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Wearing Prisms to Hear Differently:

After-Effects of Prism Adaptation on Auditory Perception

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Abstract

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

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
27 study sensorimotor plasticity is prism adaptation. It consists of pointing to visual targets while
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 / underrepresentation 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 &
50 Pettigrew, 1996; Chokron, Bartolomeo, Perenin, Helft, & Imbert, 1998). Numerous studies
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*

61 Studies using choice-reaction task paradigms showed that stimulus-response
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
67 from left to right (Dehaene, Bossini, & Giraux, 1993). As a result, when judging the distance
68 between two numbers, without using arithmetic, individuals exhibit a pseudoneglect behavior
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,
75 Priftis, Meneghello, Marenzi, & Umilta, 2006). Individuals exhibit a pseudoneglect behavior
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
78 behavior, with a shift in bisection toward the later letters (i.e., to the right) (Nicholls, Kamer,
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*

86 Auditory frequencies induce spatial association as well. As for numbers and alphabetic
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
92 auditory frequencies, stimulus-response compatibility effects in horizontal axis showed faster
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
107 domains as auditory frequencies and on experimental results showing that prism adaptation
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
110 adaptation could act on auditory frequencies perception. More precisely, the space-auditory
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
122 shift the estimated center of the auditory interval toward the higher auditory frequency.

123 **2 Material and Methods**

124 *2.1 Participants*

125 Thirty-six adults participated voluntarily in the experiment. All participants were
126 healthy, with normal or corrected to normal vision, and without auditory deficit. Participants
127 were randomly divided into two groups of 18 participants: Group L (9 females, 9 males, mean
128 age = 22.56, $SE = 0.78$ years), and Group R (11 females, 7 males, mean age = 21.22, $SE =$
129 0.70 years). All participants were right-handed according to the Edinburgh Handedness
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
134 experiment. **Although congenital amusia were not assessed,** none of the participants has
135 reported hearing loss or any difficulties to perform the auditory interval bisection judgment.

136 *2.2 Material and procedure*

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

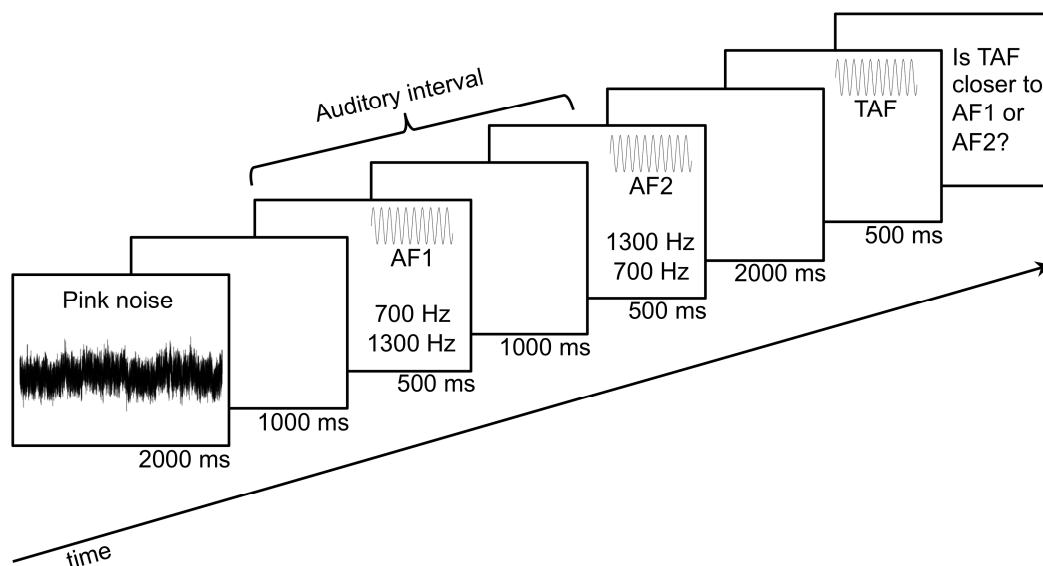
144 For both groups experimental procedure was divided into three periods: the pretest
145 (before prism adaptation: auditory interval bisection judgment and open-loop pointing task),
146 the prism adaptation procedure, and the posttest (after prism adaptation: open-loop pointing
147 task, auditory interval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

148 2.2.1 *Auditory interval bisection judgment*

149 Two auditory frequencies, 700 Hz and 1300 Hz, were used to define an auditory
150 interval, the objective center of which was 1000 Hz. Fifteen other auditory frequencies (800
151 Hz, 850 Hz, 900 Hz, 920 Hz, 940 Hz, 960 Hz, 980 Hz, 1000 Hz, 1020 Hz, 1040 Hz, 1060 Hz,
152 1080 Hz, 1100 Hz, 1150 Hz, and 1200 Hz) were used as target auditory frequencies within
153 the auditory interval. These auditory frequencies were very simple auditory sinewave
154 frequencies, which have no relation to the musical system and its equal temperament. All the
155 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.



