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Wearing Prisms to Hear Differently:

After-Effects of Prism Adaptation on Auditory Perception

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## 2 Abstract

3 Numerous studies showed that, after adaptation to a leftward optical deviation, 4 pseudoneglect behavior (overrepresentation of the left part compared to the right part of the 5 space) becomes neglect-like behavior (overrepresentation of the right part compared to the 6 left part of the space). Cognitive after-effects have also been shown in cognitive processes 7 that are not intrinsically spatial in nature, but show spatial association as numbers or letters. 8 The space-auditory frequency association (with low frequencies on the left and high 9 frequencies on the right) raises the question of whether prism adaptation can produce after-10 effects on auditory perception. We used a new experimental protocol, named the 'auditory 11 interval bisection judgment', where participants had to estimate what limit of an auditory 12 interval (low or high) a target frequency was closer to. We calculated the subjective auditory 13 interval center. In pretest, there was a spontaneous bias of the subjective center of the auditory 14 interval toward the lower limit. That was the first demonstration of pseudoneglect behavior in 15 auditory frequency representation. ANOVA realized on all participants did not show significant results of prism adaptation, but a posteriori analyses on musicians showed that, 16 17 after adaptation to a leftward optical deviation, there were more target frequencies perceived 18 as closer to the lower limit of the auditory interval. This result corroborates the shift of the 19 subjective center of the auditory interval toward high frequency limit. These innovative 20 results are discussed in terms of putative neural substrates underpinning the transfer of 21 visuomotor plasticity to auditory frequency perception.

22

#### 23 1 Introduction

#### 24 1.1 Prism adaptation

25 Sensorimotor plasticity allows the production of an appropriate motor response in 26 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 27 28 wearing prisms that shift the visual field laterally. At the beginning of the exposure, 29 participants make pointing errors in the direction of the optical deviation. On the basis of these 30 error signals, participants gradually improve their performance until they achieve an accurate 31 behavior. When the prisms are removed, the sensorimotor correlations revert to an 32 inappropriate state, and the pointing movements are shifted in the direction opposite to the 33 prismatic shift (e.g., Redding, Rossetti, & Wallace, 2005). These sensorimotor after-effects 34 can be explained by proprioceptive, visual, and motor control changes (e.g., Kornheiser, 35 1976).

#### 36 1.2 Prism adaptation acts on space representation

37 After-effects of prism adaptation are not restricted to sensorimotor level but extend as 38 well into spatial cognition (see Michel, 2006; 2016, for reviews ). The term 'cognitive', used 39 to depict after-effects, refers to the fact effects are not bound to the usual framework of 40 compensatory sensorimotor after-effects, but also involve mental abilities such as judgment, 41 comparison, and space representation (mental image of the space mapped across the brain). 42 Line-bisection task is an invaluable tool to assess space representation. In its perceptual 43 version, participants are requested to judge whether a line has been transected to the left or the 44 right of its true center. The estimation of the center of the line is usually characterized by a 45 leftward pseudoneglect bias corresponding to a mental overrepresentation of the left part of 46 the space / underpresentation of the right part of the space (e.g., McCourt & Jewell, 1999).

47 This pseudoneglect behavior, due to right hemisphere dominance in visuospatial processes 48 (e.g., Fink, Marshall, Weiss, & Zilles, 2001), could be modulated by attentional orientation as 49 spatial cueing (e.g., Milner, Brechmann, & Pagliarini, 1992) or reading habits (Brodie & Pettigrew, 1996; Chokron, Bartolomeo, Perenin, Helft, & Imbert, 1998). Numerous studies 50 51 showed that after adaptation to a leftward optical shift, pseudoneglect becomes neglect-like 52 behavior, with a mental overrepresentation of the right part of the space / underrepresentation 53 of the left part of the space (Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; Fortis, 54 Goederth, & Barrett, 2011; Michel, Pisella, et al., 2003; Michel, Rossetti, Rode, & Tilikete, 55 2003; Nijboer, Vree, Dijkerman, & Van der Stigchel, 2010; Schintu et al., 2014; Striemer & 56 Danckert, 2010). Neglect simulation was not only described in peripersonal space 57 representation, but also occurred in extrapersonal (Berberovic & Mattingley, 2003; Michel, 58 Vernet, Courtine, Ballay, & Pozzo, 2008), and bodily space representations (Michel, Rossetti,

59 et al., 2003).

