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1 **Unilateral vestibular deafferentation impairs** 2 **embodied spatial cognition**

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35 **Abstract**

1
2 36 A growing number of studies indicate that cognitive complaints are common in patients with peripheral
3
4 37 vestibular disorders. A better understanding of how vestibular disorders influence cognition in these
5
6 38 patients requires a clear delineation of the cognitive domains affected by vestibular disorders. Here, we
7
8 39 compared the consequences of left and right vestibular neurectomy on third-person perspective taking
9
10 40 – a visuo-spatial task requiring mainly own-body mental imagery, and on 3D objects mental rotation
11
12 41 imagery – requiring object-based mental imagery but no perspective taking. Patients tested one week
13
14 42 after a unilateral vestibular neurectomy and a group of age- and gender-matched healthy participants
15
16 43 played a virtual ball-tossing game from their own first-person perspective (1PP) and from the
17
18 44 perspective of a distant avatar (third-person perspective, 3PP). Results showed larger response times in
19
20 45 the patients with respect to their controls for the 3PP taking task, but not for the 1PP task and the 3D
21
22 46 objects mental imagery. In addition, we found that only patients with left vestibular neurectomy
23
24 47 presented altered 3PP taking abilities when compared to their controls. This study suggests that
25
26 48 unilateral vestibular loss affects mainly own-body mental transformation and that only left vestibular
27
28 49 loss seems to impair this cognitive process. Our study also brings further evidence that vestibular signals
29
30 50 contribute to the sensorimotor bases of social cognition and strengthens the connections between the so
31
32 51 far distinct fields of social neuroscience and human vestibular physiology.

33 52

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35 54

36 55 **Keywords**

37 56 Perspective taking, Vestibular system, Unilateral vestibular loss, Mental imagery, 3D object mental
38 57 rotation

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58 Introduction

59 A growing number of studies indicate that cognitive complaints are common in patients with vestibular
60 disorders (reviewed in [1, 2]). For example, a recent epidemiological study in US adults revealed that
61 patients with vestibular vertigo have an eight-fold increase in the odds of reporting impaired memory
62 and attention, limiting their activities [3]. A better understanding of how vestibular disorders influence
63 cognition in these patients requires a clear delineation of the cognitive domains affected by vestibular
64 disorders. Yet, the paucity of publications reporting negative findings makes it difficult to identify the
65 cognitive domains impaired and spared in patients with vestibular disorders.

66 Several studies have compared populations of patients with vestibular disorders and controls,
67 with mixed findings depending on the aetiology, on unilateral vs bilateral vestibular loss, history of the
68 disease and the cognitive task. Popp *et al.* [4], for example, showed that bilateral vestibular loss impaired
69 visuospatial abilities, processing speed, short-term memory and executive functions, whereas unilateral
70 vestibular loss impaired only visuospatial abilities and processing speed. Spatial memory was impaired
71 in navigation studies using locomotion [5] and virtual reality tasks [6]. Vestibular disorders also
72 impaired space representation when participants were not moving or displaced at all, such as during
73 mental rotation of bodies and non-corporeal objects [7–10]. We note that it remains unclear from these
74 studies if vestibular disorders impair more egocentric (*i.e. own-body*) mental imagery or object-based
75 mental imagery.

76 Another debated question concerns the consequences of left vs right peripheral vestibular
77 disorders on cognition. A rationale for this question is the anatomical and functional asymmetry within
78 the vestibulo-thalamo-cortical system. Neuroimaging studies have reported a predominance of
79 vestibular processing in the right cerebral hemisphere in right-handed participants, and an overall
80 dominance of the projections from one labyrinth to the ipsilateral cerebral hemisphere [11, 12]. As
81 various cognitive tasks involve differently lateralized brain areas, different effects of left and right
82 vestibular disorders on cognition can be predicted. Only few studies have tackled directly this question,
83 and overall their findings were controversial, showing stronger impairments in left [13] or right [14]
84 vestibular disorders, or equal impairments in left and right vestibular disorders [4].