177

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

181 2.2.2 Visuomanual open-loop pointing task

182 In the pretest and posttest conditions and at the end of the experiment, 10 open-loop
 183 pointing trials (i.e., without visual control during movement execution) were performed using
 184 liquid crystal goggles to occlude vision during movement execution. A sagittal target (black
 185 sticker dot, diameter 6 mm) was placed 45 cm from the edge of the table. Participants
 186 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
199 diameter) was placed on the nail of the right index fingertip. The spatial resolution for
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

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

215 2.3 *Data Analysis*

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

221 For the auditory interval bisection judgment, two measures were computed. The first
222 one corresponded to the mean percentage of responses indicating proximity to the lower
223 auditory frequency limit of the auditory interval (700 Hz). When AF1 or AF2 of the auditory
224 interval was 700 Hz, and the participant answered “closer” to AF1 or AF2 respectively, the
225 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
235 quoted as 0. The resulting percentages were plotted as a function of the frequency of TAF,
236 from 800 Hz to 1200 Hz. These data were then fitted with a sigmoid function, and the

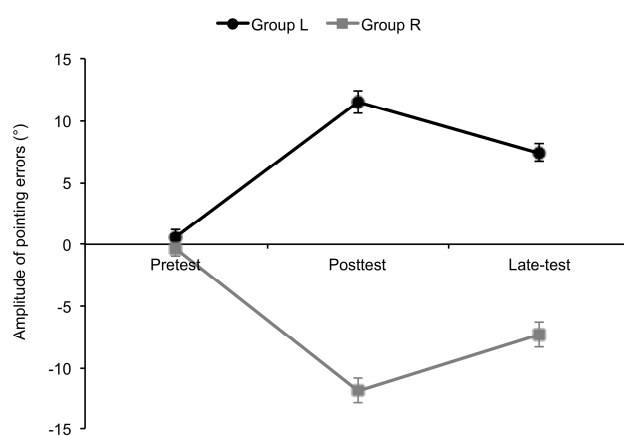
237 frequency value on the x-axis corresponding to the frequency at which the participant
238 provided a percentage of 50% was specified, and corresponded to the subjective center of the
239 auditory interval.

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

242 3 Results

243 3.1.1 Sensorimotor after-effects

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



251
252 Figure 2. Amplitude of visuomanual open-loop pointing errors for pretest and posttest as a function of deviation
253 (Group L, Group R). Error bars indicate standard errors.

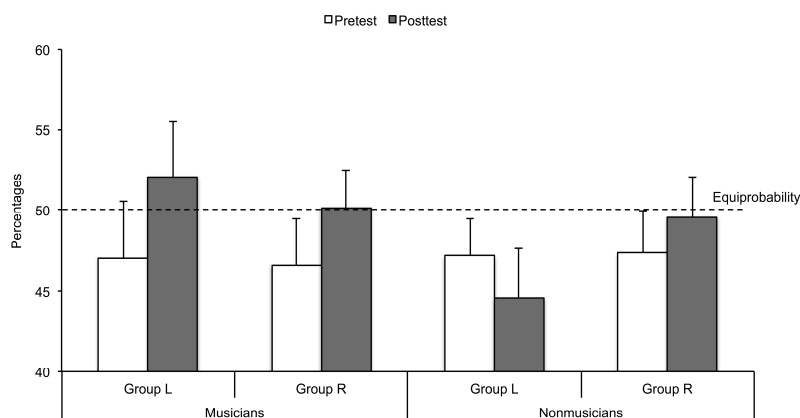
254 3.1.2 *Auditory interval bisection judgment*255 3.1.2.1 *Percentages*

256 *T*-test comparisons were first performed to evaluate whether the mean percentages of
257 responses indicating proximity to the lower auditory frequency limit of the auditory interval
258 were different from 50% in pretest. The mean percentages were significantly lower than 50%,
259 [$M = 47.09$, $SE = 1.31$, $t(35) = -2.22$, $p = .033$, $d = 0.38$].