## 60 1.3 Prism adaptation acts on mental scales with spatial association

Studies using choice-reaction task paradigms showed that stimulus-response 61 62 compatibility effects (e.g., faster and more accurate performance when the spatial position of 63 the button to press (i.e., response) is compatible with the spatial features of the stimulus) also 64 occur when the stimuli are not intrinsically spatial but considered as activating a mental spatial 65 representation (Proctor & Cho, 2006). The mental number line is thought to have a left-to-66 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 67 between two numbers, without using arithmetic, individuals exhibit a pseudoneglect behavior 68 69 by misbisecting the mental distance toward the smaller numbers (i.e., to the left) (Loftus, 70 Nicholls, Mattingley, Chapman, & Bradshaw, 2009; Longo & Lourenco, 2007). Adaptation to 71 a leftward optical deviation was responsible for neglect-like behavior, with a shift in bisection

72 toward the large numbers (i.e., to the right) (Loftus, Nicholls, Mattingley, & Bradshaw, 2008). 73 The mental alphabetic line has also a left-to-right organization with early letters on the left 74 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 75 76 by misbisecting the mental distance toward early letters (i.e., to the left) (Nicholls & Loftus, 77 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, 78 79 & Loftus, 2008). As for number and alphabetic features, humans represent time along a spatial 80 continuum (to associate the past with the left space and the future with the right space; Bonato, 81 Zorzi, & Umilta, 2012). Perception of temporal durations can also be changed following 82 prismatic adaptation (Anelli, Ciaramelli, Arzy, & Frassinetti, 2016). Taken together these 83 results underline that prism adaptation acts on the representation of stimuli with spatial 84 association.

## 85 1.4 Space-auditory frequency association in horizontal axis

Auditory frequencies induce spatial association as well. As for numbers and alphabetic 86 87 letters, auditory frequencies are represented along a mental line with low frequencies on the 88 left and high frequencies on the right. This assertion is based on stimulus-response 89 compatibility effect that occurs when the same spatial code is shared by both stimulus and 90 response coding processes (e.g., Dehaene et al., 1993; Fias, Brysbaert, Geypens, & 91 d'Ydewalle, 1996; Rusconi, Kwan, Giordano, Umilta, & Butterworth, 2006). Concerning auditory frequencies, stimulus-response compatibility effects in horizontal axis showed faster 92 93 and more accurate responses to low frequencies on the left and to high frequencies on the 94 right. This spatial association is more pronounced in musicians than in nonmusicians (Lidji, 95 Kolinsky, Lochy, & Morais, 2007; Rusconi et al., 2006). The space-auditory frequency 96 association has also been elegantly illustrated by the modulation of space representation by

97 hearing different auditory frequencies (Ishihara et al., 2013). When participants were asked to 98 mark the midpoint of a given line with a pen (manual line-bisection task) while they were 99 listening to a pitch via headphones, lower frequency produced leftward bisection biases 100 whereas higher frequency produced rightward biases. More generally, cross-modal effects on 101 the allocation of spatial resources can also be illustrated by the reduction of the leftward bias 102 in line bisection when binaural auditory white noise was heard (Cattaneo, Lega, Vecchi, & 103 Vallar, 2012). Altogether these results underline the left-to-right association between space 104 and auditory frequency.

