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Wearing prisms to hear differently: After-effects of prism adaptation on auditory perception

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ABSTRACT

Numerous studies showed that, after adaptation to a leftward optical deviation, pseudoneglect behavior (overrepresentation of the left part compared to the right part of the space) becomes neglect-like behavior (overrepresentation of the right part compared to the left part of the space). Cognitive after-effects have also been shown in cognitive processes that are not intrinsically spatial in nature, but show spatial association as numbers or letters. The space-auditory frequency association (with low frequencies on the left and high frequencies on the right) raises the question of whether prism adaptation can produce after-effects on auditory perception. We used a new experimental protocol, named the 'auditory interval bisection judgment', where participants had to estimate what limit of an auditory interval (low or high) a target frequency was closer to. We calculated the subjective auditory interval center. In pre-test, there was a spontaneous bias of the subjective center of the auditory interval toward the lower limit. That was the first demonstration of pseudoneglect behavior in auditory frequency representation. ANOVA realized on all participants did not show significant results of prism adaptation, but a posteriori analyses on musicians showed that, after adaptation to a leftward optical deviation, there were more target frequencies perceived as closer to the lower limit of the auditory interval. This result corroborates the shift of the subjective center of the auditory interval toward high frequency limit. These innovative results are discussed in terms of putative neural substrates underpinning the transfer of visuomotor plasticity to auditory frequency perception.

1. Introduction

1.1. *Prism adaptation*

Sensorimotor plasticity allows the production of an appropriate motor response in reaction to environmental or bodily changes throughout life. One of the classical models to study sensorimotor plasticity is prism adaptation. It consists of pointing to visual targets while wearing prisms that shift the visual field laterally. At the beginning of the exposure, participants make pointing errors in the direction of the optical deviation. On the basis of these error signals, participants

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gradually improve their performance until they achieve an accurate behavior. When the prisms are removed, the sensorimotor correlations revert to an inappropriate state, and the pointing movements are shifted in the direction opposite to the prismatic shift (e.g., Redding, Rossetti, & Wallace, 2005). These sensorimotor after-effects can be explained by proprioceptive, visual, and motor control changes (e.g., Kornheiser, 1976).

1.2. *Prism adaptation acts on space representation*

After-effects of prism adaptation are not restricted to sensorimotor level but extend as well into spatial cognition (see Michel, 2006; 2016, for reviews). The term 'cognitive', used to depict after-effects, refers to the fact effects are not bound to the usual framework of compensatory sensorimotor after-effects, but also involve mental abilities such as judgment, comparison, and space representation (mental image of the space mapped across the brain). Line-bisection task is an invaluable tool to assess space representation. In its perceptual version, participants are requested to judge whether a line has been transected to the left or the right of its true center. The estimation of the center of the line is usually characterized by a leftward pseudoneglect bias corresponding to a mental overrepresentation of the left part of the space/underpresentation of the right part of the space (e.g., McCourt & Jewell, 1999). This pseudoneglect behavior, due to right hemisphere dominance in visuospatial processes (e.g., Fink, Marshall, Weiss, & Zilles, 2001), could be modulated by attentional orientation as spatial cueing (e.g., Milner, Brechmann, & Pagliarini, 1992) or reading habits (Brodie & Pettigrew, 1996; Chokron, Bartolomeo, Perenin, Helft, & Imbert, 1998). Numerous studies showed that after adaptation to a leftward optical shift, pseudoneglect becomes neglect-like behavior, with a mental overrepresentation of the right part of the space/underrepresentation of the left part of the space (Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; Fortis, Goederth, & Barrett, 2011; Michel, Pisella, et al., 2003; Michel, Rossetti, Rode, & Tilikete, 2003; Nijboer, Vree, Dijkerman, & Van der Stigchel, 2010; Schintu et al., 2014; Striemer & Danckert, 2010). Neglect simulation was not only described in peripersonal space representation, but also occurred in extrapersonal (Berberovic & Mattingley, 2003; Michel, Vernet, Courtine, Ballay, & Pozzo, 2008), and bodily space representations (Michel, Rossetti, et al., 2003).

