Modifying auditory perception with prisms? Aftereffects of prism adaptation on a wide auditory spectrum in musicians and nonmusicians

Clémence Bonnet a, *, Bénédicte Poulin-Charronnat b, Patrick Bard b, Carine Michel a

a INSERM UMR1093-CAPS, Université Bourgogne Franche-Comté, UFR des Sciences du Sport, F-21000 Dijon, France
b Université Bourgogne Franche-Comté, LEAD - CNRS UMR5022, Université de Bourgogne, Pole AAFE, 11 Esplanade Erasme, 21000 Dijon, France

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ABSTRACT

Prism adaptation consists of pointing to visual targets while wearing prisms that shift the visual field laterally. The aftereffects are not restricted to sensorimotor level but extend to spatial cognition. There is a link between spatial representation and auditory frequency, with an association of low frequencies on the left side and high frequencies on the right side of space. The present study aimed first at evaluating the representation of auditory frequencies on a wide range of frequencies in musicians and nonmusicians. We used the ‘auditory interval bisection judgment’ within three auditory intervals. The results showed a pseudoneglect behavior in pretreatment in musicians and nonmusicians for high frequency intervals, reflecting a perceptual bias of the subjective interval center toward lower frequencies. The second aim of the present study was to evaluate the aftereffects of prism adaptation on an expanded auditory spectrum. The results showed aftereffects of adaptation to a leftward optical deviation for high frequency intervals in musicians and nonmusicians. Adaptation to a leftward optical deviation affects the auditory perception on an extended auditory spectrum, by shifting the subjective interval center toward high frequencies. The present study provides innovative data about representation of auditory perception and its modulation by prism adaptation.

1. Introduction

1.1. Sensorimotor plasticity and prism adaptation

Sensorimotor plasticity is defined by our capacity to produce an appropriate motor response in reaction to environmental (e.g., hypergravity or microgravity) or bodily (e.g., when growing up) changes. A classical experimental paradigm for studying sensorimotor plasticity is prism adaptation. It consists of pointing to visual targets while wearing prisms that shift the visual field laterally (Stratton, 1896). Before prism exposure, participants’ pointing is accurate. As soon as the prisms are worn, participants make pointing errors in the direction of the optical deviation. Based on error signals, they correct their trajectory and gradually improve their performance to make accurate pointing movements. After prisms’ removal, participants make pointing errors in the direction opposite to the prismatic shift (e.g., Redding & Wallace, 1996). These sensorimotor aftereffects of prism adaptation can be explained by visual, proprioceptive, and motor control changes (e.g., Kornheiser, 1976; Redding et al., 2005).

1.2. Prism adaptation effects on spatially valued elements

Prism adaptation acts on the sensorimotor level but also affects spatial cognition (see Michel, 2006, 2016, for reviews). The cognitive level refers to our ability to build a mental image of the space mapped across the brain (Bisiach et al., 1979). Cognitive aftereffects of prism adaptation were mainly highlighted thanks to the line-bisection task (e.g., Colent et al., 2000), which 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 (e.g., Milner et al., 1992). Performance in healthy participants is characterized by a leftward bias of the line center estimation corresponding to a mental over-representation of the left part of space, and an under-representation of the right part of space (e.g., McCourt & Jewell, 1999). Called pseudoneglect (see, Jewell & McCourt, 2000, for review), this behavior is due to the dominance of the right hemisphere in visuo-spatial processes (e.g., Corballis, 2003; Zago et al., 2017). Following adaptation to a leftward optical deviation, pseudoneglect becomes a neglect-like behavior (i.e., a shift to the right of the estimated center), with a mental over-representation of the right part of space, and an

* Corresponding author.
E-mail address: clemence.bonnet@u-bourgogne.fr (C. Bonnet).

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under-representation of the left part of space (e.g., Colent et al., 2000; Fortis et al., 2011; Michel, Pisella, et al., 2003; Michel, Rossetti, et al., 2003).

Furthermore, there are nonspatial elements which activate mental spatial representation. For instance, in the visual domain, numbers are represented on a left-to-right mental horizontal scale. Small numbers (e.g., 1, 2) are associated with the left part of this horizontal scale, while large numbers (e.g., 9, 10) are associated with the right part of this horizontal scale (Dehaene et al., 1993). Letters are also spatially represented on a left-to-right mental horizontal line. Early letters (e.g., A, B) are represented on the left side and later letters (e.g., Y, Z) on the right side of this horizontal line (Zorzi et al., 2006). These horizontal mental scales were observed thanks to stimulus-response compatibility studies, which showed that participants were faster and more accurate to press the response key when it was compatible with the spatial feature of the stimulus (e.g., pressing the left key for smaller numbers). In both cases (numerical and alphabetical mental lines), when healthy participants have to estimate the center between two stimuli (two numbers or two letters), they show a pseudoneglect bias toward the smaller numbers and the early letters (i.e., to the stimuli with left spatial correspondence; Loftus et al., 2009; Longo & Lourenco, 2007; Nicholls & Loftus, 2007). After adaptation to a leftward optical deviation, as for the line-bisection task, this bias becomes a neglect-like behavior, with a shift of the subjective estimation of the interval center toward the larger numbers and later letters (i.e., to the stimuli with right spatial correspondence; Loftus et al., 2008; Nicholls et al., 2008). All these data demonstrate that leftward optical deviation also modulates the mental representation of spatially valued elements.