85 The present study aims at clarifying the vestibular contributions to visuo-spatial perspective
86 taking. While the environment is usually experienced from an egocentric *first-person perspective* (1PP),
87 humans can simulate someone else’s viewpoint, referred to as *third-person perspective* (3PP) taking.
88 3PP taking is an important component of social cognition which contributes to understand others and
89 anticipate their actions. There is evidence suggesting that 3PP taking is a strongly embodied process
90 involving egocentric mental imagery [15]. Here, we compared patients one week after right or left
91 vestibular neurectomy and healthy participants involved in a virtual ball-tossing game [16, 17] played
92 either from their own viewpoint (1PP), or from the viewpoint of a distant avatar – thus requiring 3PP
93 taking. Patients were tested in the acute stage of a unilateral vestibular deafferentation, when brain

94 metabolism disorganization is maximal [18], to document the impact of the vestibular tone imbalance
95 on 3PP taking abilities. Performances were compared to those from 3D objects mental rotation, requiring
96 object-based mental imagery, but no perspective-taking. Given evidence of a vestibular contribution to
97 the perspectival experience [16, 19, 20], and overlapping neural mechanisms for vestibular information
98 processing and perspective-taking [21], we hypothesized that unilateral vestibular deficits would impair
99 3PP taking more than object-based mental imagery.

102 **Methods**

103 **Patients**

104 We tested 23 patients (13 women; mean age \pm SD: 51 ± 12 years) before and 7 days after a unilateral
105 vestibular neurectomy. Cognitive tests were performed 7 days after the surgery. All patients were right-
106 handed (Edinburgh Handedness inventory: $79 \pm 22\%$). Twenty-one patients were operated on for an
107 acoustic neuroma (grade 2, 3 or 4 from Koos classification [22]) and two patients for Menière's disease
108 (**Table 1**). Menière's disease patients had a pure unilateral vestibular pathology, with normal video head
109 impulse test (vHIT) and hearing on their contralesional ear. Twelve patients received a left neurectomy
110 and 11 a right neurectomy using the retrosigmoid approach ($n = 20$) or the translabyrinthine approach
111 ($n = 3$). Depending on the size of the neuroma and the operating approach, the neurectomy aimed at
112 removing the vestibular nerve totally ($n = 19$) or partially ($n = 4$). Before and 7 days after neurectomy,
113 patients received standard otoneurological examinations including a pure tone audiometry (SCR
114 Electroniques, France), a bithermal caloric test and a vHIT (Synapsys, France), as well as measurement
115 of vestibulo-ocular responses on a rotating chair (Synapsys, France) and of the subjective visual vertical
116 (Framiral, France). Patients were compared to 23 age- and gender-matched healthy volunteers (13
117 women, 52 ± 12 years). They were right-handed ($86 \pm 25\%$) and had no history of otoneurological and
118 psychiatric disease.

120 **Ethics statement**

121 All participants were informed about the study and gave their written informed consent. Experimental
122 procedures were approved by the local Ethics Committee (CPP Sud-Méditerranée II, 2011-A01221-40)
123 and followed the Declaration of Helsinki.

125 **Visual stimuli and tasks**

126 **3PP taking task.** Participants were involved in a virtual ball-tossing game [16]. Visual stimuli showed
127 6 avatars around a circle (see **Figure 1A** and the legend, for details). Participants were instructed to
128 adopt the perspective of the avatar holding the ball (identified by a blue T-shirt) and from this position
129 to toss the ball to the avatar wearing a red T-shirt. They indicated as quickly and as accurately as possible

130 whether they had to toss the ball to the right or left, by pressing on a respond pad [16]. There was no
131 time limit to answer. The experiment was a 5 *Angle of visuo-spatial perspective taking* (5 positions of
132 the avatar holding the ball: $\pm 60^\circ$, $\pm 120^\circ$ and 180°) \times 4 *positions of the avatar* receiving the ball ($\pm 60^\circ$
133 and $\pm 120^\circ$ with respect to the avatar holding the ball) design, with four repetitions of each of the 20
134 stimuli. Participants completed 80 trials divided into 4 blocks of 20 trials presented in a random order.

