Research report

Preservation of perceptual integration improves temporal stability of bimanual coordination in the elderly: An evidence of age-related brain plasticity

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HIGHLIGHTS

- How auditory and/or visual stimuli affect bimanual coordination in the elderly?
- Both auditory and audio-visual stimuli enhance stability of coordination in the elderly.
- Attentional and sensorimotor-related neural activations are increased in the elderly.
- Perceptual integration of auditory stimulations is preserved in the elderly.

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ABSTRACT

Despite the apparent age-related decline in perceptual-motor performance, recent studies suggest that the elderly people can improve their reaction time when relevant sensory information are available. However, little is known about which sensory information may improve motor behaviour itself. Using a synchronization task, the present study investigates how visual and/or auditory stimulations could increase accuracy and stability of three bimanual coordination modes produced by elderly and young adults. Neurophysiological activations are recorded with ElectroEncephaloGraphy (EEG) to explore neural mechanisms underlying behavioural effects. Results reveal that the elderly stabilize all coordination modes when auditory or audio-visual stimulations are available, compared to visual stimulation alone. This suggests that auditory stimulations are sufficient to improve temporal stability of rhythmic coordination, even more in the elderly. This behavioural effect is primarily associated with increased attentional and sensorimotor-related neural activations in the elderly but similar perceptual-related activations in elderly and young adults. This suggests that, despite a degradation of attentional and sensorimotor neural processes, perceptual integration of auditory stimulations is preserved in the elderly. These results suggest that perceptual-related brain plasticity is, at least partially, conserved in normal aging.

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1. Introduction

Aging seems to be characterized by inevitable decline in perceptual-motor performance, as proved by slowness in reaction times and movement times and by decreased accuracy and fluency when the elderly perform psychomotor tasks [1–3]. One obvious example of this effect can be found in bimanual coordination which is continuous rhythmical movements of the upper limbs [5–8]. Experimentally, temporal accuracy and stability of a bimanual coordination can be explored with a synchronization paradigm that requires to tap right and left index fingers in synchrony with a required timing pattern specified by a stimulus. In healthy adults, two modes of coordination are proved to be accurate and stable: the so-called inphase coordination relates to simultaneous movements of homologous muscle groups and antiphase coordination mode corresponds to alternated activation of homologous muscle groups. The inphase coordination mode is characterized by greater stability than antiphase one [9,10]. Intermediate coordination modes are harder to perform, as proved by their low accuracy and stability without learning [11,12].

Most of the studies investigating the effect of aging on bimanual coordination reveal a significant degradation of bimanual
coordination but inconsistent results can be found in the literature. For instance, Serrien and collaborators require young adults and older participants to produce inphase and antiphase coordination by doing flexions and extensions with their elbows in accordance with an auditory stimulation at 1 Hz [13]. Results suggest that upper-limb performance is resistant to age-related deficits for both inphase and antiphase coordination modes. Using a visual stimulation, Lee and collaborators asked young and older participants to realize the inphase and antiphase coordination modes with two slide carriages at 1 and 2 Hz. Results indicate that, whatever the frequency, elderly produce lower temporal stability than younger participants for both the inphase and antiphase coordination modes [14]. Bangert and collaborators require young and older participants to perform continuous coordination (circle drawing) and discrete tasks (inphase and antiphase tapping fingers) at 0.8, 1 and 1.2 Hz in synchrony with a visual stimulation. They found that age-related deterioration of movements is particularly found for the antiphase discrete tapping. The elderly produced antiphase coordination less stably than the younger participants (no difference for inphase) [15]. Using an auditory stimulation, Wishart and collaborators asked young and older participants to produce bimanual inphase and antiphase coordination modes at different frequencies (0.5, 1, 1.5, 2 Hz) [8]. They found that antiphase is less stable for elderly but only when the required movement frequency is high (beyond 1.5 Hz). It is possible that the differences between these results refer to the type of coordination (discrete tapping or continuous coordination) or to the required frequency of the coordination (from 0.5 Hz to 2 Hz). But one other possible explanation of the apparent discrepancy between these results relates to the sensory modality of the stimulation available to produce the required coordination.

Firstly, auditory sensory modality seems to induce greater improvement on motor performance than visual modality. Previous results of Fraisse [16] proved that auditory stimulation gives rise to faster unimanual reaction times than visual stimulation in healthy adults. More recently, Repp and Penel [17] suggest an auditory dominance on unimanual sensorimotor synchronization to rhythmic stimuli. As regard to bimanual coordination, Ronse and collaborators compared visual and auditory augmented feedback to learn intermediate coordination mode. They found an improvement of the temporal stability of a new coordination produced with auditory augmented feedback in young adults [18]. One possibility to improve the accuracy and stability of intermediate coordination is to synchronize fingers tapping with environmental information such as stimulation pacing or augmented visual feedback in young adults [19] and the elderly [20]. Debaere and collaborators tested the learning of bimanual coordination with and without augmented visual feedback in young adults. They demonstrated that augmented visual feedback facilitates this new learning and showed that different neural pathways are used when individuals practice a bimanual coordination task with and without visual feedback. Wishart and collaborators asked elderly people to produce intermediate coordination with visual feedback. They showed that with visual feedback, the older adults were able to acquire the new bimanual coordination as revealed by significant improvements in measures of accuracy and stability. However, no study has compared the effect of visual and auditory sensory modalities of a stimulation to improve stability of a bimanual coordination in the elderly.