1.3. Auditory frequencies are spatially valued elements

The association between stimuli and space exists not only in the visual domain but also in the auditory domain. As letters and numbers, auditory frequencies are represented along a left-to-right mental line with low frequencies on the left of the mental line and high frequencies on the right. This analogy, called SMARC effect (Spatial-Musical Association of Response Codes), was observed following stimulus-response compatibility experiments, in which auditory stimuli and responses share the same spatial position (Rusconi et al., 2006). Participants were faster and more accurate when left responses were associated with low frequencies and right responses with high frequencies. It is worth noting that this association is more prevalent in musicians than in nonmusicians (Lidji et al., 2007; Rusconi et al., 2006). Moreover, the space-auditory frequency association was confirmed by the modulation of space representation when listening to auditory frequencies. In a line-bisection task, hearing low frequencies shifted the subjective interval center to the left, while hearing high frequencies caused a bisection bias to the right (Ishihara et al., 2013). These results reflect the left-to-right association between auditory frequencies and space.

1.4. Prism adaptation affects auditory perception

Knowing that prism adaptation to a leftward optical deviation produces cognitive effects on spatially-valued elements and that auditory frequencies are associated with spatial location, Michel et al. (2019) have recently shown that prism adaptation modifies the perception of auditory frequencies. They used a new experimental paradigm, the ‘auditory interval bisection judgment’, which allows the estimation of the subjective center of an auditory interval, limited by two auditory frequencies. This singular auditory task was proposed by analogy with the well-known paradigm of perceptual line-bisection (see Section 1.2). Two main results were observed. First, the authors showed the existence of an auditory pseudoneglect. Before prism adaptation, there was a pseudoneglect bias in the subjective estimation of the auditory interval center toward the lower auditory frequencies. Second, they showed an effect of the adaptation to a leftward deviation on auditory frequency perception. There was a shift of the estimated auditory interval center toward the higher frequencies following adaptation to a leftward optical deviation in musicians only. The present study was in direct line with the work of Michel and collaborators.

The aim of the present study was twofold. First, we investigated the representation of auditory frequencies in a wider auditory spectrum than Michel et al. (2019) in musicians and nonmusicians. We examined whether the auditory pseudoneglect was present in this wider auditory spectrum, and if so, if its amplitude is modulated as in the visual space for which the pseudoneglect bias (i.e., leftward bias in the estimation of the line center) is more pronounced on the left part of space (see Michel, 2016 for review; Michel, Pisella, et al., 2003). If the auditory system behaves in a similar way as the visual system, the auditory pseudoneglect (i.e., bias of the estimated center of the auditory interval toward the lower interval limit) should be more pronounced for the lower frequencies of the auditory spectrum.

Second, we studied the cognitive aftereffects of prism adaptation in the wider auditory spectrum. In the visual field, the influence of adaptation to a leftward optical deviation on space representation was found to be more pronounced on the left part of space, where the leftward pseudoneglect bias is stronger (see Michel, 2016 for review; Michel, Pisella, et al., 2003). In visual line-bisection, the greater the initial leftward pseudoneglect bias is, the greater the amplitude of the rightward representational aftereffects following prism adaptation to a leftward optical deviation are (Goedert et al., 2010; Herlihey et al., 2012; Michel, Pisella, et al., 2003). If the auditory system responds to prism adaptation like the visual system, adaptation to a leftward optical deviation should induce a greater bias of the subjective center toward the higher interval limit for lower frequencies of the auditory spectrum. The more pronounced the auditory pseudoneglect is, the greater the amplitude of aftereffects of prism adaptation on auditory perception should be.

2. Experiment 1

2.1. Material and methods

2.1.1. Sample size estimation

An a priori power analysis was performed for sample size estimation based on data from the published study of Michel et al. (2019) (N = 7 for each optical deviation), and corresponding to our main hypothesis, which compared the percentages of ‘low’ responses in pretest to posttest after adaptation to a leftward optical deviation. The effect size in this study was d = −1.08, considered to be large using Cohen’s (1988) criteria. A priori analysis for a t-test comparison between two dependent means with α = 0.05 and power = 0.80, indicated that the required sample size with this effect size (G*Power 3.1; Faul et al., 2007) is approximately N = 9. Our proposed sample size of N = 12 by group is then adequate for the main objective of Experiment 1.

2.1.2. Participants

Forty-eight volunteers participated in the first experiment. They were randomly divided into two groups of 24 participants according to their musical expertise: Group M (10 females, 14 males, mean age = 23.21, SD = 2.89 years) was composed of musicians, who had more than 5 years of musical training and were still playing music (8 play the piano, 3 play the guitar, 3 play drums, 3 play the violin, 2 play the trombone, 1 plays the flute, 1 plays the electric bass, and 3 play two or three instruments: clarinet/drums, guitar/bass/drums/piano, violin/piano/singing), and Group NM (11 females, 13 males, mean age = 23.87, SD = 3.44 years) was composed of participants having no musical background or less than 5 years of musical training, and no current musical practice. Both groups were each randomly divided into two subgroups of 12 participants according to the optical deviation used during prism adaptation: Groups ML and NML were exposed to a 15° leftward optical deviation and Groups MR and NMR were exposed to a 15° rightward
optical deviation during prism adaptation procedure. All participants were healthy, with normal or corrected to normal vision, and without auditory or neurological deficits. Except six ambidextrous participants (2 ML, 1 MR, 1 NML, 2 NMR), all were right-handed according to the Edinburgh Handedness Inventory (Group ML: $M = 0.76$, $SD = 0.24$; Group MR: $M = 0.86$, $SD = 0.20$; Group NML: $M = 0.72$, $SD = 0.26$; Group NMR: $M = 0.77$, $SD = 0.23$). After being informed of the experimental procedures, all participants gave their written consent and completed a musical expertise questionnaire. They were completely naive as to the purpose of the experiment, spatial representation of auditory frequencies, and prism adaptation. They were debriefed after the experiment. The experimental protocol was carried out in accordance with the Declaration of Helsinki (1964).