1.3. *Prism adaptation acts on mental scales with spatial association*

Studies using choice-reaction task paradigms showed that stimulus-response compatibility effects (e.g., faster and more accurate performance when the spatial position of the button to press (i.e., response) is compatible with the spatial features of the stimulus) also occur when the stimuli are not intrinsically spatial but considered as activating a mental spatial representation (Proctor & Cho, 2006). The mental number line is thought to have a left-to-right organization whereby small and large numbers are represented along a spatial continuum from left to right (Dehaene, Bossini, & Giraux, 1993). As a result, when judging the distance between two numbers, without using arithmetic, individuals exhibit a pseudoneglect behavior by misbisecting the mental distance toward the smaller numbers (i.e., to the left) (Loftus, Nicholls, Mattingley, Chapman, & Bradshaw, 2009; Longo & Lourenco, 2007). Adaptation to a leftward optical deviation was responsible for neglect-like behavior, with a shift in bisection toward the large numbers (i.e., to the right) (Loftus, Nicholls, Mattingley, & Bradshaw, 2008). The mental alphabetic line has also a left-to-right organization with early letters on the left side and later letters on the right side of the space (Gevers, Reynvoet, & Fias, 2003; Zorzi, Priftis, Meneghello, Marenzi, & Umilta, 2006). Individuals exhibit a pseudoneglect behavior by misbisecting the mental distance toward early letters (i.e., to the left) (Nicholls & Loftus, 2007; Zorzi et al., 2006). Adaptation to a leftward optical deviation also produces neglect-like behavior, with a shift in bisection toward the later letters (i.e., to the right) (Nicholls, Kamer, & Loftus, 2008). As for number and alphabetic features, humans represent time along a spatial continuum (to associate the past with the left space and the future with the right space; Bonato, Zorzi, & Umilta, 2012). Perception of temporal durations can also be changed following prismatic adaptation (Anelli, Ciaramelli, Arzy, & Frassinetti, 2016). Taken together these results underline that prism adaptation acts on the representation of stimuli with spatial association.

1.4. *Space-auditory frequency association in horizontal axis*

Auditory frequencies induce spatial association as well. As for numbers and alphabetic letters, auditory frequencies are represented along a mental line with low frequencies on the left and high frequencies on the right. This assertion is based on stimulus-response compatibility effect that occurs when the same spatial code is shared by both stimulus and response coding processes (e.g., Dehaene et al., 1993; Fias, Brysbaert, Geypens, & d'Ydewalle, 1996; Rusconi, Kwan, Giordano, Umilta, & Butterworth, 2006). Concerning auditory frequencies, stimulus-response compatibility effects in horizontal axis showed faster and more accurate responses to low frequencies on the left and to high frequencies on the right. This spatial association is more pronounced in musicians than in nonmusicians (Lidji, Kolinsky, Lochy, & Morais, 2007; Rusconi et al., 2006). The space-auditory frequency association has also been elegantly illustrated by the modulation of space representation by hearing different auditory frequencies (Ishihara et al., 2013). When participants were asked to mark the midpoint of a given line with a pen (manual line-bisection task) while they were listening to a pitch via headphones, lower frequency produced leftward bisection biases whereas higher frequency produced rightward biases. More generally, cross-modal effects on the allocation of spatial resources can also be illustrated by the reduction of the leftward bias in line bisection when binaural auditory white noise was heard (Cattaneo, Lega, Vecchi, & Vallar, 2012). Altogether these results underline the left-to-right association between space and auditory frequency.

1.5. *Does prism adaptation act on auditory perception?*

Based on cognitive theories underlining that space representation interact with other metrics domains as auditory frequencies and on experimental results showing that prism adaptation acts not only on space representation but also on other features interacting with space representation (see above paragraphs 1.2, 1.3 and 1.4), we make predictions that prism adaptation could act on auditory frequencies perception. More precisely, the space-auditory frequency association (low frequencies on the left and high frequencies on the right) raises the question of the existence of after-effects of prism adaptation on auditory perception. Because adaptation to a leftward optical deviation produces a rightward bias in space representation, adaptation to a leftward optical deviation should produce an auditory bias toward high frequencies. Based on the spatial representation of auditory frequencies along a mental line with low frequencies on the left and high frequencies on the right (Lidji et al., 2007; Rusconi et al., 2006), we used a new experimental protocol, named the 'auditory interval bisection judgment', where the subjective center of an auditory interval, limited by two auditory frequencies (low and high), can be estimated. We proposed this auditory task by analogy with the well-known paradigm of perceptual line bisection task also named Landmark task (e.g., Milner et al., 1992; Schintu et al., 2014). Adaptation to a leftward optical deviation should shift the estimated center of the auditory interval toward the higher auditory frequency.

2. Material and methods

2.1. Participants

Thirty-six adults participated voluntarily in the experiment. All participants were healthy, with normal or corrected to normal vision, and without auditory deficit. Participants were randomly divided into two groups of 18 participants: Group L (9 females, 9 males, mean age = 22.56, *SE* = .78 years), and Group R (11 females, 7 males, mean age = 21.22, *SE* = .70 years). All participants were right-handed according to the Edinburgh Handedness Inventory (Group L: *M* = .82, *SE* = .05; Group R: *M* = .79, *SE* = .04). Before the experiment, the participants filled out a questionnaire about their musical background. The experimental protocol was carried out in accordance with the Declaration of Helsinki (1964). All participants were naïve as to the purpose of the experiment, and were debriefed after the experiment. Although congenital amusia were not assessed, none of the participants has reported hearing loss or any difficulties to perform the auditory interval bisection judgment.