Secondly, recent behavioural research in young adults suggests that the combination of both visual and auditory modalities can enhance unimanual sensorimotor synchronization to rhythmic stimuli [21] and to learn a new bimanual coordination mode [22]. Moreover, when young and older participants are required to respond as fast as possible to auditory, visual or audio-visual sensory stimuli, results show that audio-visual information accelerates unimanual reaction times compared to unisensory auditory, even more in the elderly than in young adults [23–25]. The effect of the combination of two sensory modalities on motor behavior suggests that the brain integrates incoming sensory information as a patterned fashion in order to adapt outgoing motor commands. The process is called multisensory integration (MI) [26,27].

Thirdly, neural mechanisms by which MI operates can be investigated with ElectroEncephaloGraphy (EEG) which measures the level of desynchronization and synchronization within local neuronal populations, capturing respectively the level of neural activation and deactivation of underlying cortical areas [28–31]. A recent review of neural correlates of MI [32] reveals that MI is associated to desynchronization in alpha frequency band (8–12 Hz), desynchronization in beta band (13–30 Hz) and synchronization in the gamma band (30–80 Hz) which reflect respectively activations of attentional (Deiber, Calbana, Ibanez, & Hauert, 2001), sensorimotor [29–31] and perceptual processes [34–36]. Investigating these activations is particularly interesting in the context of aging because the age-related decline observed in bimanual coordination can be associated with a reduction of attentional capacity especially for complex motor tasks [14,37,38]. Age-related alteration of bimanual coordination may also be due to an alteration in sensorimotor processes. More particularly, aging induce a lengthening of motor programming [39,40]. Alteration of bimanual coordination can also be attributed to degraded perceptual processes due to relative alteration of brain areas responsible for sensory integration or sensory organs themselves [41,42].

On this basis, the aim of the present study is: (1) to compare the effects of auditory and visual stimulations to improve the accuracy and stability of the bimanual coordination in the elderly compared to younger adults; (2) to investigate the possible effects of the combination of both sensory modalities on the produced coordination modes and (3) to test whether the behavioural effects are associated to additional neural activations related to sensorimotor, attentional and perceptual processes in the elderly.

2. Methods

2.1. Participants

Twenty volunteers participated in the study, including 10 young adults (eight women; 22.8 ± 1.68 years of age) and 10 elderly participants (eight women; 67.7 ± 6.58 years old). Most of young adults were students and most of elderly were recruited from club of retired teachers. All participants were right-handed, as assessed by the Edinburgh Handedness Inventory [43] (Older adults = 96 ± 8.43; Young adults = 87.32 ± 14.68). All participants were non-musicians. General cognitive functions of the elderly were assessed using the Mini-Mental State Examination [44] (maximum score = 30; MMSE = 27.8 ± 2.09). Individuals with a score less than 24 were excluded from the study, resulting in the replacement of one elderly. None of participant reported cognitive, sensory, motor or neuropsychological deficits. Participants had corrected-to-normal vision and hearing. All participants signed an informed consent before beginning the study. The study was in agreement with the University guidelines and the ethical standards laid down in the declaration of Helsinki.

2.2. Materials

One computer (X86 architecture and Windows XP Operation System) delivered visual instructions and visual pictures and/or auditory tones stimuli with Presentation software version 0.81 (Neurobehavioural Systems Inc., Albany, CA). This computer was connected via a PS2 port to a keyboard with two red-colored ‘Ctrl’
keys. Each key pressing was recorded with the Presentation software which allowed recording with a temporal precision in the tenths of milliseconds range. Visual stimuli were presented on a screen (pixel resolution: 1280 \times 1024, frame rate: 100 Hz) and auditory tones were delivered through two loudspeakers placed on each side of the monitor. The visual stimulations (VIS) were composed of red and blue squares (2.5 \times 2.5 cm with an average luminance of 19.68 cd/m^2) presented during 40 ms at 5 cm left and right from the center of the screen. The auditory stimulations (AUD) corresponded to low and high-pitched tones (500 and 4000 Hz respectively with an intensity of 80 dB). The multimodal stimulations (MUL) were composed of AUD and VIS stimulations presented simultaneously (low-pitched tones + red square and high-pitched tones + blue square).