105 *1.5 Does prism adaptation act on auditory perception?* 

106 Based on cognitive theories underlining that space representation interact with other metrics domains as auditory frequencies and on experimental results showing that prism adaptation 107 108 acts not only on space representation but also on other features interacting with space 109 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 110 111 frequency association (low frequencies on the left and high frequencies on the right) raises the 112 question of the existence of after-effects of prism adaptation on auditory perception. Because 113 adaptation to a leftward optical deviation produces a rightward bias in space representation, 114 adaptation to a leftward optical deviation should produce an auditory bias toward high 115 frequencies. Based on the spatial representation of auditory frequencies along a mental line 116 with low frequencies on the left and high frequencies on the right (Lidji et al., 2007; Rusconi 117 et al., 2006), we used a new experimental protocol, named the 'auditory interval bisection 118 judgment', where the subjective center of an auditory interval, limited by two auditory 119 frequencies (low and high), can be estimated. We proposed this auditory task by analogy with 120 the well-known paradigm of perceptual line bisection task also named Landmark task (e.g.,

- 121 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.

#### 123 **2** Material and Methods

## 124 2.1 Participants

Thirty-six adults participated voluntarily in the experiment. All participants were 125 126 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 127 128 age = 22.56, SE = 0.78 years), and Group R (11 females, 7 males, mean age = 21.22, SE =0.70 years). All participants were right-handed according to the Edinburgh Handedness 129 130 Inventory (Group L: M = 0.82, SE = 0.05; Group R: M = 0.79, SE = 0.04). Before the 131 experiment, the participants filled out a questionnaire about their musical background. The 132 experimental protocol was carried out in accordance with the Declaration of Helsinki (1964). 133 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 134 135 reported hearing loss or any difficulties to perform the auditory interval bisection judgment.

#### 136 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 degrees 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 degrees (Optique Peter, Lyon, France). The total visual field with the goggles was 105 degrees, 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).

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## 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 ms.

156 The complete sequence of events for one trial is displayed in Figure 1. In order to 157 avoid auditory memory influences of previous stimuli, each trial began by a pink noise of 158 2,000 ms (a pink noise has a power per Hertz that decreases as the frequency increases, and 159 sounds like a cascade). After a silent interval of 1,000 ms, the auditory interval was presented. 160 It consisted in the sounding of two auditory frequencies of 500 ms each separated by a silent 161 interval of 1,000 ms. The two auditory frequencies were 700 Hz and 1300 Hz, whose the 162 order of presentation was counterbalanced. For one half of the trials, the first auditory 163 frequency (AF1) was 700 Hz, and the second one (AF2) was 1300 Hz, and vice versa for the 164 second half of the trials. The auditory interval was followed by a silent interval of 2,000 ms, 165 before the presentation of the target auditory frequency (TAF), which also lasted 500 ms. 166 TAF could take 15 frequency values, with extreme frequency values (i.e., 800 Hz, 850 Hz, 167 1150 Hz, and 1200 Hz) repeated four times, while all the remaining frequency values were 168 repeated six times. This resulted in 82 trials, which were pseudorandomly ordered. The use of

169 all the range of frequencies between AF1 and AF2 was justified by the need of obtaining the 170 best slope as possible for having the best estimation of the subjective midpoint (based on the 171 probability of the individual responses, see below). The same TAF could not be repeated in 172 two successive trials. A different random order of trials was used for each participant, and for 173 both pretest and posttest. The participants had to indicate whether the TAF was closer to AF1 174 or AF2 of the auditory interval. The experimenter scored the response of the participants in an 175 Excel file. The participants began the auditory interval bisection judgment by four training 176 items to ensure that they had clearly understood the instructions.



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Figure 1. Sequence of events for one trial of the auditory interval bisection judgment. Each trial began by a pink
noise of 2,000 ms, 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.