2.1.3. Experimental procedure

For all groups, the experimental procedure was divided into four sessions: a pretest (before prism adaptation: auditory interval bisection judgment and open-loop pointing task), the prism adaptation procedure, a posttest (after prism adaptation: open-loop pointing task, auditory interval bisection judgment), and a late-test (open-loop pointing task; see Fig. 1).

2.1.3.1. Auditory interval bisection judgment. Three auditory intervals were used, two frequencies defined each of them (AF1 and AF2) and nine other auditory frequencies were used as target auditory frequencies (TAF) within the auditory intervals (see Table 1). All the auditory frequencies were pure tones created with Amadeus Pro software and lasted 500 ms.

The paradigm was the same as the one used by Michel et al. (2019), and every trial followed the event sequence displayed in Fig. 2. Each trial began by a pink noise (2000 ms) to avoid auditory memory influences of previous stimuli. After a silence of 500 ms, the participants listened to the auditory interval. The two auditory limits of the auditory interval were presented separated by a silence of 500 ms. The order of presentation of both frequencies was counterbalanced, with AF1/AF2 for half of the trials and the reverse for the other half. For I1, AF1 was 200 Hz and AF2 was 800 Hz (half of the trials: 200 Hz–800 Hz, the other half: 800 Hz–200 Hz), for I2, AF1 was 1850 Hz and AF2 was 2450 Hz (half of the trials: 1850 Hz–2450 Hz, the other half: 2450 Hz–1850 Hz), and for I3 AF1 was 3500 Hz and AF2 was 4100 Hz (half of the trials: 3500 Hz–4100 Hz, the other half: 4100 Hz–3500 Hz). A silence of 1000 ms followed the presentation of the auditory interval and the TAF was then presented during 500 ms. For every interval, TAF could take nine frequency values with four extreme values (frequencies close to the auditory limits; e.g., 1950 Hz, 2000 Hz, 2300 Hz, 2350 Hz for I2) repeated four times, all the other values were repeated six times. Finally, the auditory interval bisection judgment was composed by 46 trials per interval, resulting in 138 trials, pseudo-randomized for each participant. The same interval could not be presented in two successive trials, and the same was true for the TAF. A pseudo-randomized order was used for each participant, for both pretest and posttest, which were split into two equivalent blocks. In this auditory interval bisection judgment, participants had to indicate to the experimenter if the TAF was closer to the low or to the high limit of the interval, by answering ‘low’ or ‘high’. At the end of every trial, the experimenter scored the response in the PsyScope software, which was used to present the stimuli.

The participants began by a training, in which they had to distinguish the low and high limits of the intervals later used in the experiment, then they performed four training trials of the auditory interval bisection judgment (with auditory frequencies close to the limits of an interval not used in the experiment; 700 Hz–1300 Hz) to ensure that they clearly understood the instructions. All participants reported that they had neither difficulty (1) to distinguish between the low and the high limit for each interval, nor (2) to perform the auditory interval bisection judgment.

2.1.3.2. Visuo-manual open-loop pointing task. To ensure the development of the sensorimotor realignment, participants completed an open-loop pointing task (i.e., without visual control during movement execution) in pretest (i.e., before prism adaptation), in posttest (immediately after prism adaptation), and in last-test session (at the end of experiment). They comfortably sat in a chair in front of the adaptation table with their head aligned with the body axis using a chinrest. For each session, they had to perform ten open-loop pointing trials, with their vision occluded during movement execution, making them unaware of the sensorimotor aftereffects of prism adaptation. The sagittal target (black dot, diameter 6 mm) was placed 45 cm from the edge of the table, and the starting hand position was placed 11 cm from the edge of the table. At the beginning of each trial, the experimenter passively placed the participants’ right index finger in the starting position and asked them to make accurate movements at a natural speed to the sagittal target. The sensorimotor aftereffects of prism adaptation were

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Auditory frequencies used during auditory interval bisection judgment in Experiment 1. AF: auditory frequency; AF1: low limit of the auditory interval; AF2: high limit of the auditory interval; TAF: target auditory frequency.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Auditory interval</td>
<td>AF1</td>
</tr>
<tr>
<td>Interval 1</td>
<td>200 Hz</td>
</tr>
<tr>
<td>Interval 2</td>
<td>1850 Hz</td>
</tr>
<tr>
<td>Interval 3</td>
<td>3500 Hz</td>
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</tbody>
</table>

Fig. 1. Experimental paradigm used in Experiments 1 and 2. M: musicians; NM: nonmusicians; PA: prism adaptation; ML: musicians exposed to a Leftward optical deviation; MR: musicians exposed to a Rightward optical deviation; NML: nonmusicians exposed to a Leftward optical deviation; NMR: nonmusicians exposed to a Rightward optical deviation.
Fig. 2. Sequence of events for each trial of the auditory interval bisection judgment for interval I2. The event sequence was similar for all three intervals, only the frequencies used were different. Each trial began by a pink noise followed by a silence of 500 ms. The two auditory limits of the auditory interval (AF1 and AF2) were then presented separated by a silence of 500 ms. A silence of 1000 ms followed the presentation of the auditory interval and the target auditory frequency (TAF) was then presented during 500 ms. Participants had to indicate if they perceived the TAF closer to the low or the high limit of the interval.

assessed by the difference in pointing errors between mean performance in posttest and mean performance in pretest for each participant (immediate aftereffects: posttest performance minus pretest performance). At the end of the experiment, ten open-loop pointing trials were performed to ensure that sensorimotor plasticity persisted during the auditory task in posttest, and until the end of the experiment (late aftereffects: last-test performance minus pretest performance). All arm movements 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 computer program in Matlab (Mathworks, Natick, MA).