In parallel, a second computer recorded the EEG signal (Active II, Biosemi Inc., Amsterdam, The Netherlands) at 2048 Hz from 64 active electrodes placed on the scalp in accordance with the International 10–20 System. Impedance at all electrodes was kept below 5 kΩ. Acquisition of the timing of stimuli, key pressing and EEG was managed by the Presentation software.

2.3. Task

The participants were asked to produce three bimanual coordination modes with fingers tapping in synchrony with VIS or AUD or MUL stimulations. They had to synchronize their right index finger tapping on a right 'Ctrl' key with low-pitched tones and/or red squares and they had to synchronize their left index finger's tapping with high-pitched tones and/or blue squares. The inphase coordination mode (INPHASE) corresponded to simultaneous tapping of both fingers in synchrony with the stimulations; the antiphase (ANTI) and intermediate (INTER) coordination modes corresponded to alternative tapping of the right and left fingers in synchrony with the stimulations. The tempo (T), that is the temporal delay between two taps of the right index finger, was fixed at 1 second. The right-left inter-tap (IT), that is the temporal delay between the tapping of the right and left index, was 0 ms for INPHASE, 500 ms for ANTI and 250 ms for INTER coordination. To sum up, nine conditions were required, combining three sensory modalities (VIS, AUD or MUL) and three coordination modes (INPHASE, ANTI, INTER).

2.4. Procedure

The experiment was conducted in a dark and silent room. Participants were invited to sit on a chair with their head at a distance of 80 cm from a computer screen. The computer keyboard was adjusted so that the forearms of the participant were comfortably placed on the table and their index positioned on each red-colored key. In order to standardize the position and to avoid artifacts on the EEG signal, they had to keep the same position during the whole experience.

Three sessions were proposed. First, participants performed the so-called “control task”. A visual stimulus “Ready?” was presented on the screen until the participant pressed the right “Ctrl” key of the keyboard. One of the 9 conditions was proposed. The participant was asked to keep her/his hands on the table without moving and to focus her/his attention on the stimuli without tapping. At the end of the trial an indication “End of the trial” was presented on the screen. The participant started the following trial when she/he was ready. Each trial of the “Control task” lasted 20 s and each condition consisted in a block of 5 trials for a total of 200 stimulations for each condition. Each condition was counterbalanced between participants to avoid fatigue and order effects. The EEG signal were recorded during the whole session.

Just after the “Control task”, the “Familiarization” consisted in tapping the “Ctrl” keys in synchrony with the stimulation according to one trial of one of the 9 experimental conditions randomly selected. Other trials could be performed if necessary (1 to 3 in average). EEG signal was not recorded during this session. No feedback was given. We just ensured that each participant understood the task.

Finally, participants produced each of the 9 conditions of the “Experimental task”. Each experimental trial lasted 20 s and each condition corresponded to one block of 5 trials for a total of 200 stimulations and 200 corresponding taps (100 right and 100 left) for each condition. No explicit feedback was given. Each condition of the “Experimental task” was counterbalanced between participants to avoid fatigue and order effects. Both behavioural and EEG data were recorded.

2.5. Data analysis

2.5.1. Behavioural data

First, the Relative Phase (RP) was computed for each condition and each participant. RP is the temporal delay between IT divided by T and multiplied by 360°. RP is expressed in degrees and gives theoretically 0° for INPHASE, 180° for ANTI and 90° for INTER. We computed the Absolute Error (AE) of the RP which is the absolute difference between the required and the produced RP, and Standard Deviation (SD) of the RP. AE informs about the accuracy of the produced coordination mode and SD reflects its temporal stability.

2.5.2. EEG data

We pre-processed the raw EEG data as follows. EEG data were 3–100 Hz filtered with second-order, zero-lag Butterworth type. Subsequently, the data were down-sampled to 1024 Hz to reduce computation time and memory storage. Visual inspection of EEG data allowed to interpolate bad channels and EEG data were referenced to an average reference. The continuous dataset was segmented into epochs from –250 ms to 750 ms locked to the visual/auditory stimuli corresponding to the right finger's tap (i.e., red square or/and low-pitched tones). Hence, each epoch contained one right and one left fingers taps. An independent component analysis was applied on EEG data in order to detect and correct blink artifacts. Finally, we rejected aberrant epochs with a deviation standard over 5 SD in order to obtain the cleanest possible signal (mean: 8.225 ± 1.12 rejected epochs for all participants of the RP).

After the pre-processing, a spectral analysis of brain oscillatory activity was performed to determine EEG power (Pow) with a Fast Fourier Transform. For the time epoch, Pow was calculated in the gamma (30–80 Hz), alpha (8–12 Hz) and beta (13–30 Hz) frequency bands over three regions of interest (ROIs): respectively the frontal cortex (F1, F2, F3, F4, Fz), the parietal cortex (P1, P2, P3, P4, Pz) and the centro-parietal cortex (C1, C2, C3, C4, Cz, CP1, CP2, CP3, CP4, CPz). Pow data were transformed using a logarithmic function in order to reduce the effects of inter-participants and inter-electrodes variability. Finally, we computed the Task-Related Power (TRPow) which is the power spectrum specifically associated to the bimanual tapping in each condition by subtracting the Pow of the “Control task” from each corresponding Pow of the “Experimental task” [28].