135
136 **1PP task.** Five avatars were shown in the visual scene (**Figure 1B**) and the hands holding the ball in the
137 front of the scene indicated that participants had to toss the virtual ball from their 1PP [16]. Participants
138 indicated as quickly and accurately as possible whether they had to toss the ball to their right or left (to
139 the avatar located at $\pm 60^\circ$, $\pm 120^\circ$) without time limit. Each of the four visual stimuli was repeated four
140 times in one block of 16 trials presented in a random order.

141
142 **Visual detection task.** A visual detection task [16] was used to control for potential attentional and visual
143 differences between groups of participants (**Figure 1C**). In 10 trials, one avatar held a ball, while in 10
144 other trials, no ball was shown. Participants were instructed to detect as quickly and as accurately as
145 possible that there was a ball in the visual scene, without time limit. Participants completed one block
146 of 20 trials presented in a random order.

147
148 **3D objects mental rotation task.** Twenty out of 23 patients were involved in a 3D objects mental rotation
149 task [9]. Pairs of identical or different 3D objects were presented side by side on a computer screen
150 (**Figure 1D**). When identical, the second object was rotated with respect to the first object by 20° , 40°
151 or 80° . We instructed participants to imagine a rotation of one of the objects to align it with the other
152 and to indicate as quickly and as accurately as possible whether the objects were identical or different.
153 There was no time limit to answer. There were two blocks of 36 pairs of objects, of which 24 were
154 identical and 12 were different. Pairs of objects were presented randomly within each block, and the
155 presentation of the blocks was counterbalanced.

156 157 **Experimental procedures**

158 Participants were tested while comfortably sitting on a chair with their head maintained by a forehead
159 and chin rest. SuperLab 4.5 (Cedrus Corporation, USA) was used to present visual stimuli on a computer
160 screen (64.4×49.4 cm) placed 50 cm in front of the participants. Thirteen patients and controls first
161 completed the 1PP task and then the 3PP taking task, while the others started with the 3PP taking task.
162 All participants finished with the visual detection task and the 3D objects mental rotation task.
163 Participants took short breaks after each block and task. Before the experiment, they trained to each task
164 with a random selection of 10 trials. **After the experiment, participants filled out a questionnaire about
165 the strategies they used. They indicated whether it happened during the experiment they imagined**

166 rotating the entire visual scene with the avatars to solve the 3PP taking task. If it was the case, they were
167 asked to rate how often they did it, using a 7-point Likert scale ranging from ‘rarely’ to ‘all the time’.

170 Data analysis

171 For each participant and task, we calculated the mean response times (RTs) and percentage of errors.
172 Trials yielding incorrect answers were discarded from the analysis of the RTs and we excluded trials for
173 which RTs exceeded 2 standard deviations of the participant’s grand average. As the Shapiro-Wilk test
174 revealed not normally distributed RTs for most of the dependent variables, we used a log transformation
175 and applied repeated-measures ANCOVA when this procedure led to normal distribution. Variables that
176 remained non-normally distributed and the percentage of errors were analysed using non-parametric
177 procedures (SPSS 25, IBM Corporation, USA). Differences were considered significant when $P < 0.05$.
178 One outlier participant was excluded for the 3PP taking task (RTs > 16 s), as well as one participant for
179 the 1PP and visual detection tasks, resulting in a total of 22 patients and 22 controls in the final analysis.

180 We used partial correlations to calculate the relation between 13 clinical parameters (Table 1)
181 and performance in the cognitive tasks. To minimize the risk of false positives, we used Bonferroni-
182 corrected α level of $P < 0.05/13$ for statistical significance ($P < 0.0039$).

185 Results

186 3PP taking task

187 **Response times.** RTs were first analysed using a repeated-measures ANCOVA with Angle of 3PP taking
188 as within-subject factor, Group and Gender as between-subject factors, and Age as covariate. Age was
189 significantly related to RTs ($F_{1,39} = 12.19$, $P < 0.005$), whereas Gender was not ($F_{1,39} = 0.08$, $P = 0.77$).
190 Importantly, we found a significant effect of the Group after controlling for the effect of Age ($F_{1,39} =$
191 4.40 , $P < 0.05$). **Figure 2A** shows significantly larger RTs for 3PP taking in patients than in controls.
192 As expected, the analysis shows a significant effect of the Angle of 3PP taking ($F_{3,107} = 2.78$, $P < 0.05$),
193 with longer RTs for larger angles of perspective taking (Greenhouse-Geisser correction, $\epsilon = 0.69$). There
194 was no significant interaction between Angle and Group, or with the covariate. RTs were not
195 significantly related to the grade of the neuroma (Kruskal-Wallis test, $P > 0.05$) (**Figure 2B**).