260 A repeated measures ANOVA with Session (pretest, posttest) as within-subject factor
261 and Deviation (Group L, Group R) as between-subject factor, performed on the percentages
262 of responses indicating proximity to the lower auditory frequency limit of the auditory
263 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
274 referred to as nonmusicians ($N = 22$). Group L was composed of 7 musicians (Musical
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
 278 significantly different from 50%, and there was no significant difference between musicians
 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
 281 Session was observed [$F(1, 12) = 9.259, p = .01, \eta_p^2 = .436$]. Planned comparisons showed a
 282 significant effect of Session for Group L [$F(1, 12) = 6.39, p = .026$], with an increase in
 283 percentages of responses indicating proximity to the lower auditory frequency limit of the
 284 auditory interval for posttest compared to pretest, but not for Group R [$p > .10$]. For the
 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.



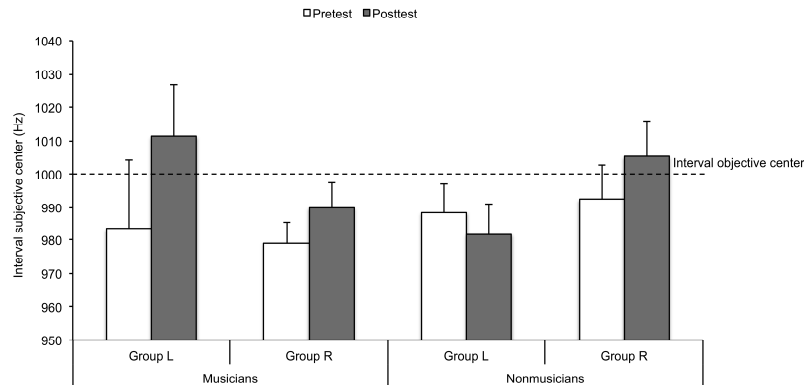
288
 289 Figure 3. Percentages for pretest and posttest as a function of deviation (Group L, Group R) and musical
 290 expertise (musicians, nonmusicians). Error bars indicate standard errors.

291 3.1.2.2 Subjective center

292 *T*-test comparisons were first performed to evaluate whether the mean subjective
 293 center of the auditory interval was different from the objective center (1000 Hz). Taken
 294 together, the mean subjective center of all musicians and nonmusicians was significantly
 295 lower than 1000 Hz, [$M = 986.84, SE = 5.69, t(35) = -2.314, p = .027, d = 0.39$].

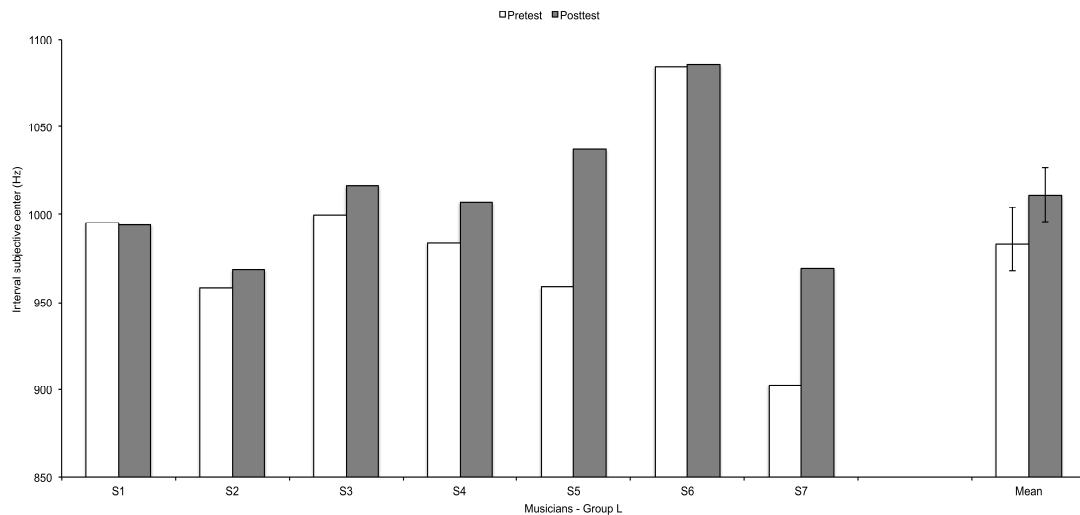
296 A 2×2 (Session [pretest, posttest] \times Deviation [Group L, Group R]) repeated
 297 measures ANOVA showed no significant effects [$p > .10$]. As for percentages, we expected
 298 to find a shift of the auditory interval toward the higher auditory frequency for all participants
 299 irrespectively of their musical expertise. Nevertheless the identification a posteriori of two
 300 groups of participants (musicians and nonmusicians) allowed detailing the results. Figure 4
 301 displayed the results for musicians and nonmusicians. Taken separately, the subjective center
 302 of neither musicians nor nonmusicians was significantly different from 1000 Hz [$M = 981.20$,
 303 $SE = 10.53$, $t(13) = -1.785$, $p = .098$; $M = 990.43$, $SE = 6.55$, $t(21) = -1.460$, $p = .159$,
 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,
 306 posttest] \times Deviation [Group L, Group R]) repeated measures ANOVA, conducted for
 307 musicians, showed a significant effect of Session [$F(1, 12) = 7.189$, $p = .02$, $\eta_p^2 = .375$].