2.1.3.3. Prism adaptation procedure. Immediately following the pretest, participants wore prismatic goggles and their head was kept aligned with the body axis by using a chin rest. Nine visual colored targets (sticker dots; diameter: 6 mm, space interdots: 4 cm) were placed 45 cm from the edge of the table. Participants performed a closed-loop pointing task (i.e., with vision of the hand during the movement). They were asked to point to the targets as quickly and as accurately as possible and returned at the starting position at a natural speed. Vision of the starting hand position was occluded to ensure the optimal development of the adaptation (Redding & Wallace, 1997). Every 3 s, the experimenter instructed participants verbally on which of the nine targets to point, according to a random sequence. The prism adaptation procedure involved four blocks of 81 pointing trials (total number of movements: 324). Participants relaxed for 1 min, eyes closed, at the end of each pointing block. The prism adaptation procedure lasted about 20 min.

2.1.3.4. Data analysis. For the auditory interval bisection judgment, the mean percentage of ‘low’ responses given by the participants was computed separately for the three intervals (I1, I2, and I3). This percentage indicates the proportion of target auditory frequencies considered as closer to the lower auditory frequency limit of the auditory interval (I1: 200 Hz; I2: 1850 Hz; I3: 3500 Hz) and suggested an approximate estimation of the auditory interval center (Michel et al., 2019). As illustrated in Fig. 3, a weak percentage of ‘low’ responses would indicate that participants perceived some of the low auditory targets as closer to the high frequency limit of the auditory interval, because they were perceived as higher than the subjective center (see top panel of Fig. 3). This would mean that there would be an auditory bias in the estimation of the interval center toward the lower frequencies in regard to the objective center. In contrast, a high percentage of ‘low’ responses would mean that participants perceived some of the higher auditory targets as closer to the low frequency limit of the auditory interval, because they were perceived as lower than the subjective center (see bottom panel of Fig. 3). This would suggest an auditory bias in the estimation of the interval center toward the higher frequencies in regard to the objective center.

After computing the percentage of ‘low’ responses, the participants’ subjective center of the auditory interval was precisely defined by fitting the data with a sigmoid function. The subjective center of the auditory interval is the frequency for which participants provided 50% of responses closer to the lower frequency limit and 50% of responses closer to the higher frequency limit of the auditory interval (Michel et al., 2019).

For the visuo-manual open-loop pointing task, pointing angular errors were 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, with negative values corresponding to leftward errors and positive value to rightward errors.

The statistical analyses were carried out using the Statistica software (version 7.1). Normality of the data was verified with a Shapiro-Wilk test. When data were normal (p > .05), we used parametric analyses (repeated measures ANOVA and LSD post-hoc). Otherwise (p < .05), we used nonparametric analysis (Friedman ANOVA and Wilcoxon test). Results were considered to be significant at p < .05.
2.2. Results

2.2.1. Sensorimotor aftereffects on visuo-manual open-loop pointing task

Repeated measures ANOVA with Session (pretest, posttest, late-test) as within-subject factor and Deviation (Left, Right) as between-subject factor were carried out for musicians and nonmusicians separately (Group ML vs. Group MR; Group NML vs. Group NMR). The results, displayed in Fig. 4, showed a significant effect of Deviation for both musicians and nonmusicians, [Group M: \(F(1, 22) = 131.48, p < .001, \eta^2_p = 0.86\); Group NM: \(F(1, 22) = 115.87, p < .001, \eta^2_p = 0.84\)], and a Session \(\times\) Deviation interaction for both musicians and nonmusicians, [Group M: \(F(2, 44) = 178.02, p < .001, \eta^2_p = 0.89\); Group NM: \(F(2, 44) = 142.15, p < .001, \eta^2_p = 0.84\)]. Sensorimotor aftereffects were illustrated by a significant difference between pretest and posttest and between pretest and late-test when participants were exposed to both leftward and rightward optical deviations [LSD post-hoc: pretest vs. posttest, all \(p < .001\); pretest vs. late-test, all \(p < .001\)].

2.2.2. Performance on auditory interval bisection judgment in pretest

First, \(t\)-test comparisons were performed to evaluate whether the mean percentages of ‘low’ responses were different from 50% in the pretest. The mean percentage was not significantly different from 50% for \(I_1\), but it was significantly lower than 50% in musicians and nonmusicians for \(I_2\) [Group M: \(M = 39.22, SD = 11.01, t(23) = 4.79, p < .001\); Group NM: \(M = 39.22, SD = 11.01, t(23) = -4.79, p < .001\)].

Fig. 3. Schematic representation of the measurement of the percentage of ‘low’ responses.
Top panel: A weak percentage of ‘low’ responses would indicate that participants perceived some of the low target auditory frequencies as closer to the high frequency limit of the auditory interval. As a consequence, the subjective center would be lower than the objective center of the auditory interval.
Bottom panel: A high percentage of ‘low’ responses would indicate that participants perceived some of the higher target auditory frequencies as closer to the low frequency limit of the auditory interval. As a consequence, the subjective center would be higher than the objective center of the auditory interval.