2.2. Material and procedure

Both groups differed by the optical deviation used during prism exposure. Group L was exposed to 15° leftward optical deviation and Group R was exposed to a 15° rightward optical deviation. We used prisms that shifted the vision 15° to the left (Group L) or to the right (Group R) without changing the width. The goggles were fitted with wide field point-to-point lenses creating an optical shift of 15° (Optique Peter, Lyon, France). The total visual field with the goggles was 105°, including 45 degrees of binocular vision.

For both groups experimental procedure was divided into three periods: the pretest (before prism adaptation: auditory interval bisection judgment and open-loop pointing task), the prism adaptation procedure, and the posttest (after prism adaptation: open-loop pointing task, auditory interval bisection judgment and last open-loop pointing task).

2.2.1. Auditory interval bisection judgment

Two auditory frequencies, 700 Hz and 1300 Hz, were used to define an auditory interval, the objective center of which was 1000 Hz. Fifteen other auditory frequencies (800 Hz, 850 Hz, 900 Hz, 920 Hz, 940 Hz, 960 Hz, 980 Hz, 1000 Hz, 1020 Hz 1040 Hz, 1060 Hz, 1080 Hz, 1100 Hz, 1150 Hz, and 1200 Hz) were used as target auditory frequencies within the auditory interval. These auditory frequencies were very simple auditory sinewave frequencies, which have no relation to the musical system and its equal temperament. All the frequencies were pure tones created with Amadeus Pro software, and lasted 500 msec.

The complete sequence of events for one trial is displayed in Fig. 1. In order to avoid auditory memory influences of

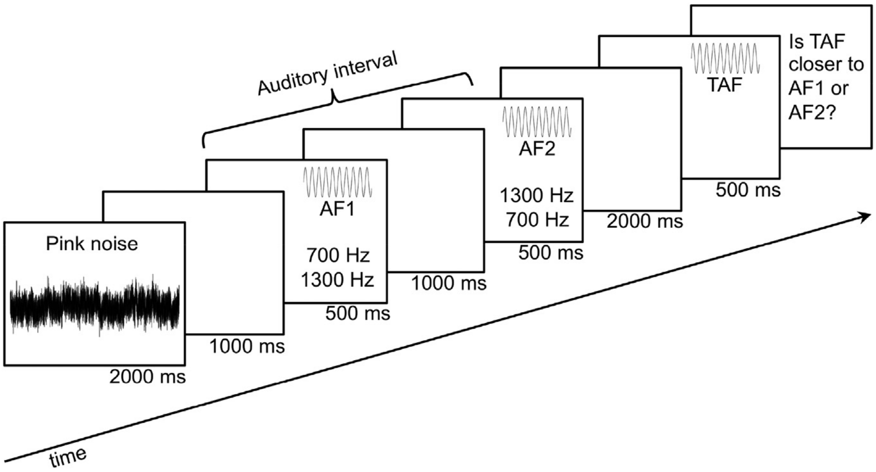

Fig. 1 – Sequence of events for one trial of the auditory interval bisection judgment. Each trial began by a pink noise of 2,000 msec, followed by AF1 and AF2 that defined the auditory interval, and finally by TAF for which the participants had to indicate whether it is closer to AF1 or AF2.

previous stimuli, each trial began by a pink noise of 2,000 msec (a pink noise has a power per Hertz that decreases as the frequency increases, and sounds like a cascade). After a silent interval of 1,000 msec, the auditory interval was presented. It consisted in the sounding of two auditory frequencies of 500 msec each separated by a silent interval of 1,000 msec. The two auditory frequencies were 700 Hz and 1300 Hz, whose the order of presentation was counterbalanced. For one half of the trials, the first auditory frequency (AF1) was 700 Hz, and the second one (AF2) was 1300 Hz, and vice versa for the second half of the trials. The auditory interval was followed by a silent interval of 2,000 msec, before the presentation of the target auditory frequency (TAF), which also lasted 500 msec. TAF could take 15 frequency values, with extreme frequency values (i.e., 800 Hz, 850 Hz, 1150 Hz, and 1200 Hz) repeated four times, while all the remaining frequency values were repeated six times. This resulted in 82 trials, which were pseudorandomly ordered. The use of all the range of frequencies between AF1 and AF2 was justified by the need of obtaining the best slope as possible for having the best estimation of the subjective midpoint (based on the probability of the individual responses, see below). The same TAF could not be repeated in two successive trials. A different random order of trials was used for each participant, and for both pretest and posttest. The participants had to indicate whether the TAF was closer to AF1 or AF2 of the auditory interval. The experimenter scored the response of the participants in an Excel file. The participants began the auditory interval bisection judgment by four training items to ensure that they had clearly understood the instructions.