## 181 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

187 using a chin-rest. The starting hand position was placed 11 cm from the edge of the table. 188 Participants were asked to make accurate movements at a natural self-paced speed to the 189 single sagittal target. Before movement onset, participants' right index finger was passively 190 placed by the experimenter in the starting position. The after-effects of adaptation were 191 assessed by the difference in the pointing errors between mean performance in posttest and 192 mean performance in pretest for each participant (immediate after-effects: posttest minus 193 pretest performance). At the end of the experiment, 10 open-loop pointing trials were 194 performed to assess whether the sensorimotor plasticity persisted until the end of the 195 experiment (late after-effects: last performance minus pretest performance). 196 All arm movements for the visuomanual open-loop pointing task (before and after 197 prism exposure) were recorded using 3 TV-cameras (sampling frequency 60 Hz) of an 198 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 199 200 movement measurements was less than 1 mm. Data processing was performed using custom 201 software written in Matlab (Mathworks, Natick, MA).

202 2.2.3 Prism adaptation procedure

203 Prism adaptation procedure followed the pretest. Participants wore prismatic goggles 204 and their head was kept aligned with the body axis by using a chin-rest. They were asked to 205 perform a closed-loop pointing task (with vision of the hand during the movement). Nine 206 visual targets (colored sticker dots; diameter 6 mm, space inter-dots: 4 cm) were placed 45 cm 207 from the edge of the table. The participants pointed as fast as possible to the targets and 208 returned near the start position at a natural speed. Vision of the starting position of the hand 209 was occluded to ensure the optimal development of the adaptation (Redding & Wallace, 210 1997). Every 5 seconds participants pointed alternately to one of the nine visual targets 211 indicated randomly by the experimenter. The adaptation procedure involved 4 blocks of 75

pointing trials (total number of movements: 300). Participants relaxed for 1 minute (eyes
closed) at the end of each pointing block. The total duration of the adaptation procedure lasted
for about 28 min.

215 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.

226 The second measure was computed to fit the data with a sigmoid function in order to 227 obtain the participants' subjective center of the auditory interval. The subjective center of the 228 auditory interval is the frequency for which participants were at 50 % of responses closer to 229 the lower frequency limit and 50 % of responses closer to the higher frequency limit of the 230 auditory interval. This point of equiprobability provided a measure of the subjective center of 231 the auditory interval. In order to evaluate the subjective center, percentages of responses 232 indicating proximity to the higher frequency limit of the auditory interval (1300 Hz) were 233 computed. When AF1 or AF2 of the auditory interval was 1300 Hz, and the participant 234 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, 235 236 from 800 Hz to 1200 Hz. These data were then fitted with a sigmoid function, and the

- 237 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 theauditory interval.
- 240 Results were considered to be significant at p < .05. Means (± standard errors) are
- 241 presented in the Results section.

#### 242 **3 Results**

## 243 3.1.1 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] (Figure 2).



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Figure 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.

## 254 3.1.2 Auditory interval bisection judgment

#### 255 3.1.2.1 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 = 0.38].

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].

264 Based on the literature of cognitive after-effects of prism adaptation and on spatial 265 association of auditory frequencies (see introduction), we expected to find an increase of the 266 mean percentages of responses indicating proximity to the lower auditory frequency limit of 267 the auditory interval for all participants irrespectively of their musical expertise. Nevertheless 268 the musical expertise questionnaire used to better know the musical level of the participants 269 allowed us to identify a posteriori two groups of participants: musicians and nonmusicians. 270 Hereafter, participants having more than 5 years of musical training and still making music 271 will be referred to as musicians (N = 14; 4 play the piano, 5 play the guitar, 1 plays trumpet, 272 and 4 play two or three instruments (piano/guitar, piano/flute, piano/guitar/cajon, 273 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 274 275 Expertise: M = 13.43 years; SD = 4.16) and 11 nonmusicians. Group R was composed of 7 276 musicians (Musical Expertise: M = 12.86 years; SD = 4.18) and 11 nonmusicians as well.