Fig. 4. Amplitude of pointing errors for pretest, posttest, and late-test as a function of the deviation in musicians (Group ML, Group MR) and nonmusicians (Group NML, Group NMR). Error bars indicate standard errors. Positive values indicate rightward pointing errors from the visual target. Negative values indicate leftward pointing errors from the visual target.
Fig. 5. Percentages of ‘low’ responses for pretest as a function of interval (I1, I2, I3) and musical expertise (M, NM). Error bars indicate standard errors. Filled squares indicate significant pseudoneglect. The 50% line indicates the point of equiprobability for which the participants provided 50% ‘low’ and 50% ‘high’ responses. A mean percentage significantly lower than 50% indicates an auditory pseudoneglect.
pseudoneglect is increased in the left hemispace and absent in the right hemispace. In the auditory domain, it seems to be different. In a large auditory spectrum, pseudoneglect appears absent in low frequencies (i.e., to the left, by reference to SMARC effect; see Section 1.3) and present in high frequencies (i.e., to the right, by reference to SMARC effect; see Section 1.3). The possible influence of the auditory workspace used in the experiment must be considered in the modulation of pseudoneglect. The absence of pseudoneglect for the lower interval could be explained by the use of a wide workspace, which was biased toward high frequencies. Two intervals out of three, I2 and I3, have frequencies higher than 1080 Hz. Perceptually, frequencies lower than 400 Hz are considered low, frequencies between 400 Hz and 1600 Hz are considered median, and frequencies higher than 1600 Hz are considered high (Bagot, 1999). Then, in Experiment 1, frequencies of I1 (200 Hz–800 Hz) could be perceived as low, frequencies between 400 Hz and 1600 Hz as median, and frequencies higher than 1600 Hz as high. Participants could mainly respond ‘high’ for target auditory frequencies in I2 and I3, and ‘low’ for target auditory frequencies in I1 in an absolute way (and not in comparison with the low and high limits of the intervals as requested in the auditory interval bisection judgment). This perceptual bias would be more pronounced in nonmusicians than in musicians, as suggested by the variation of the percentages of ‘low’ responses. This perceptual response bias could have modulated the expression of pseudoneglect in the wide auditory spectrum used. Furthermore, another argument developed in the general discussion section, proposed that the perception of the lower interval was more sensitive leading to a masking of pseudoneglect.

Second, prism adaptation to a leftward optical deviation produced an increase of the percentage of ‘low’ responses, in musicians for I2 and for I3. After adaptation to a leftward optical deviation, musicians perceived more target auditory frequencies as closer to the low limit of the auditory interval, suggesting a bias of the estimation of the auditory interval center toward the high limit of the auditory intervals (see bottom of Fig. 3). This result replicates the result obtained in the study of Michel et al. (2019) and extends the presence of aftereffects of adaptation to a leftward optical deviation on a wider auditory spectrum, toward high frequencies (auditory intervals: 1850 Hz–2450 Hz; 3500 Hz–4100 Hz). For the lower interval I1, no aftereffects of prism adaptation were observed. The perceptual response bias could also apply and might have masked the effect of prism adaptation. Furthermore, the absence of auditory pseudoneglect for I1 could explain the absence of effects of prism adaptation. One interpretation would be that, like in the visual domain, the aftereffects of prism adaptation in the auditory domain would be dependent on the presence of pseudoneglect (Goedert et al., 2010; see Michel, 2016 for review).

Finally, the effects of adaptation to a leftward optical deviation were shown for the first time in nonmusicians, but for I2 only. As mentioned in the above paragraph, the absence of pseudoneglect in I1 could explain the absence of aftereffects of prism adaptation. Concerning the absence of aftereffects of prism adaptation for I3 in nonmusicians, it is possible that the task was too difficult in high frequencies for musically untrained participants. The smallest variation of frequency (Hz) between two

Fig. 6. Percentages of ‘low’ responses for pretest and posttest as a function of interval (I1, I2, I3) and optical deviation (Group ML, Group MR) in musicians. Error bars indicate standard errors. The 50% line indicates the point of equiprobability for which the participants provided 50% ‘low’ and 50% ‘high’ responses.

Fig. 7. Percentages of ‘low’ responses for pretest and posttest as a function of interval (I1, I2, I3) and optical deviation (Group NML, Group NMR) in nonmusicians. Error bars indicate standard errors. The 50% line indicates the point of equiprobability for which the participants provided 50% ‘low’ and 50% ‘high’ responses.
The auditory pseudoneglect was observed in a wide auditory spectrum toward higher frequencies, regardless of the musical expertise. Prism perceptual response bias raises the question of the difficulty of the auditory task for non-musicians and, for the first time, in nonmusicians. Experiment 1 also adapted to a left optical deviation affects auditory perception in musicians. Although the horizontal representation of auditory frequencies is less pronounced in nonmusicians (Lidji et al., 2007), the experimental design of Experiment 2 was set up to be optimal, and then to strengthen the effects observed with nonmusicians.

3. Experiment 2

3.1. Materials and methods

3.1.1. Sample size estimation

A statistical a priori power analysis was performed for sample size estimation. The analysis parameters were the same as in the Experiment 1 (see Section 2.1.1). Our proposed sample size of N = 11 by group is then adequate for the main objective of Experiment 2.

3.1.2. Participants

Twenty-two volunteer nonmusician participants, who did not take part in Experiment 1, participated in Experiment 2 (15 females, 7 males, mean age = 22.09, SD = 2.35). All were healthy, with normal or corrected to normal vision, and without auditory or neurological deficits. Except two ambidextrous participants (1 L, 1 R), all were right-handed according to the Edinburgh Handedness Inventory (Group L: M = 0.74, SD = 0.16; Group R: M = 0.81, SD = 0.26). Participants were randomly divided into two groups of eleven participants according to the optical deviation used during prism adaptation: Group L was exposed to a 15° leftward optical deviation and Group R was exposed to a 15° rightward optical deviation. After being informed of the experimental procedures, all participants signed their written consent and completed a musical expertise questionnaire. They were completely naive as to the purpose of the experiment, spatial representation of auditory frequencies, and prism adaptation. They were debriefed after the experiment. The experimental protocol was carried out in accordance with the Declaration of Helsinki (1964).