196 In a second analysis, we explored how the side of neurectomy influenced 3PP taking. We found
197 that patients with left neurectomy showed significantly larger RTs than their age and gender-matched
198 controls ($F_{1,17} = 6.81$, $P < 0.05$) (**Figure 2A**). There was no other significant main effect or interaction,
199 but Age was significantly related to RTs ($F_{1,17} = 8.04$, $P < 0.05$). By contrast, patients with right
200 neurectomy did not differ from their controls ($F_{1,17} = 0.04$, $P = 0.84$) (**Figure 2A**). The effect of Angle
201 of 3PP taking was not significant after Greenhouse-Geisser correction ($F_{2,38} = 2.53$, $P = 0.09$), but the

202 effect of Age was significant ($F_{1,17} = 7.74, P < 0.05$). Direct comparison of patients' performance with
203 left and right neurectomy did not reveal significant differences in RTs ($F_{1,17} = 2.42, P = 0.14$). Thus, the
204 effect of Group observed in the whole-population analysis seems to arise from altered 3PP taking mainly
205 in patients with left neurectomy. We note that this result cannot be accounted for by different **vestibular**
206 **functions** in patients with left and right neurectomy (see **Table 1**).

207
208 **Errors.** Friedman's tests revealed an effect of the Angle of 3PP taking on the percentage of errors in
209 patients ($\chi^2_{(4)} = 25.7, P < 0.001$) and controls ($\chi^2_{(4)} = 37.8, P < 0.001$) (**Figure 2C**). However, Mann-
210 Whitney tests did not reveal a significant effect of the Group ($-60^\circ: P = 0.13; -120^\circ: P = 0.16; 180^\circ: P$
211 $= 0.33; +120^\circ: P = 0.44; +60^\circ: P = 0.08$).

212
213 **Questionnaire about 3PP taking strategies.** 18/22 patients (82%) and 19/22 controls (86%) reported
214 they never imagined rotating the entire visual scene to solve the task, whereas 4/22 patients (18%) and
215 3/22 controls (14%) reported they "sometimes" imagined rotating the visual scene. No participant
216 reported having used this strategy "all the time". Strategies were reported in similar proportion in the
217 whole sample of patients and controls ($\chi^2 = 0.17, P = 0.68$), and in similar proportion in patients with
218 left and right vestibular neurectomy ($\chi^2 = 1.22, P = 0.27$).

219 **First-person perspective task**

220
221 RTs between the whole sample of patients and the controls did not differ (Mann-Whitney test, $U = 244,$
222 $P = 0.55$) (**Figure 2D**). Similar analyses for patients with left and right neurectomy revealed no
223 differences between the groups (left: $U = 22, P = 0.15$; right: $U = 40, P = 0.48$). As the percentages of
224 errors were very low, they were not analysed.

225 **Visual detection task**

226
227 RTs were significantly longer in the whole sample of patients when compared to the controls (Mann-
228 Whitney test, $U = 287, P < 0.05$) (**Figure 2D**). RTs differed between the patients with left neurectomy
229 and their controls ($U = 113, P < 0.05$), but they were not different between the patients with right
230 neurectomy and their controls ($U = 40, P = 0.63$). As the percentages of errors were very low, they were
231 not analysed.