277 Taken separately, the mean percentages of neither musicians nor nonmusicians were significantly different from 50%, and there was no significant difference between musicians 278 279 and nonmusicians [ps > .10]. Similar ANOVAs were performed separately for musicians and 280 nonmusicians. The results are presented in Figure 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 281 significant effect of Session for Group L [F(1, 12) = 6.39, p = .026], with an increase in 282 283 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 284 285 nonmusicians, the ANOVA showed no significant effect [ps > .10]. Prism adaptation to a 286 leftward optical deviation resulted in numerous target frequencies perceived as being closer to 287 the lower frequency of the auditory interval in musicians only.



Figure 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.

291 3.1.2.2 Subjective center

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*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 = 0.39]. 296 A  $2 \times 2$  (Session [pretest, posttest]  $\times$  Deviation [Group L, Group R]) repeated 297 measures ANOVA showed no significant effects [ps > .10]. As for percentages, we expected 298 to find a shift of the auditory interval toward the higher auditory frequency for all participants 299 irrespectively of their musical expertise. Nevertheless the identification a posteriori of two 300 groups of participants (musicians and nonmusicians) allowed detailing the results. Figure 4 displayed the results for musicians and nonmusicians. Taken separately, the subjective center 301 302 of 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 = .159,303 304 respectively]. There was no significant difference between the mean subjective center of the 305 auditory interval of musicians and nonmusicians [p > .10]. Similar 2 × 2 (Session [pretest, posttest] × Deviation [Group L, Group R]) repeated measures ANOVA, conducted for 306 musicians, showed a significant effect of Session [ $F(1, 12) = 7.189, p = .02, \eta_p^2 = .375$ ]. 307



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Figure 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.

311 Planned comparisons showed a significant effect of Session for Group L [F(1, 12) =312 7.46, p = .018], with a higher subjective center for posttest compared to pretest, but not for the 313 Group R [p < .10].



Figure 5. Subjective center for pretest and posttest as for the musicians of the Group L. Error bars indicatestandard errors.

317 For the nonmusicians, no significant effect was observed [ps > .10]. Prism adaptation 318 to a leftward optical deviation resulted in shifting the subjective center of the auditory interval 319 toward the higher auditory frequency in musicians only.

#### 320 4 Discussion

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321 The main objective of the present study was to investigate the influence of prism 322 adaptation on auditory perception. Two major results were observed in our experiment. First, 323 we proposed a new task named auditory interval bisection judgment, and observed the first 324 demonstration of a bias toward the lower limit for the estimation of the center of the auditory 325 interval. This spontaneous bias corresponds to pseudoneglect behavior in auditory frequency 326 representation. Second, prism adaptation to a leftward optical deviation produced an increase 327 of the designation of the lower frequency limit of the auditory interval in musicians. After 328 prism adaptation to a leftward optical deviation, the musicians are more inclined to perceive 329 the target frequencies as closer to the lower limit of the auditory interval. This result 330 corroborated the shift of the estimation of the auditory interval center toward the high 331 frequency limit following adaptation to a leftward optical deviation in musicians.

## 332 4.1 First demonstration of pseudoneglect in auditory perception

333 In the present experiment we proposed an auditory interval bisection judgment to 334 explore the mental representation of auditory frequencies. This task allowed investigating whether frequencies were uniformly represented throughout an auditory interval or whether 335 336 they are characterized by a nonuniform representation as for pseudoneglect in space 337 representation (e.g., Milner et al., 1992). The first important result of our study was the bias 338 observed toward the lower limit of the auditory interval when the subjective center of the 339 auditory interval was estimated. It appears that lower frequencies of the interval were 340 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 341 342 low frequencies on the left and high frequencies on the right), this bias corresponds with a 343 pseudoneglect expression on auditory frequency perception.