3.1.3. Experimental procedure

The procedure was the same as in Experiment 1 (Section 2.1.3; see Fig. 1), except that two main changes were applied to make the auditory interval bisection judgment easier and try to reduce the potential perceptual response bias.

First, the frequencies of the ‘extreme’ intervals (I1, I3) were modified to be closer to those of the median interval I2 (see Table 2), resulting in a reduced amplitude of the auditory spectrum used in Experiment 2 compared to Experiment 1. Second, the trials were presented blocked by interval (and not randomized as in Experiment 1). For instance, participants listened to trials of I1 during the first block, then trials of I3 for the second block, and so on. There was a total of six blocks (two by intervals), each of them composed of 23 pseudo-randomized trials. In the first half of the auditory interval bisection judgment task, three blocks (one for each interval) were presented, and the other three blocks were presented in the second half of the task. The same interval could not be presented in two successive blocks. Within each block, the order of presentation of the limits (AF1 and AF2) was pseudo-randomized and the same TAF could not be presented in two successive trials. In total, 138 trials were presented in six blocks, randomized for each participant, and for both pretest and posttest. The instruction was the same as in Experiment 1, participants had to judge if the TAF was closer to the low or the high limit of the interval, by answering ‘low’ or ‘high’.

3.1.4. Data analysis

The analyses were the same as in Experiment 1 (see Section 2.1.3.4).

3.2. Results

3.2.1. Sensorimotor aftereffects on visuo-manual open-loop pointing task

We used a nonparametric analysis because data were not normal (Shapiro-Wilk test: p < .05). A Friedman ANOVA was performed for each optical deviation and showed a significant effect of leftward and rightward deviation (all ps < .001). The sensorimotor aftereffects were illustrated by a significant difference between pretest and posttest and between pretest and late-test after prism adaptation for both optical deviations [Wilcoxon test: pretest vs. posttest, ps < .01; pretest vs. late-test, ps < .01] (Fig. 8).

3.2.2. Performance on auditory interval bisection judgment in pretest

3.2.2.1. Percentages. As in Experiment 1, t-test comparisons were performed to evaluate whether the mean percentages of ‘low’ responses presented in the second half of the task. The same interval could not be presented in two successive blocks. Within each block, the order of presentation of the limits (AF1 and AF2) was pseudo-randomized and the same TAF could not be presented in two successive trials. In total, 138 trials were presented in six blocks, randomized for each participant, and for both pretest and posttest. The instruction was the same as in Experiment 1, participants had to judge if the TAF was closer to the low or the high limit of the interval, by answering ‘low’ or ‘high’.

3.1.4. Data analysis

The analyses were the same as in Experiment 1 (see Section 2.1.3.4).

3.2. Results

3.2.1. Sensorimotor aftereffects on visuo-manual open-loop pointing task

We used a nonparametric analysis because data were not normal (Shapiro-Wilk test: p < .05). A Friedman ANOVA was performed for each optical deviation and showed a significant effect of leftward and rightward deviation (all ps < .001). The sensorimotor aftereffects were illustrated by a significant difference between pretest and posttest and between pretest and late-test after prism adaptation for both optical deviations [Wilcoxon test: pretest vs. posttest, ps < .01; pretest vs. late-test, ps < .01] (Fig. 8).

3.2.2. Performance on auditory interval bisection judgment in pretest

3.2.2.1. Percentages. As in Experiment 1, t-test comparisons were performed to evaluate whether the mean percentages of ‘low’ responses
were different from 50% in the pretest. The mean percentage of ‘low’ responses was significantly higher than 50% in I1 (M = 54.25, SD = 7.98; t(21) = 2.50, p < .02, d = 0.53), and was not significantly different from 50% in I2 (M = 49.01, SD = 8.15; t(21) = –0.57, p > .10, d = 0.12). There is a trend of ‘low’ responses to be lower than 50% in I3 (M = 45.35, SD = 11.09; t(21) = –1.96, p = .06, d = 0.42).

3.2.2.2. Subjective center. For every interval, t-test comparisons were performed to evaluate whether the mean subjective center of the auditory interval was different from the objective center (I1: 900 Hz; I2: 2150 Hz; I3: 3400 Hz). Even if the mean subjective center seemed to be lower than the objective center for I2, M = 2149.30, and for I3, M = 3376.39, the difference between the subjective center and the objective center was not statistically significant for the three intervals, p > .10 for I1, p > .50 for I2 and p > .10 for I3.

3.2.3. Aftereffects of prism adaptation on auditory interval bisection judgment

3.2.3.1. Percentages. Repeated measures ANOVA with Session (pretest, posttest) and Interval (I1, I2, I3) as within-subject factors were performed on the percentages of ‘low’ responses for leftward deviation and rightward deviation separately (Fig. 9). For the group L, a significant effect of Session, F(1, 10) = 20.77, p = .001, η² = 0.67, and an Interval × Session interaction, F(2, 20) = 4.07, p = .03, η² = 0.29, were observed, with an increase of the percentages of ‘low’ responses for I2 and I3 in posttest compared to pretest [LSD Post-hoc, I2: p < .01, I3: p < .001]. There were no significant effects for the group R, all ps > .10. This second result indicated that prism adaptation to a leftward optical deviation influences auditory perception in high frequencies (I2 and I3) but not in medium frequencies (I1).