308



309 Figure 4. Subjective center for pretest and posttest as a function of deviation (Group L, Group R) and musical
 310 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 [$p < .10$].



314

315 Figure 5. Subjective center for pretest and posttest as for the musicians of the Group L. Error bars indicate
 316 standard 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

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
335 whether frequencies were uniformly represented throughout an auditory interval or whether
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
341 consider the spatial continuum representation of auditory frequencies from left to right (with
342 low frequencies on the left and high frequencies on the right), this bias corresponds with a
343 pseudoneglect expression on auditory frequency perception.

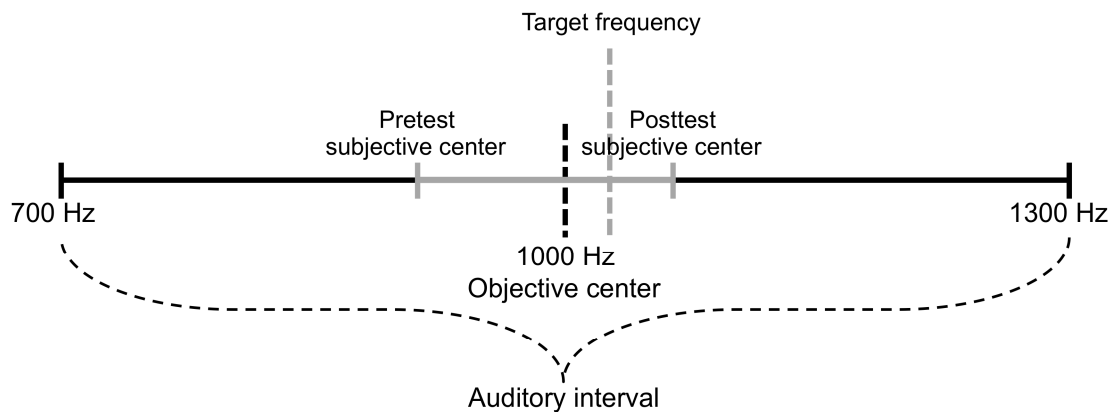
344 Pseudoneglect is well documented in space representation (e.g., McCourt & Jewell,
345 1999). The tendency to be biased toward the left-hand side of space is a robust and consistent
346 behavior classically described in visuospatial line-bisection task where participants are asked
347 to indicate 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

357 memory (McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007), or when they had to
358 completely build novel mental representations created from aural-verbal descriptions (Brooks,
359 Logie, McIntosh, & Della Sala, 2011). Pseudoneglect occurs on the representation of stimuli
360 with spatial association such as numbers (Loftus, Nicholls, et al., 2009; Longo & Lourenco,
361 2007) or alphabetic letters (Gevers et al., 2003; Zorzi et al., 2006) that are represented along a
362 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
370 frequencies from left to right, the pseudoneglect observed on auditory interval bisection is a
371 coherent result.

372 4.2 *Prism adaptation acts on auditory perception*

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



380

381 Figure 5. A representation of the shift of subjective center observed in musicians after prism adaptation to a left
 382 optical deviation.

383

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 pretest 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 (pseudoneglect) 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,
416 Webeling, ter Wal, Groet, & van Zandvoort, 2004) and pain perception (Sumitani et al.,
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.

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

426 Danckert, Ferber, & Goodale, 2008; Luauté et al., 2009), whereas the anterior intraparietal
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
435 substrate of cognitive after-effects that could also support the present results (Chapman et al.,
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
443 system (right hemisphere activation) and dorsal attentional system (left hemisphere
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
447 patients (Jacquin-Courtois et al., 2010; Tissières et al., 2017) and modulate the activation of
448 neural substrate involved in auditory attention in normals (Tissières et al., 2018). Furthermore
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

451 representation (Lidji et al., 2007; Rusconi et al., 2006), the effect of prism adaptation on the
452 right posterior parietal cortex could explain the change in auditory perception. Furthermore the
453 right temporal cortex being directly involved in pitch perception (Hyde, Peretz, & Zatorre,
454 2008; Peretz & Zatorre, 2005), effect of prism adaptation on temporal cortex could also
455 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
460 subjective center toward the higher frequency limit of the auditory interval after adaptation to
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
466 directly comparing a group of pianists with a group of nonpianists. Furthermore a larger
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.

473 6 References

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