2.5.3. Statistics

Statistical Age (2) × Coordination (3) × Modality (3) analyses of variance (ANOVA) with repeated measures on Coordination and Modality were carried out on each dependent variable: AE, SD and TRPow in the gamma, alpha and beta bands. For each ANOVA, the homogeneity of variance was verified and the F, ddl and p values were corrected with the Greenhouse–Geisser correction if
necessary. As post hoc, pairwise comparisons between all pairs of each dependent variable were computed using non-pooled error terms (i.e., by computing separate paired-samples t-tests [45]) and using sequentially acceptable step-up Bonferroni procedure [46]. For each analysis, the p value was fixed at \( p \leq 0.05 \).

### 3. Results

#### 3.1. Behavioural results

##### 3.1.1. Absolute error (AE) of RP

The ANOVA revealed an Age effect on AE (\( F(1,18) = 13.653; \; p = 0.002; \; \eta^2 = 0.431 \)). Whatever the Coordination and the Modality, AE was lower for Young adults (AE = 9.13 \pm 8.239°) compared to the Elderly (AE = 19.67 \pm 7.48°) (Fig. 1a).

The ANOVA revealed also a Modality effect on AE (\( F(2,36) = 4.021; \; p = 0.026; \; \eta^2 = 0.182 \)). Whatever the Age and the Coordination, AE was lower for AUD (13.39 \pm 16.51°) than for VIS (17.23 \pm 18.60°). Moreover, AE was lower for MUL (12.59 \pm 11.97°) than for VIS (t(10) = 2.823; \; p = 0.019 and t(10) = 2.525; \; p = 0.032).

A Coordination effect was also significant on AE (\( F(1.22, 22.07) = 17.751; \; p = 0.000; \; \eta^2 = 0.496 \)). t test revealed that the AE differ significantly between INPHASE and INTER (t(10) = 6.854; \; p = 0.000) and between ANTI and INTER (t(10) = 5.052; \; p = 0.000) indicating that AE was lower for INPHASE (7.96 \pm 4.60°) and ANTI (9.84 \pm 9.81°) than INTER (25.40 \pm 21.69°) whatever the Age and the Modality.

##### 3.1.2. Standard deviation (SD) of RP

The ANOVA revealed an Age effect on SD (\( F(1,18) = 7.639; \; p = 0.012; \; \eta^2 = 0.298 \)). This effect suggests that, whatever the Coordination and the Modality, SD was lower for Young adults (SD = 8.58 \pm 3.68°) compared to the Elderly (SD = 13.71 \pm 9.79°) (Fig. 1b).

The ANOVA revealed a Modality effect on SD (\( F(1.27, 22.86) = 17.42; \; p = 0.000; \; \eta^2 = 0.492 \)). t test showed a significant

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**Fig. 1.** The top panels display the mean Absolute Error (a) and Standard Deviation (b) of the Relative Phase (SD) for YOUNG and ELDERLY participants. Vertical bars represent the inter-individual variability (standard deviation). The middle panels represent the TRPow in beta (13–30 Hz) frequency band over centro-parietal cortex (C1, C2, C3, C4, Cz, CP1, CP2, CP3, CP4, C4z) (c) and the TRPow in alpha (8–12 Hz) frequency band over parietal cortex (P1, P2, P3, P4, Pz) (d) and the bottom panel represents the TRPow in gamma (30–80 Hz) frequency band over frontal cortex (F1, F2, F3, F4, Fz) (e) for YOUNG and ELDERLY participants. The horizontal line in the box interior represents the median, the length of the box represents the interquartile range (the distance between the 25th and the 75th percentiles), the vertical lines issuing from the box extend to the minimum values above the 25th percentiles and the maximum values below 1.5 of the 75th percentiles and the dots, if any, represent the minimum values below 1.5 of the 25th percentiles and the maximum values above 1.5 of the 75th percentiles. *** \( p < 0.05 \) and ### \( p = 0.057 \). ns indicates a non-significant difference.
difference between AUD and VIS ($t(10)=5.524; p=0.000$) and between MUL and VIS ($t(10)=7.343; p=0.000$). Whatever the Age and the Coordination, SD was lower for AUD ($9.31 \pm 5.71$) and MUL ($10.45 \pm 7.31$) compared to VIS ($13.68 \pm 9.41$).

The ANOVA revealed a Coordination effect on SD ($F(1,45, 26.12)=39.492; p=0.000; \eta^2=0.687$) indicating that SD was lower for INPHASE compared to INTER ($t(10)=12.92; p=0.000$) and ANTI ($t(10)=8.354; p=0.000$) whatever the Age and the Coordination (Fig. 2).