3.2.3.2. Subjective center. Normality was not confirmed for I1 (in pretest and posttest), and for I3 (in posttest) but it was for I2. A Wilcoxon test, used for data of I1 and I3, showed no significant aftereffects of prism adaptation for both optical deviations, all ps > .10. For I2, a t-test showed a significant effect of leftward optical deviation, t(11) = –2.35, p = .04, d = 0.27 (pretest: M = 2140.35 Hz; posttest: M = 2166.50 Hz) (Fig. 10). This effect of adaptation to a leftward optical deviation was illustrated by a shift of the subjective interval center toward the higher frequencies. Concerning the rightward prism adaptation there were no significant results, all ps > .10.

![Fig. 9. Percentages of ‘low’ responses for pretest and posttest as a function of the participants I1, I2, I3 and optical deviation (Left, Right). Error bars indicate standard errors. The 50% line indicates the point of equi-probability for which the participants provided 50% ‘low’ and 50% ‘high’ responses.](image)

![Fig. 10. Subjective center for pretest and posttest as a function of deviation (Left, Right) for Interval I2. Error bars indicate standard errors.](image)

3.3. Discussion of Experiment 2

Two main results emerge from this second experiment. First, no significant auditory pseudoneglect was observed for nonmusicians. This result is not in agreement with the result of Experiment 1. The variability of pseudoneglect that can be observed in the general population could explain the difference between the results of Experiment 1 and Experiment 2 (McCourt & Jewell, 1999). Nevertheless, there is a trend for mean percentage of ‘low’ responses to be lower than 50% in I3. Concerning the high percentage of ‘low’ responses for I1, it could be linked to the perceptual response bias already mentioned in Experiment 1.

Second, for percentages of low responses, auditory aftereffects of prism adaptation to a leftward optical deviation occurred in I2 and in I3 in nonmusicians. After prism adaptation to a leftward optical deviation, nonmusician participants answered more often ‘low’, suggesting that they perceived the target auditory frequencies more often closer to the low limit of the auditory interval. This observation may suggest a bias of the estimation of the auditory interval center toward the high limit of the auditory intervals that is consistent with our hypothesis and with the results obtained for musicians in Experiment 1. Like in Experiment 1, no effect was shown for the interval with the lower frequencies (i.e., 600 Hz–1200 Hz) probably because of the absence of pseudoneglect in I1. Moreover, adaptation to a leftward optical deviation modified the subjective interval center, by producing a shift toward the higher frequency limit for I2 only. The effects of adaptation to a leftward optical deviation in I2 are in accordance with those observed for the measure of percentage of ‘low’ responses and show that adaptation to a leftward optical
deviation can also affect the auditory perception in nonmusicians. It is likely that the mean percentage of 'low' responses is a more sensitive tool than the estimation of the interval center to evaluate the auditory modulation produced by prism adaptation in the auditory interval bisection judgment task. The percentage of 'low' responses allows the assessment of auditory modulations produced by prism adaptation in both I2 and I3, whereas the subjective interval center detects only changes in I2.

Altogether, the results of Experiment 2 supported the innovative results of Experiment 1. The action of adaptation to a leftward optical deviation on high auditory frequencies was confirmed in participants without musical expertise. This experiment showed for the first time that, under certain circumstances, adaptation to a leftward optical deviation can shift the subjective auditory center toward the high frequencies in nonmusicians.

4. General discussion

The two main objectives of the present study were (1) to investigate the representation of auditory frequencies in a wide auditory spectrum, and (2) to evaluate the aftereffects of prism adaptation on auditory frequency representation in this wide auditory spectrum. In Experiment 1, participants exhibited a percentage of 'low' responses smaller than 50% whatever their musical expertise for high auditory frequency intervals, suggesting an estimation of the interval center which was shifted toward lower frequencies. Named auditory pseudoneglect, this behavior, which was observed for high frequencies of the auditory spectrum, was not observed for low/median frequencies. Furthermore, innovative aftereffects of prism adaptation to a leftward optical deviation were observed in a wide auditory spectrum under certain circumstances. Experiment 1 showed an increase of the percentage of 'low' responses in musicians for the higher auditory frequency intervals (i.e., I2 and I3). A similar effect was observed in nonmusicians for I2 only. Experiment 2, in which the auditory interval bisection judgment task was made easier, showed an increase of the percentage of 'low' responses in nonmusicians for both the higher auditory frequency intervals (i.e., I2 and I3). These results were the first demonstration of aftereffects of prism adaptation in auditory interval bisection judgment in nonmusicians.

4.1. Auditory pseudoneglect

In accordance with the results observed by Michel et al. (2019), the present study showed an auditory response bias called auditory pseudoneglect. The innovative aspect of our results is the presence of this bias on a wide auditory spectrum, for high frequencies. The orientation of attention toward the left part of space (e.g., Milner et al., 1992) and the association between low auditory frequencies and left part of space (e.g., Lidji et al., 2007) could explain the response bias toward low frequencies observed in the auditory interval bisection judgment. A perceptual reason could explain the absence of pseudoneglect in the lower interval in Experiment 1 (i.e., 200 Hz–800 Hz). The auditory frequency is physically expressed in Hertz (Hz) and perceptually expressed in Mel (Stevens et al., 1937). While the frequency of audible sounds can reach 20,000 Hz, on the perceptual scale they can only reach about 2400 Mels (Zwicker & Feldtkeller, 1981). The Mel scale follows a logarithmic growth (Stevens et al., 1937). Below 500 Hz, the values in Mel are almost identical to the values in Hertz. Beyond 500 Hz, the curve is ceiling and two distant frequencies in Hz become closer when expressed in Mel (Zwicker & Feldtkeller, 1981). In our study, all intervals had the same physical width of 600 Hz. Perceptually, the lower interval I1 of Experiment 1 was larger (576 Mels) than the higher intervals I2 (238 Mels) and I3 (150 Mels). The perception of auditory frequencies in I1 matched more to the physical expression of these frequencies and should perceptually be more accurate than for intervals I2 and I3, for which the discrimination of the auditory frequencies could be more complicated, making the auditory interval bisection judgment more difficult to perform. This might lead to a masked expression of the pseudoneglect bias. A complementary analysis made on correct responses for the three intervals was in agreement with this argument for nonmusicians, although it was not for musicians, who obtained higher scores of correct responses for the three intervals.