2.2.2. *Visuomanual open-loop pointing task*

In the pretest and posttest conditions and at the end of the experiment, 10 open-loop pointing trials (i.e., without visual control during movement execution) were performed using liquid crystal goggles to occlude vision during movement execution. A sagittal target (black sticker dot, diameter 6 mm) was placed 45 cm from the edge of the table. Participants comfortably sat in a chair in front of a table and kept their head aligned with the body axis using a chin-rest. The starting hand position was placed 11 cm from the edge of the table. Participants were asked to make accurate movements at a natural self-paced speed to the single sagittal target. Before movement onset, participants' right index finger was passively placed by the experimenter in the starting position. The after-effects of adaptation were assessed by the difference in the pointing errors between mean performance in posttest and mean performance in pretest for each participant (immediate after-effects: posttest minus pretest performance). At the end of the experiment, 10 open-loop pointing trials were performed to assess whether the sensorimotor plasticity persisted until the end of the experiment (late after-effects: last performance minus pretest performance).

All arm movements for the visuomanual open-loop pointing task (before and after prism exposure) were recorded using 3 TV-cameras (sampling frequency 60 Hz) of an optoelectronic system of motion analysis (Smart, B.T.S., Italy). One reflective marker (1 cm diameter) was placed on the nail of the right index fingertip. The spatial resolution for movement measurements was less than 1 mm. Data processing was performed using custom software written in Matlab (Mathworks, Natick, MA).

2.2.3. *Prism adaptation procedure*

Prism adaptation procedure followed the pretest. Participants wore prismatic goggles and their head was kept aligned with the body axis by using a chin-rest. They were asked to perform a closed-loop pointing task (with vision of the hand during the movement). Nine visual targets (colored sticker dots; diameter 6 mm, space inter-dots: 4 cm) were placed 45 cm from the edge of the table. The participants pointed as fast as possible to the targets and returned near the start position at a natural speed. Vision of the starting position of the hand was occluded to ensure the optimal development of the adaptation (Redding & Wallace, 1997). Every 5 sec participants pointed alternately to one of the nine visual targets indicated randomly by the experimenter. The adaptation procedure involved 4 blocks of 75 pointing trials (total number of movements: 300). Participants relaxed for 1 min (eyes closed) at the end of each pointing block. The total duration of the adaptation procedure lasted for about 28 min.

2.3. *Data analysis*

For the visuomanual open-loop pointing task, the pointing angular error was calculated as the difference between the starting position to target position vector and the starting position to final index fingertip position vector. Pointing errors from the sagittal target were expressed in degrees to refer to the optical deviation used during prism exposure. Leftward errors were assigned a negative value and rightward errors a positive value.

For the auditory interval bisection judgment, two measures were computed. The first one corresponded to the mean percentage of responses indicating proximity to the lower auditory frequency limit of the auditory interval (700 Hz). When AF1 or AF2 of the auditory interval was 700 Hz, and the participant answered “closer” to AF1 or AF2 respectively, the response was quoted as 1, otherwise it was quoted as 0.

The second measure was computed to fit the data with a sigmoid function in order to obtain the participants' subjective center of the auditory interval. The subjective center of the auditory interval is the frequency for which participants were at 50% of responses closer to the lower frequency limit and 50% of responses closer to the higher frequency limit of the auditory interval. This point of equiprobability provided a measure of the subjective center of the auditory interval. In order to evaluate the subjective center, percentages of responses indicating proximity to the higher frequency limit of the auditory interval (1300 Hz) were computed. When AF1 or AF2 of the auditory interval was 1300 Hz, and the participant answered “closer” to AF1 or AF2 respectively, the response was quoted as 1, otherwise it was quoted as 0. The resulting percentages were plotted as a function of the frequency of TAF, from 800 Hz to 1200 Hz. These data were then fitted with a sigmoid function, and the frequency value on the x-axis corresponding to the frequency at which the participant provided a percentage of 50% was specified, and corresponded to the subjective center of the auditory interval.

Results were considered to be significant at $p < .05$. Means (±standard errors) are presented in the Results section.

3. Results

3.1. Sensorimotor after-effects

When pretest performance in open-loop visuomanual pointing task was compared with *t*-test, there was no significant difference between both groups [$p > .10$]. A repeated measures ANOVA with Session (pretest, posttest, late-test) as within-subject factor and Deviation (Group L and Group R) as between-subject factor showed a significant main effect of Deviation [$F(1, 34) = 180.20$, $p < .001$, $\eta_p^2 = .841$], and a Session × Deviation interaction [$F(2, 68) = 191.96$, $p < .001$, $\eta_p^2 = .849$]. Following adaptation, after-effects were significantly different from zero in both groups in posttest and late-test [all $ps < .001$] (Fig. 2).

3.2. Auditory interval bisection judgment

3.2.1. Percentages

T-test comparisons were first performed to evaluate whether the mean percentages of responses indicating proximity to the lower auditory frequency limit of the auditory interval were different from 50% in pretest. The mean percentages were significantly lower than 50%, [$M = 47.09$, $SE = 1.31$, $t(35) = -2.22$, $p = .033$, $d = .38$].