The ANOVA revealed also a significant Age x Coordination interaction on SD ($F(2,36)=3.875; p=0.029; \eta^2=0.177$). t-test revealed that, for the Elderly, the SD differ significantly between INTER and INPHASE ($t(10)=5.951; p=0.000$) and between ANTI and INPHASE ($t(10)=4.375; p=0.001$). For Young adults, t-test also revealed that the SD differ significantly between INTER and INPHASE ($t(10)=16.298; p=0.000$) and between ANTI and INPHASE ($t(10)=8.814; p=0.000$). As shown in Fig. 3, these results suggest that SD was lower for INPHASE compared to ANTI and INTER even more for the Elderly.

A Coordination x Modality was also found on SD ($F(4,72)=2.919; p=0.027; \eta^2=0.139$). t-test revealed that SD differ significantly for ANTI between VIS et AUD ($t(10)=5.90; p=0.000$) and between VIS et MUL ($t(10)=5.34; p=0.000$). This suggests that SD was lower for AUD and/or MUL compared to VIS even more for ANTI (Fig. 4a).

Finally, the ANOVA revealed a significant Age x Modality interaction on SD ($F(2,36)=4.436; p=0.019; \eta^2=0.197$). t-tests revealed that the SD differed significantly between Young adults and the Elderly in VIS ($t(10)=3.792; p=0.004$) in AUD ($t(10)=3.453; p=0.007$) and in MUL ($t(10)=2.572; p=0.030$). As shown in Fig. 4, whatever the Coordination, SD was higher for the Elderly compared to Young adults, even more for VIS. Even if t-test revealed a difference between Young adults and the Elderly in all Coordination and Modality, Fig. 5 showed that the difference is larger for VIS.

### 3.2. EEG results

#### 3.2.1. TRPow in the beta frequency band (13–30 Hz) over centro-parietal regions

The ANOVA indicated a marginal Age effect ($F(1,18)=4.116; p=0.057; \eta^2=0.186$) suggesting that TRPow tended to be lower for the Elderly ($−1.036 \pm 1.332 \mu V^2$) compared to Young adults ($−0.216 \pm 0.692 \mu V^2$) (Fig. 1c).

As illustrated in Fig. 2, the ANOVA revealed a main Coordination effect ($F(2,36)=7.027; p=0.002; \eta^2=0.281$). t-test revealed a significantly difference between INPHASE and ANTI.

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**Fig. 2.** The top panel displays the Standard Deviation of the Relative Phase (SD) for each of the 3 Coordination: INTER, ANTI and INPHASE for all participants whatever the Modality. Vertical bars represent the inter-individual variability. The bottom panel represents the scalp maps with the TRPow in beta (13–30 Hz) frequency band for all participants whatever the Modality (the nose is represented at the top of the map). Blue color represents high negative TRPow (i.e., activation). Black circles represent the ROI over centro-parietal cortex (C1, C2, C3, C4, Cz, P1, P2, P3, P4, CP1).

**Fig. 3.** The top panel displays the Standard Deviation of the Relative Phase (SD) for each of the 3 Coordination: INTER, ANTI and INPHASE for Young Adults (white square) and the Elderly (black square) whatever the Modality. Vertical bars represent the inter-individual variability. The bottom panel represents the scalp maps with the TRPow in alpha (8–12 Hz) frequency band for Elderly (top) and Young (down) whatever the Modality (the nose is represented at the top of the map). Blue color represents high negative TRPow (i.e., activation). Black circles represent the ROI over parietal cortex (P1, P2, P3, P4, Pz).
Fig. 4. For each of the 3 Modalities: VIS, AUD and MUL and the 3 Coordination: INTER, ANTI and INPHASE for all participants: (a) Standard Deviation of the Relative Phase (SD) and (b) TRPow in the gamma (30–80Hz) frequency band. The positive values in TRPow represent synchronization (i.e., activation). Vertical bars represent the inter-individual variability.

Fig. 5. The top panel displays the Standard Deviation of the Relative Phase (SD) for each of the 3 Modality: VIS, AUD and MUL for all participants whatever the Coordination. Vertical bars represent the inter-individual variability. The bottom panel represents the scalp maps with the TRPow in gamma (30–80Hz) frequency band for all participants whatever the Coordination (the nose is represented at the top of the map). Red color represents high positive TRPow (i.e., activation). Black circles represent the ROI over frontal cortex (F1, F2, F3, F4, Fz).

\( t(10) = 4.452; p = 0.001 \) and between INPHASE and INTER coordination \( t(10) = 2.620; p = 0.027 \). Values of beta TRPow was lower in INTER and ANTI compared to INPHASE whatever the Age and Modality.

3.2.2. TRPow in the alpha frequency band (8–12 Hz) over parietal regions

The ANOVA revealed an Age effect \( F(1,18) = 14.887; p = 0.001; \eta^2 = 0.452 \); TRPow of the Elderly was lower than Young adults whatever the Coordination and the Modality \((-1.710 \pm 1.596\, \mu V^2\) and \(0.991 \pm 1.321\, \mu V^2\) respectively) (Fig. 1d).

