounts for the increased variability of isofrequency tapping and in particular for the loss of bimanual advantage with aging.

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