4.2. Auditory perception and prism adaptation

The aftereffects of adaptation to a leftward optical deviation occur with stimuli spatially represented, like numbers (Loftus et al., 2008) and letters (Nicholls et al., 2008). Auditory frequencies have also been shown to be spatially valued elements, with low frequencies mentally represented to the left and high frequencies mentally represented to the right along a horizontal mental line (see Section 1.3). Space representation depends on orientation of attention (e.g., McCourt & Jewell, 1999; Milner et al., 1992). The right hemisphere, especially the right posterior parietal cortex, is dominant in visuo-spatial processes in healthy people (Fierro et al., 2000; Fink et al., 2001). The right hemisphere is also dominant in auditory perception (e.g., Hyde et al., 2008) and in pitch discrimination (Lageoïs-chauvel et al., 2001; Zatorre, 1998; Zatorre & Belin, 2001), specifically in the temporal cortex where the Heschl gyrus is considered as the 'pitch center' (Hall & Pack, 2009). The right temporal cortex is also involved during prism exposure to leftward optical deviation (Lauaté et al., 2009). Aftereffects of prism adaptation may be mediated by the differential hemispheric activation of both hemispheres. This change of hemispheric balance in favor to the left hemisphere and in detriment to the right hemisphere (Schiuuto et al., 2016) could explain the modification of leftward representational bias (i.e., toward low frequencies in the present study) into rightward representational bias (i.e., toward high frequencies in the present study) (for a review see Michel, 2016).

4.3. Cerebral plasticity in auditory perception

The cerebral plasticity could explain the differences observed in the present investigation between musicians and nonmusicians. Aftereffects of prism adaptation were demonstrated for the first time in nonmusician participants in Experiment 1 and for both high frequency intervals in Experiment 2, after making the auditory interval bisection judgment easier with a blocked presentation by interval and with a more reduced auditory spectrum than in Experiment 1. Nonmusicians and musicians do not adopt the same cognitive strategies when they analyze auditory frequencies. It has been shown that during mental imaging of music, nonmusicians have a ‘feeling’ strategy, whereas musicians tend to spontaneously visualize intervals (Altenmüller et al., 2000). In the same vein, during an informal debriefing, musician participants of the present study reported a horizontal spatial representation of the auditory intervals that could make the task easier to perform. Furthermore, musical training could modify the auditory network to achieve a superior ability for auditory imagery and processing of music (Herholz et al., 2008). Compared to nonmusicians, musicians have a different cerebral organization of the auditory cortex, correlated with better pitch perception ability (Gaser & Schlaug, 2003; Schneider et al., 2002; for a review see Zatorre et al., 2001). Consequently, musicians are more sensitive to frequency variations than nonmusicians. This could explain why pseudoneglect bias and aftereffects of adaptation to a leftward optical deviation appear to be more stable in musicians than in nonmusicians.

4.4. Physical frequency vs. perceptual frequency

In order to better understand the involvement of the perceptual scale in the auditory interval bisection judgment task, objective and subjective centers of Experiment 2 were converted from Hertz (physical unit) into Mel (perceptual unit) according to the following mathematical formula (e.g., Kamath et al., 2019).
This conversion allowed the comparison of the perceptual subjective centers (Mel) to the perceptual objective centers (Mel), instead of the comparison of the subjective centers (Hz) to the physical objective centers (Hz) in the results section of Experiment 2. Even if for I2 and I3 the perceptual subjective centers (I2: M = 1581.89 Mels, SD = 17.23; I3: M = 1985.47 Mels, SD = 20.16) were lower than perceptual objective centers (I2: M = 1582.29 Mels; I3: M = 1992.14 Mels), no significant auditory pseudoneglect was shown. Furthermore, prism adaptation to a leftward optical deviation shifted the perceptual subjective center toward the high limit of the interval for I2 (M = 1586.59 Mels, SD = 19.95), as in Experiment 2 when data were analyzed in Hertz (see Section 3.2).

It is worth noting here that physical auditory frequency did not match to perceptual auditory frequency beyond 500 Hz (Zwicker & Feldtkeller, 1981). When expressed in Mel, auditory frequency limits are perceptually closer. They are all the closer as auditory frequencies increase. For instance, for I3 of Experiment 2, the physical auditory interval was 600 Hz whereas the perceptual auditory interval was almost 165 Mels. The auditory intervals used in the present study were physically equal but perceptually different, making auditory perception unequal between auditory intervals. In further experimental paradigms, it would be more appropriate to define the width of auditory intervals directly in Mel.

5. Conclusion

The present study allows a better understanding of the representation of auditory frequencies in a wide auditory spectrum. The auditory pseudoneglect seemed to be present in the high frequencies of the auditory intervals used in the present study were physically equal but perceptually different, making auditory perception unequal between auditory intervals. In further experimental paradigms, it would be more appropriate to define the width of auditory intervals directly in Mel.

CB, BPC and CM participated in the elaboration of the experimental protocol, made the statistical analysis, and wrote the paper. PB participated in the elaboration of the experimental design and data analyses.

References