The effect of Modality was significant \( F(1,47,26.62) = 4.466; p = 0.030; \eta^2 = 0.198 \). A paired sample t-test revealed that the TRPow differed significantly between VIS and AUD \( t(10) = 3.089; p = 0.013 \) and between VIS and MUL \( t(10) = 3.932; p = 0.003 \) indicating that TRPow was lower for VIS \((-0.47 \pm 2.02\, \mu V^2\) and MUL \((-0.71 \pm 1.61\, \mu V^2\) whatever the Age and the Coordination.

As illustrated in Fig. 3, the ANOVA revealed an Age × Coordination interaction \( F(2,36) = 5.351; p = 0.009; \eta^2 = 0.229 \), t-test revealed that for Young adults, the TRPow differed significantly between ANTI and INTER \( t(10) = 2.621; p = 0.027 \) and between ANTI and INPHASE \( t(10) = 3.086; p = 0.013 \). For the elderly INTER was both different from ANTI \( t(10) = 3.365; p = 0.007 \) and INPHASE \( t(10) = 2.287; p = 0.047 \). This suggests that for Young adults, TRPow was lower in ANTI compared to INTER and INPHASE coordination. For the Elderly, TRPow was lower for INTER compared to ANTI and INPHASE coordination.

Finally, the ANOVA revealed an Age × Coordination × Modality interaction \( F(4,72) = 5.384; p = 0.000; \eta^2 = 0.230 \). As represented in Table 1, whatever the Coordination mode, the TRPow was lower for the Elderly compared to Young adults even more for the VIS condition. There was no significant difference between the Elderly and Young adults for INPHASE produced with the AUD Modality and for ANTI produced with the MUL Modality.

3.2.3. TRPow in the gamma frequency band (30–80 Hz) over frontal regions

The ANOVA performed on TRPow revealed no effect of Age \( F(1,18) = 1.577; p = 0.226 \).

A significant effect of Modality was revealed \( F(2,36) = 5.251; p = 0.009; \eta^2 = 0.226 \). A paired sample t-test revealed that the TRPow differed significantly between VIS and AUD \( t(10) = 4.604; p = 0.001 \) and between VIS and MUL \( t(10) = 2.417; p = 0.003 \).

| Table 1 | Means and standard deviations of the TRPow \((\mu V^2)\) in the alpha frequency band (8–12 Hz) over the parietal cortex for Young adults and Elderly performing the INTER, ANTI and INPHASE Coordination modes produced in accordance with the VIS, AUD and MUL modalities. |
|--------|-------------------------------------------------|-------------|----------|-------------|--------|
|        | Modality | Young      | Elderly   | r        | p         | Significance |
| VIS    | INTER    | -0.274 (1.195) | -2.092 (1.691) | 3.548    | 0.006      | -         |
|        | ANTI     | -0.469 (1.118) | -1.795 (1.530) | 2.818    | 0.020      | -         |
|        | INPHASE  | -0.788 (2.202) | -1.873 (1.230) | 2.559    | 0.030      | -         |
| AUD    | INTER    | 1.216 (1.490)  | -2.599 (2.348) | 6.019    | 0.000      | ***       |
|        | ANTI     | 0.169 (1.765)  | -1.125 (1.031) | 2.568    | 0.030      | -         |
|        | INPHASE  | 0.459 (1.639)  | -0.945 (1.345) | 2.677    | ns         | ***       |
| MUL    | INTER    | -0.262 (1.270) | -1.653 (0.983) | 3.496    | 0.006      | ***       |
|        | ANTI     | -0.422 (0.573) | -1.390 (1.724) | 2.206    | ns         | ***       |
|        | INPHASE  | 1.096 (1.556)  | -1.652 (1.497) | 5.465    | 0.000      | ***       |

\*p < 0.05.  \**p < 0.01.
illustrated in Fig. 5, whatever the Age and the Coordination, the TRPow was lower for AUD and MUL compared to VIS.

The ANOVA revealed a Coordination × Modality interaction ($F(2,62,47.25) = 3.384; p = 0.030; \eta^2 = 0.158$). t-test revealed a significantly difference only for ANTI between VIS and AUD ($t(10) = 5.0393; p = 0.000$), AUD and MUL ($t(10) = 2.348; p = 0.0433$), VIS and MUL ($t(10) = 4.1786; p = 0.002$). As shown in Fig. 4b, in ANTI, TRPow was higher for VIS compared to MUL and was higher for MUL compared to AUD.