232 **3D objects mental rotation**

233
234 **Response times.** A repeated-measures ANCOVA revealed a significant main effect of Angular disparity
235 (Greenhouse-Geisser correction, $\epsilon = 0.67: F_{1,3,47} = 18.95, P < 0.0001$), with longer RTs for larger angles
236 of mental rotation. In contrast with the 3PP taking task, there was no significant effect of the Group
237 ($F_{1,35} = 0.15, P = 0.71$) (**Figure 3A**). We found no significant effect of Age ($F_{1,35} = 3.07, P = 0.09$) and

238 Gender ($F_{1,35} = 0.47, P = 0.50$), but there was a significant interaction of Angular disparity \times Age ($F_{1,3,47}$
239 $= 3.01, P < 0.05$). Similar analyses conducted separately for patients with left and right neurectomy
240 revealed no effect of the Group (left: $F_{1,15} = 0.09, P = 0.78$; right: $F_{1,15} = 0.03, P = 0.87$) (**Figure 3A**).

241
242 **Errors.** Friedman's tests revealed a significant effect of Angular disparity in patients ($\chi^2_{(2)} = 27.3, P <$
243 0.0001) and in controls ($\chi^2_{(2)} = 22.7, P < 0.0001$), with more errors for larger angles of mental rotation
244 (**Figure 3B**). Mann-Whitney tests showed a statistical trend for higher percentage of errors in patients
245 than in controls for 20° ($U = 269, P = 0.06$), but not for 40° ($U = 249, P = 0.19$) and 80° ($U = 260, P =$
246 0.11).

247 **Clinical data and their correlation with visuo-spatial cognition**

248 **Table 1** shows that overall the two groups of patients did not differ with respect to their clinical
249 status, with the exception of worse postural performance in patients with right than left vestibular
250 loss, and a larger proportion of cophosis at D+7 in the patients with left vestibular neurectomy. There
251 was an important variability in the presurgical vestibular functions, owing to the different locations
252 and grades of the neuroma [22]. Thus, we calculated partial correlations between clinical parameters
253 and cognitive performance, while controlling for the effects of age (as RTs for 3PP taking were
254 related to age). There was no significant correlation between clinical parameters and cognitive
255 performance at a Bonferroni-corrected α level. The only statistical trend was a positive correlation
256 between the deficit at the caloric test measured at D-1 and the average RTs (log transform) for the
257 3PP taking task ($r = 0.596, P = 0.007$). No such trend was found for the correlation between the other
258 cognitive tasks and clinical parameters recorded at D-1 and D+7.

260 **Discussion**

261 **Different effect of vestibular disorders on egocentric vs object-based mental imagery**

262 The present data show that patients tested one week after unilateral vestibular neurectomy had impair
263 3PP taking abilities, as revealed by longer RTs in patients than in controls. Interestingly, no deficit was
264 found when patients were required to toss the virtual ball from their 1PP, that is, when no own-body
265 mental transformation was necessary. This indicates that deficits in 3PP taking were not merely related
266 to attentional or oculomotor deficits to explore the visual scene and to discriminate left/ right orientations
267 (**see below**). Rather, our results speak in favour of a more specific vestibular contribution to perspective
268 taking and highlight the specific role of vestibular information in embodied spatial cognition [23].
269 Another recent study, in which patients with objective balance deficits were required to imitate lateral
270 body tilts of an avatar, showed longer movement latencies and more errors in the patients [7]. Our results

274 are also in line with a previous study in healthy participants using the same 3PP taking task, showing
275 that natural vestibular stimulation (on a rotating chair) helped to adopt the perspective of a distant avatar
276 when the directions of the physical rotation and simulated viewpoint were congruent [16].

277 Although our participants were trained to use explicitly own-body mental imagery during the
278 3PP taking task, we cannot exclude that some of them used other strategies, such as simulating a ‘bird
279 perspective’ of the visual scene or mixed egocentric/allocentric strategies depending on the avatar’s
280 position. Debriefing questionnaires confirmed that most participants complied to the instructions and
281 used mainly an egocentric strategy. Importantly, as mixed egocentric/allocentric strategies were reported
282 in similar proportions in the patients and the controls, strategies cannot account for the different 3PP
283 taking abilities between the groups.

284 In contrast with the 3PP taking task, the unilateral vestibular neurectomy had no effect on 3D
285 object mental imagery. There are only few studies about the consequences of vestibular disorders on
286 object-based mental imagery and they showed divergent results. Impaired object-based mental imagery
287 seems to depend on the extent of the vestibular loss, as patients with bilateral loss were the most impaired
288 [8, 9], and on the compensation stage, as deficits were found only in the early stage after vestibular
289 neurectomy [9, 10].