A repeated measures ANOVA with Session (pretest, posttest) as within-subject factor and Deviation (Group L, Group R) as between-subject factor, performed on the percentages of responses indicating proximity to the lower auditory frequency limit of the auditory interval showed no significant effects [$ps > .10$].

Based on the literature of cognitive after-effects of prism adaptation and on spatial association of auditory frequencies (see introduction), we expected to find an increase of the mean percentages of responses indicating proximity to the lower auditory frequency limit of the auditory interval for all participants irrespectively of their musical expertise. Nevertheless the musical expertise questionnaire used to better know the musical level of the participants allowed us to identify a posteriori two groups of participants: musicians and nonmusicians. Hereafter, participants having more than 5 years of musical training and still making music will be referred to as musicians ($N = 14$; 4 play the piano, 5 play the guitar, 1 plays trumpet, and 4 play two or three instruments (piano/guitar, piano/flute, piano/guitar/cajon, piano/guitar/bass), and participants having less than 5 years of musical training will be referred to as nonmusicians ($N = 22$). Group L was composed of 7 musicians (Musical Expertise: $M = 13.43$ years; $SD = 4.16$) and 11 nonmusicians. Group R was composed of 7 musicians (Musical Expertise: $M = 12.86$ years; $SD = 4.18$) and 11 nonmusicians as well.

Taken separately, the mean percentages of neither musicians nor nonmusicians were significantly different from 50%, and there was no significant difference between musicians and nonmusicians [$ps > .10$]. Similar ANOVAs were performed separately for musicians and nonmusicians. The results are presented in Fig. 3. For the musicians, a significant effect of Session was observed [$F(1, 12) = 9.259$, $p = .01$, $\eta_p^2 = .436$]. Planned comparisons showed a significant effect of Session for Group L [$F(1, 12) = 6.39$, $p = .026$], with an increase in percentages of responses indicating proximity to the lower auditory frequency limit of the auditory interval for posttest compared to pretest, but not for Group R [$p > .10$]. For the nonmusicians, the ANOVA showed no significant effect [$ps > .10$]. Prism adaptation to a leftward optical deviation resulted in numerous target frequencies perceived as being closer to the lower frequency of the auditory interval in musicians only.

3.2.2. Subjective center

T-test comparisons were first performed to evaluate whether the mean subjective center of the auditory interval was different from the objective center (1000 Hz). Taken together, the mean subjective center of all musicians and nonmusicians was significantly lower than 1000 Hz, [$M = 986.84$, $SE = 5.69$, $t(35) = -2.314$, $p = .027$, $d = .39$].

A 2 × 2 [Session (pretest, posttest) × Deviation (Group L, Group R)] repeated measures ANOVA showed no significant effects [$ps > .10$]. As for percentages, we expected to find a shift of the auditory interval toward the higher auditory frequency for all participants irrespectively of their musical expertise. Nevertheless the identification a posteriori of two groups of participants (musicians and nonmusicians) allowed detailing the results. Fig. 4 displayed the results for musicians and nonmusicians. Taken separately, the subjective center of

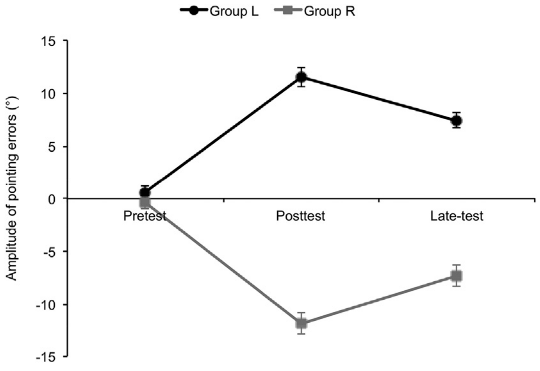

Fig. 2 – Amplitude of visuomanual open-loop pointing errors for pretest and posttest as a function of deviation (Group L, Group R). Error bars indicate standard errors.

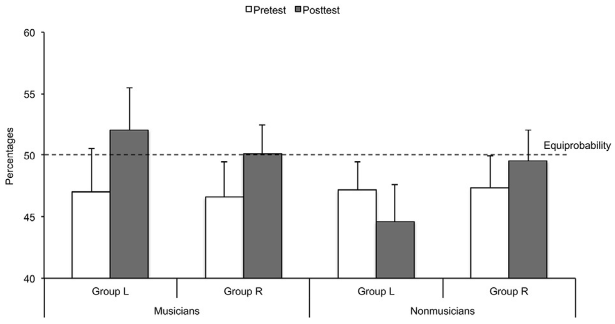

Fig. 3 – Percentages for pretest and posttest as a function of deviation (Group L, Group R) and musical expertise (musicians, nonmusicians). Error bars indicate standard errors.