4. Discussion

The purpose of this study was to compare the effects of auditory and/or visual stimulations to increase temporal accuracy and stability of bimanual coordination in the elderly. Associated EEG activations were also investigated. Globally, no behavioural benefit from multimodal stimulations is found. The elderly stabilized bimanual coordination with both auditory and audio-visual stimulations compared to visual stimulation, hence suggesting that auditory information is sufficient to improve coordination despite aging. This effect is globally associated with higher attentional and sensorimotor-related activations but similar neural perceptual activations in the elderly compared to young adults. This suggests a global degradation of attentional and sensorimotor neural processes but a preservation of perceptual integration of auditory information in the elderly.

4.1. Age-related decrease in the temporal stability of the most complex coordination modes

Firstly, for all participants, the inphase and antiphase coordination modes are produced more accurately compared to the intermediate coordination mode whatever the modality of the sensory stimulations. Moreover, the inphase mode is more stable than the antiphase and intermediate modes. This result is in accordance with previous findings showing that the antiphase mode is produced with the same level of accuracy but lower stability than the inphase mode [9] and that the intermediate mode is less accurate and stable than the inphase and antiphase modes without practice [11]. At a neural level, the inphase mode induced less desynchronization of neural populations in the beta frequency band over the sensorimotor cortex than the antiphase and intermediate modes. Given that a desynchronization in the beta band over sensorimotor cortex is associated with sensorimotor processes [28,30,31], one can deduce that the greater stability of the inphase coordination mode is associated with lower sensorimotor activations. This result is in accordance with previous findings showing that the production of inphase coordination requests less brain activations than the production of antiphase coordination [47–49].

Secondly, as expected, the elderly globally produced less accurate and stable coordination compared to young adults. Moreover, the elderly have a tendency to increase neural desynchronization in the beta frequency band over the sensorimotor cortex, which suggests that they need greater activation of sensorimotor processes to produce bimanual coordination (Fig. 1c). Elderly also present a global increase in the neural desynchronization in the alpha frequency band over the parietal cortex which suggests a recruitment of attentional processes (Fig. 1d). The age-related decrease in the temporal motor stability and additional neural recruitments are more marked for the intermediate and antiphase modes compared to the inphase mode. This is consistent with many studies showing that the less stable coordination is more degraded with age [7,8]. At a neural level, elderly produced the intermediate coordination mode with additional neural activity in alpha band over parietal cortex. This suggests that the production of the less stable coordination is associated with greater activation of attentional processes in the elderly (Fig. 3). All in all, additional recruitment of sensorimotor and attentional processes are not associated to an improvement in accuracy or stability in the elderly (Fig. 1a and b). This could reflect a failed effort to attempt to stabilize bimanual coordination by recruiting additional neural resources. In the literature on aging, this phenomenon refers to a neural “dedifferentiation” and reflects age-related difficulties in recruiting specialized neural mechanisms and additional activations which are not relevant to improve performance [37].

4.2. Visual information leads to the lowest temporal stability in both young and elderly participants

In both young adults and the elderly, visual stimulation induces the lowest level of accuracy and temporal stability. At a neural level, two processes can be discussed. Firstly, visual stimulation induces greater neural desynchronization in the alpha band over the parietal cortex whatever the age and coordination (see bottom Panel of Fig. 3). As the level of (de)synchronization over parietal cortex refers to attentional processes [33], one can deduce that visual stimulations require more attentional activations than auditory and audio-visual stimulations. To our knowledge, the increased level of attention allocated to visual information compared to auditory information has not been documented. However, Repp and Penel [17] highlighted that synchronization to visual stimulation is more affected by auditory distractors compared to the introduction of visual distractors during synchronization with auditory stimulation. This result confirms our finding showing that visual information recruits more attentional resources than auditory information. Hence, the recruitment of additional attentional for visual information could be linked to the lesser stability of bimanual coordination. Secondly, visual stimulation induces greater neural synchronization in the gamma band over the frontal cortex whatever the age and coordination (see bottom Panel of Fig. 3). As neural synchronization in the gamma frequency band over frontal cortex has been associated to perceptual processes [34–36], it is possible that visual stimulation is less perceptible than auditory and audio-visual stimulations. This result is in accordance with Fraisse [16] who proposed that visual processes have a poorer temporal resolution than auditory processes [17]. This suggests that the visual system is less efficient to perceive finely temporal information compared to auditory system. On the contrary, visual stimuli bring more spatial information than auditory stimuli [50]. Given that our paradigm implies temporal rather than spatial synchronization, the spatial saliency of visual stimuli was not necessary to improve the temporal stability of the relative phase.