344 Pseudoneglect is well documented in space representation (e.g., McCourt & Jewell, 345 1999). The tendency to be biased toward the left-hand side of space is a robust and consistent 346 behavior classically described in visuospatial line-bisection task where participants are asked 347 to indicate the center of a horizontal line (see Brooks, Della Sala, & Darling, 2014; McCourt 348 & Jewell, 1999, for reviews). This spatial bias to the left hand side in line bisection has been 349 referred to as 'pseudoneglect' (Bowers & Heilman, 1980) by analogy to the performance of 350 right-hemisphere impaired patients with left unilateral spatial neglect who show spatial larger 351 biases towards the right hand-side of the space (Nijboer, Kollen, & Kwakkel, 2013; Robertson 352 & Marshall, 1993). The 'pseudoneglect' term now refers to the general tendency of healthy 353 people to preferentially attend to the left side of space (Hatin, Tottenham, & Oriet, 2012). A 354 number of studies have revealed that a representational form of pseudoneglect exists beyond 355 the direct visuospatial processes. Pseudoneglect, for instance, was shown when participants 356 were asked to mentally represent a stimulus that had been previously seen and retrieved from

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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.

363 As for all pseudoneglect expressions, pseudoneglect on auditory frequency perception 364 could be explained by a leftward contralateral activation-orientation due to right hemisphere 365 dominance in visuospatial functions (Benton & Tranel, 1993; Fink et al., 2001). Space 366 representation depends on orientation of attention; the part of the space where attention is 367 oriented is mentally overrepresented (e.g., Milner et al., 1992). If we consider the spontaneous 368 leftward orientation of attention (e.g., Loftus, Nicholls, et al., 2009), the associated 369 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 370 371 coherent result.

#### 372 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.



Figure 5. A representation of the shift of subjective center observed in musicians after prism adaptation to a leftoptical deviation.

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384 As displayed in Figure 5, a target, with a frequency comprised between the subjective 385 centers observed in pretest and posttest, will be perceived as closer to the higher frequency of 386 the auditory interval before prism adaptation (because higher than the prettest subjective 387 center), but the same frequency will be perceived as closer to the lower frequency of the 388 auditory interval after leftward prism adaptation (because lower than the posttest subjective 389 center). This result may suggest that the overrepresentation of the low frequencies / 390 underrepresentation of the high frequencies of the interval (pseudoneglect) was replaced by an 391 overrepresentation of the high frequencies / underrepresentation of the low frequencies of the 392 interval following adaptation to a leftward optical deviation.

393 It is worth underlying, however, that after-effects on auditory perception occurred only 394 in musicians, meaning that auditory frequency representation may be more sensitive to prism 395 perturbation in participants with a robust spatial association for auditory frequencies (Lidji et 396 al., 2007; Rusconi et al., 2006). Further investigations will allow a better understanding of the 397 sensitivity of musicians for the auditory response of prism adaptation. These after-effects in 398 auditory perception come within the scope of well-known effects of prism adaptation on the 399 representation of spatial stimuli or stimuli with spatial association (see Michel, 2006; 2016, for 400 reviews).