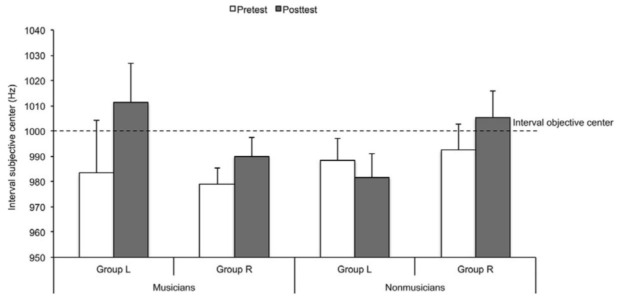

Fig. 4 – Subjective center for pretest and posttest as a function of deviation (Group L, Group R) and musical expertise (musicians, nonmusicians). Error bars indicate standard errors.

neither musicians nor nonmusicians was significantly different from 1000 Hz [$M = 981.20$, $SE = 10.53$, $t(13) = -1.785$, $p = .098$; $M = 990.43$, $SE = 6.55$, $t(21) = -1.460$, $p = .159$, respectively]. There was no significant difference between the mean subjective center of the auditory interval of musicians and nonmusicians [$p > .10$]. Similar 2 × 2 [Session (pretest, posttest) × Deviation (Group L, Group R)] repeated measures ANOVA, conducted for musicians, showed a significant effect of Session [$F(1, 12) = 7.189$, $p = .02$, $\eta_p^2 = .375$].

Planned comparisons showed a significant effect of Session for Group L [$F(1, 12) = 7.46$, $p = .018$], with a higher subjective center for posttest compared to pretest (Fig. 5), but not for the Group R [$p < .10$].

For the nonmusicians, no significant effect was observed [$ps > .10$]. Prism adaptation to a leftward optical deviation resulted in shifting the subjective center of the auditory interval toward the higher auditory frequency in musicians only.

4. Discussion

The main objective of the present study was to investigate the influence of prism adaptation on auditory perception. Two major results were observed in our experiment. First, we proposed a new task named auditory interval bisection judgment, and observed the first demonstration of a bias toward the lower limit for the estimation of the center of the auditory interval. This spontaneous bias corresponds to pseudoneglect behavior in auditory frequency representation. Second, prism adaptation to a leftward optical deviation produced an increase of the designation of the lower frequency limit of the auditory interval in musicians. After prism adaptation to a leftward optical deviation, the musicians are more inclined to perceive the target frequencies as closer to the lower limit of the auditory interval. This result corroborated the shift of the estimation of the auditory interval center toward the high frequency limit following adaptation to a leftward optical deviation in musicians.

4.1. *First demonstration of pseudoneglect in auditory perception*

In the present experiment we proposed an auditory interval bisection judgment to explore the mental representation of auditory frequencies. This task allowed investigating whether frequencies were uniformly represented throughout an auditory interval or whether they are characterized by a nonuniform representation as for pseudoneglect in space representation (e.g., Milner et al., 1992). The first important result of our study was the bias observed toward the lower limit of the auditory interval when the subjective center of the auditory interval was estimated. It appears that lower frequencies of the interval were overrepresented and/or that higher frequencies of the interval were underrepresented. If we consider the spatial continuum representation of auditory frequencies from left to right (with low frequencies on the left and high frequencies on the right), this bias corresponds with a pseudoneglect expression on auditory frequency perception.

Pseudoneglect is well documented in space representation (e.g., McCourt & Jewell, 1999). The tendency to be biased toward the left-hand side of space is a robust and consistent behavior classically described in visuospatial line-bisection task where participants are asked to indicate the center of a horizontal line (see Brooks, Della Sala, & Darling, 2014; McCourt & Jewell, 1999, for reviews). This spatial bias to the left hand side in line bisection has been referred to as ‘pseudoneglect’ (Bowers & Heilman, 1980) by analogy to the performance of right-hemisphere impaired patients with left unilateral spatial neglect who show spatial larger biases

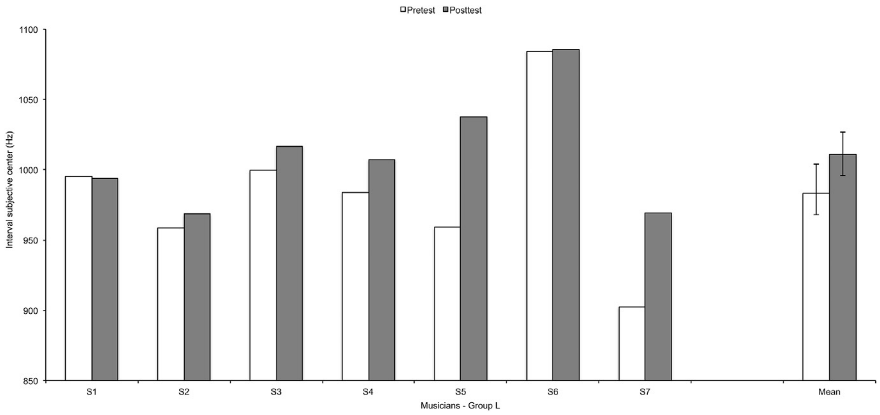

Fig. 5 – Subjective center for pretest and posttest for the musicians of the Group L. Error bars indicate standard errors.