A closer look into our results suggests that, for all participants, the temporal stability is the lowest for the antiphase coordination mode produced with visual stimulation (Fig. 4a). For this condition, more neural activity is found in the gamma band over frontal cortex (Fig. 4b). This suggests that participants activate more perceptual-related neural resources for visual perception of the antiphase pattern. The perception of stimuli within three coordination modes differs by the temporal delay between the two stimuli. The antiphase mode presents the largest temporal delay (500 ms), followed by the intermediate mode (250 ms) and finally by the inphase mode (0 ms). Taken together, behavioural and EEG results suggest that visual stimulations request more perceptual integration when the temporal delay is the largest. This leads us to think that, when the required tempo is 1 s, we don’t perceive antiphase as a whole but as separate stimuli. Hence, whatever the age, the low behavioural stability of the antiphase coordination mode could be linked to a greater effort to perceive visual stimuli specifying the antiphase pattern.
4.3. Both auditory and audio-visual stimulations stabilize bimanual coordination even more in the elderly

Contrary to our behavioural hypotheses, we found no benefit of audio-visual stimulation compared to auditory stimulation on temporal stability of coordination. This suggests that audio-visual stimulations do not provide additional information compared to auditory stimulations to improve temporal stability of bimanual coordination. One possible explanation is that, contrary to previous studies investigating MI, our stimuli were highly discriminatory. The literature reports a “principle of inverse effectiveness”. This rule stipulates that components of a multisensory stimulus are more effectively integrated when the salience of those components is relatively weak [27,51–53]. In other words, when an auditory or visual stimulus is presented just above perceptual threshold level, the gain produced by bimodal audio-visual presentation is greater than when the individual stimuli are highly salient. In our study, it is possible that the absence of difference in performance between auditory and audio-visual stimulations comes from an efficient perception of non-ambiguous stimuli. This hypothesis is corroborated by our EEG results revealing no difference in neural activations related to perceptual processes (i.e. frontal gamma synchronization) during auditory and audio-visual stimulations (bottom panel of Fig. 4).

Another hypothesis is that auditory stimulations are enough to improve temporal components of rhythmic motor behaviour [17,54]. Previous studies exploring how periodic sensory information impacts continuous bimanual coordination showed that synchronizing particular points of a movement cycle with environmental stimulations can improve both spatial and temporal stability of coordination [55,56]. This phenomenon is called “anchoring” [55–57]. Anchoring to auditory stimulations has been proved to stabilize the relative phase of the inphase and antiphase coordination modes [55] and to reduce the spontaneous destabilization of antiphase coordination when the frequency of movements increases [56]. Our results show that the stability of the relative phase of the antiphase mode is increased with auditory (and audio-visual) stimulations compared to visual stimulations (Fig. 4a), probably because anchoring is facilitated with auditory compared to visual stimulations. This effect is less obvious for the inphase and intermediate coordination modes. It is possible that the inphase coordination mode is very stable whatever the modality of the stimulations because of the required frequency which is rather low (1 Hz). On contrary, the intermediate coordination mode presents a low stability whatever the modality of the stimulations. This result is in accordance with previous results suggesting that anchoring induced by auditory stimulations has a limited impact to stabilize the relative phase of the intermediate coordination mode [57]. According to our results, visual stimulations do not seem to bring additional information to auditory stimulations in order to improve the temporal stability of the relative phase of the intermediate coordination mode.

Another interesting result is that the greater effectiveness of auditory and audio-visual stimulations compared to visual stimulations on the temporal stability of the produced bimanual coordination modes is more pronounced in the elderly. This behavioural improvement seems to be mainly associated to an age-related preservation of perceptual integration of auditory stimuli and, to a lesser extent, of attentional processes directed to the simplest (inphase and antiphase) patterns. Firstly, young and elderly participants presented similar neural synchronization in the gamma frequency band over frontal cortex (see Fig. 5). Behavioural improvement without additional activations in the elderly compared to young adults suggest a preservation of perceptual integration of auditory stimulations in the elderly. This finding clearly reflect a preserved brain plasticity in the elderly and contrasts with previous results which report a “compensation” mechanism which corresponds to a behavioural improvement with additional neural activations [37,58]. Secondly, the auditory or audio-visual stimulations were associated to similar attentional activations in young and elderly participants, but only for the inphase or antiphase coordination modes (see Table 1). More precisely, in the elderly, the attentional effort was reduced for the inphase coordination mode produced with auditory stimulations and for the antiphase coordination mode produced with audio-visual stimulations. The first result could be explained by the fact that auditory stimulations for inphase is reduced to one stimulus (fusion of two tones) which reduces the attention paid to discriminate the stimuli, even more in the elderly. The second result highlights the effectiveness of audio-visual stimulations to reduce attentional effort to produce antiphase coordination in the elderly. Taken together, these results suggest that, for the simplest coordination modes performed with auditory or audio-visual stimulations, the elderly are able to improve behavioural performance without recruiting additional attention. Once again, this phenomenon suggests a relative preservation of attentional processes with aging in order to improve the temporal motor stability but only for the simplest bimanual coordination.

5. Conclusion

To conclude, despite the global age-related deterioration of attentional and sensorimotor neural processes already which is classically described in the literature, our results suggest a preservation of perceptual integration of the auditory or audio-visual stimulations which could, at least partially, contribute to the improvement of stability of bimanual coordination in the elderly. These results are very encouraging to further investigate how the availability of different sensory stimulations could lead to age-related behavioural improvements and brain plasticity.

References