401 Indeed in the field of space representation, it is now well established that adaptation to 402 a leftward optical deviation changes an overrepresentation of the left part of the space / 403 underrepresentation of the right part of the space (pseudonglect) into an overrepresentation of 404 the right part of the space / underrepresentation of the left part of the space (neglect-like 405 behavior; see Michel 2006, 2016 for reviews). Prism adaptation has a strong impact on space 406 representation whatever the dimension of the space, peripersonal (Colent et al., 2000; Michel, 407 Pisella, et al., 2003), extrapersonal (Berberovic & Mattingley, 2003; Michel et al., 2008), or 408 bodily (Michel, Rossetti, et al., 2003), and whatever the spatial nature of the task, direct as in 409 line bisection (e.g., Michel, Pisella, et al., 2003), or with association as in mental numbers 410 (Loftus et al., 2008), or letter scales (Nicholls et al., 2008). The influence of prism adaptation 411 also extends to other cognitive processes such as spatial attention (e.g., Loftus, Vijayakumar, 412 & Nicholls, 2009), hierarchical processing (Bultitude & Woods, 2010; Reed & Dassonville, 413 2014), and even on cross-modal functions independent from sensorimotor processes involved 414 in visuomanual adaptation such as haptic tasks (McIntosh, Rossetti, & Milner, 2002), tactile 415 extinction (Maravita et al., 2003), tactile threshold and proprioceptive perception (Dijkerman, Webeling, ter Wal, Groet, & van Zandvoort, 2004) and pain perception (Sumitani et al., 416 417 2007). To illustrate cross-modal effects of prism exposure, it could be mentioned that neglect 418 occurs throughout auditory manifestations as rightward bias in sound location or dichotic 419 listening (e.g., Bellmann, Meuli, & Clarke, 2001), rightward shift in auditory subjective 420 straight ahead (e.g., Kerkhoff, Artinger, & Ziegler, 1999), and that prism can improve neglect 421 at auditory level (Jacquin-Courtois et al., 2010). Taken together with the after-effects of prism 422 adaptation on space representation and on cross-modal functions, the present after-effects on 423 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 426 427 sulcus was implicated in error detection (Danckert et al., 2008; Luauté et al., 2009), and the 428 parieto-occipital sulcus was implicated in error correction (Luauté et al., 2009). Concerning 429 neural substrates of cognitive after-effects, the bilateral activation in superior temporal cortex 430 (superior temporal sulcus, superior temporal gyrus) during the later phase of prism exposure to 431 a leftward optical deviation (Luauté et al., 2009) could mediate the effects of prism adaptation 432 on cognitive spatial representations, and more particularly the effect of prism adaptation on 433 auditory frequencies shown in the present experiment. Other investigations have highlighted 434 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., 435 436 2010; Crottaz-Herbette, Fornari, & Clarke, 2014; Luauté et al., 2006). Following adaptation to 437 a leftward optical deviation the change in hemispheric equilibrium to the detriment of the right 438 hemisphere and in favor of the left hemisphere (Schintu et al., 2016) could be responsible for 439 the representational transformation from leftward representational bias (pseudoneglect) to 440 rightward representational bias (neglect-like behavior) (Michel, 2016). Based on fMRI study 441 using a simple visual detection task, Crottaz-Herbette and collaborators (2017) proposed a 442 model where adaptation to a leftward prism adaptation could influence both ventral attentional system (right hemisphere activation) and dorsal attentional system (left hemisphere 443 444 activation). In order to better discuss the neural substrate that could underpinning our results, 445 we have also to consider the effect of prism adaptation on auditory perception, i.e. on 446 unexposed sensory systems. Indeed, prism adaptation can improve auditory deficit in neglect patients (Jacquin-Courtois et al., 2010; Tissières et al., 2017) and modulate the activation of 447 neural substrate involved in auditory attention in normals (Tissières et al., 2018). Furthermore 448 449 because right posterior parietal cortex is the neural substrate of space representation (Fierro et 450 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.

#### 456 **5** Conclusion

457 The present study showed two main and original results. For the first time, a 458 pseudoneglect bias was observed in auditory perception, with the subjective center of an 459 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 460 461 a leftward optical deviation in musicians. Our results are preliminary, and to better understand 462 the effect of prism adaptation on auditory frequency perception our investigation needs to be 463 extended. In the present study the musical expertise was used a posteriori, but in a future 464 study it could be possible to evaluate the "piano-effect" (Lidji et al., 2007) on the left-to-right 465 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 466 467 frame of the auditory spectrum should be used to study whether effects of prism adaptation 468 are homogeneous throughout the auditory spectrum or whether some auditory frequencies are 469 more sensitive to prism adaptation. Furthermore, the lack of auditory sensitivity to prism 470 adaptation in nonmusicians observed in the present experimental conditions also merits 471 further consideration. Taken together our preliminary work offers theoretical and clinical 472 perspectives for effects of prism adaptation on auditory perception.

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