towards the right hand-side of the space (Nijboer, Kollen, & Kwakkel, 2013; Robertson & Marshall, 1993). The ‘pseudoneglect’ term now refers to the general tendency of healthy people to preferentially attend to the left side of space (Hatin, Tottenham, & Oriet, 2012). A number of studies have revealed that a representational form of pseudoneglect exists beyond the direct visuospatial processes. Pseudoneglect, for instance, was shown when participants were asked to mentally represent a stimulus that had been previously seen and retrieved from memory (McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007), or when they had to completely build novel mental representations created from aural-verbal descriptions (Brooks, Logie, McIntosh, & Della Sala, 2011). Pseudoneglect occurs on the representation of stimuli with spatial association such as numbers (Loftus, Nicholls, et al., 2009; Longo & Lourenco, 2007) or alphabetic letters (Gevers et al., 2003; Zorzi et al., 2006) that are represented along a spatial continuum from left to right.

As for all pseudoneglect expressions, pseudoneglect on auditory frequency perception could be explained by a leftward contralateral activation-orientation due to right hemisphere dominance in visuospatial functions (Benton & Tranel, 1993; Fink et al., 2001). Space representation depends on orientation of attention; the part of the space where attention is oriented is mentally overrepresented (e.g., Milner et al., 1992). If we consider the spontaneous leftward orientation of attention (e.g., Loftus, Nicholls, et al., 2009), the associated representational pseudoneglect, and the spatial continuum for the representation of auditory frequencies from left to right, the pseudoneglect observed on auditory interval bisection is a coherent result.

4.2. *Prism adaptation acts on auditory perception*

The second important major result of our study showed that prism adaptation to a leftward optical deviation produced an increase of the designation of the lower frequency limit of the auditory interval in musicians. This means that, after adaptation to a left optical deviation, musicians perceived more target frequencies as closer to the lower frequency of the auditory interval. This result corroborated the shift of the estimated center of the auditory interval toward the higher frequency limit following adaptation to a leftward optical deviation in musicians.

As displayed in Fig. 6, a target, with a frequency comprised between the subjective centers observed in pretest and posttest, will be perceived as closer to the higher frequency of the auditory interval before prism adaptation (because higher than the prettest subjective center), but the same frequency will be perceived as closer to the lower frequency of the auditory interval after leftward prism adaptation (because lower than the posttest subjective center). This result may suggest that the overrepresentation of the low frequencies/underrepresentation of the high frequencies of the interval (pseudoneglect) was replaced by an overrepresentation of the high frequencies/underrepresentation of the low frequencies of the interval following adaptation to a leftward optical deviation.

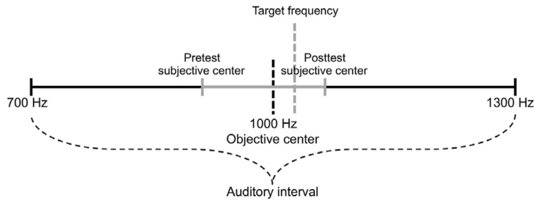

Fig. 6 – A representation of the shift of subjective center observed in musicians after prism adaptation to a left optical deviation.

It is worth underlying, however, that after-effects on auditory perception occurred only in musicians, meaning that auditory frequency representation may be more sensitive to prism perturbation in participants with a robust spatial association for auditory frequencies (Lidji et al., 2007; Rusconi et al., 2006). Further investigations will allow a better understanding of the sensitivity of musicians for the auditory response of prism adaptation. These after-effects in auditory perception come within the scope of well-known effects of prism adaptation on the representation of spatial stimuli or stimuli with spatial association (see Michel, 2006; 2016, for reviews).

Indeed in the field of space representation, it is now well established that adaptation to a leftward optical deviation changes an overrepresentation of the left part of the space/underrepresentation of the right part of the space (pseudoneglect) into an overrepresentation of the right part of the space/underrepresentation of the left part of the space (neglect-like behavior; see Michel, 2006, 2016 for reviews). Prism adaptation has a strong impact on space representation whatever the dimension of the space, peripersonal (Colent et al., 2000; Michel, Pisella, et al., 2003), extrapersonal (Berberovic & Mattingley, 2003; Michel et al., 2008), or bodily (Michel, Rossetti, et al., 2003), and whatever the spatial nature of the task, direct as in line bisection (e.g., Michel, Pisella, et al., 2003), or with association as in mental numbers (Loftus et al., 2008), or letter scales (Nicholls et al., 2008). The influence of prism adaptation also extends to other cognitive processes such as spatial attention (e.g., Loftus, Vijayakumar, & Nicholls, 2009), hierarchical processing (Bultitude & Woods, 2010; Reed & Dassonville, 2014), and even on cross-modal functions independent from sensorimotor processes involved in visuomanual adaptation such as haptic tasks (McIntosh, Rossetti, & Milner, 2002), tactile extinction (Maravita et al., 2003), tactile threshold and proprioceptive perception (Dijkerman, Webeling, ter Wal, Groet, & van Zandvoort, 2004) and pain perception (Sumitani et al., 2007). To illustrate cross-modal effects of prism exposure, it could be mentioned that neglect occurs throughout auditory manifestations as rightward bias in sound location or dichotic listening (e.g., Bellmann, Meuli, & Clarke, 2001), rightward shift in auditory subjective straight ahead (e.g., Kerkhoff, Artinger, & Ziegler, 1999), and that prism can improve neglect at auditory level (Jacquin-Courtois et al., 2010). Taken together with the after-effects of prism adaptation on space representation and on cross-modal functions, the present after-effects on auditory perception is a coherent result.

Investigation of dynamic changes in brain activity during prism exposure showed a consistent involvement of the cerebellum in spatial realignment (Chapman et al., 2010;

Danckert, Ferber, & Goodale, 2008; Luauté et al., 2009), whereas the anterior intraparietal sulcus was implicated in error detection (Danckert et al., 2008; Luauté et al., 2009), and the parieto-occipital sulcus was implicated in error correction (Luauté et al., 2009). Concerning neural substrates of cognitive after-effects, the bilateral activation in superior temporal cortex (superior temporal sulcus, superior temporal gyrus) during the later phase of prism exposure to a leftward optical deviation (Luauté et al., 2009) could mediate the effects of prism adaptation on cognitive spatial representations, and more particularly the effect of prism adaptation on auditory frequencies shown in the present experiment. Other investigations have highlighted the involvement of the inferior parietal cortex (angular gyrus, gyrus supramarginal) in the substrate of cognitive after-effects that could also support the present results (Chapman et al., 2010; Crottaz-Herbette, Fornari, & Clarke, 2014; Luauté et al., 2006). Following adaptation to a leftward optical deviation the change in hemispheric equilibrium to the detriment of the right hemisphere and in favor of the left hemisphere (Schintu et al., 2016) could be responsible for the representational transformation from leftward representational bias (pseudoneglect) to rightward representational bias (neglect-like behavior) (Michel, 2016). Based on fMRI study using a simple visual detection task, Crottaz-Herbette and collaborators (2017) proposed a model where adaptation to a leftward prism adaptation could influence both ventral attentional system (right hemisphere activation) and dorsal attentional system (left hemisphere activation). In order to better discuss the neural substrate that could underpinning our results, we have also to consider the effect of prism adaptation on auditory perception, i.e., on unexposed sensory systems. Indeed, prism adaptation can improve auditory deficit in neglect patients (Jacquin-Courtois et al., 2010; Tissieres, Elamly, Clarke, & Crottaz-Herbette, 2017) and modulate the activation of neural substrate involved in auditory attention in normals (Tissieres, Fornari, Clarke, & Crottaz-Herbette, 2018). Furthermore because right posterior parietal cortex is the neural substrate of space representation (Fierro et al., 2000; Fink et al., 2001), and that pitch tone perception has an association with space representation (Lidji et al., 2007; Rusconi et al., 2006), the effect of prism adaptation on the right posterior parietal cortex could explain the change in auditory perception. Furthermore the right temporal cortex being directly involved in pitch perception (Hyde, Peretz, & Zatorre, 2008; Peretz & Zatorre, 2005), effect of prism adaptation on temporal cortex could also underpin the change in auditory perception.

5. Conclusion

The present study showed two main and original results. For the first time, a pseudoneglect bias was observed in auditory perception, with the subjective center of an auditory interval shifted toward the lower limit of the interval. Second, there was a shift of the subjective center toward the higher frequency limit of the auditory interval after adaptation to a leftward optical deviation in musicians. Our results are preliminary, and to better understand the effect of prism adaptation on auditory frequency perception our investigation needs to be extended. In the present study the musical expertise was used a posteriori, but in a future study it could be possible to evaluate the “piano-effect” (Lidji et al., 2007) on the left-to-right representation of auditory frequencies, and how prism adaptation affects this perception by directly comparing a group of pianists with a group of nonpianists. Furthermore a larger frame of the auditory spectrum should be used to study whether effects of prism adaptation are homogeneous throughout the auditory spectrum or whether some auditory frequencies are more sensitive to prism adaptation. Furthermore, the lack of auditory sensitivity to prism adaptation in nonmusicians observed in the present experimental conditions also merits further consideration. Taken together our preliminary work offers theoretical and clinical perspectives for effects of prism adaptation on auditory perception.

Author note

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