290 Altogether, our data suggest that acute unilateral vestibular deficits affect differently visuo-
291 spatial tasks involving mostly egocentric mental imagery (3PP taking) and object-based mental imagery.
292 We propose that shared neural networks are involved in encoding own-body rotations (vestibular cortical
293 network) and in simulating own-body and viewpoint rotations (3PP taking). This proposition is first
294 supported by our previous results in healthy participants showing that whole-body rotations on a rotating
295 chair influenced 3PP taking in a direction-specific way, but not object-based mental imagery [16].
296 Second, a recent fMRI study [21] showed that clockwise/counterclockwise mental rotation of the
297 observer’s viewpoint (as used in our 3PP taking task) and galvanic vestibular stimulation both activated
298 the bilateral posterior insular cortex and the right parietal operculum (OP2), two core areas of the
299 vestibular cortical network.

300 **Different effect of right vs left vestibular disorders on perspective taking**

301 A main result of the present study is that 3PP taking abilities depended on the side of vestibular
302 deafferentation. Only patients with left neurectomy showed larger RTs in the 3PP taking task, when
303 compared to their controls. This was not the case when visuo-spatial judgements were performed from
304 their 1PP. However, patients with left neurectomy were also slower for the visual detection task. This
305 indicates that left vestibular loss is more likely to disturb the mechanisms of egocentric own-body mental
306 imagery and alertness than the mechanisms of visuo-spatial tasks that do not require egocentric mental
307 imagery (i.e., 1PP task and 3D object mental rotation). It is difficult to compare our data with previous
308 studies as only few of them have investigated spatial cognition with respect to the side of the vestibular
309 loss. In line with our findings, Saj *et al.* [13] found that only left vestibular neurectomy significantly
310

311 deviated the perceived straight ahead. Left cathodal galvanic vestibular stimulation also impaired mental
1 312 imagery in healthy participants [24], while only left-warm caloric vestibular stimulation distorted their
2 313 body schema [25]. However, opposite data have been reported, with slower recovery of the subjective
3 314 visual vertical in right vestibular neuritis [26], and a **trend** for poorer spatial navigation in right vestibular
4 315 deficits [14]. **Another study reported no effect of the side of the vestibular loss on cognitive deficits [4].**
5 316 The discrepancy between these data may be related to the diversity of the spatial functions tested,
6 317 involving different brain areas.

11 318 Why would left vestibular neurectomy impair 3PP taking? Neuroimaging studies have
12 319 emphasized a right hemispheric dominance of vestibular processing in right-handed participants [11] –
13 320 as were our participants. Accordingly, a stronger impact of right vestibular neurectomy on 3PP taking
14 321 can be expected. Our results do not support this hypothesis. However, they are in line with neuroimaging
15 322 data showing different compensation patterns in acute right and left vestibular neuritis, with a shift of
16 323 the dominant ascending input from the ipsilateral to the contralateral pathways [18]. Alternatively, based
17 324 on results from a diffusion tensor imaging study of the vestibulo-thalamo-cortical pathways [12], we
18 325 predict that right vestibular neurectomy would predominantly disrupt multisensory processing in the
19 326 right parieto-insular cortex, whereas left neurectomy is more likely to disrupt multisensory processing
20 327 *bilaterally* in this area. We propose that left vestibular neurectomy evoked deficits in 3PP taking by
21 328 disrupting bilateral areas underpinning 3PP taking. Of note, an fMRI study [17] described the neural
22 329 correlates of 3PP taking in a virtual ball-tossing game similar to that used in the present study. 3PP
23 330 taking, when compared to 1PP, activated bilaterally the anterior insula and medial frontal cortices, as
24 331 well as the left inferior parietal lobe. As 3PP taking involves a bilateral network of insular and parieto-
25 332 frontal areas, we anticipate that it is very likely more affected by predominantly bilateral vestibulo-
26 333 thalamo-cortical projections from the left vestibular receptors [12].

38 334 **Role of visuo-spatial attention and alertness**

40 335 **Patients had longer RTs than controls in the visual detection task, and RTs for the 3PP taking task and**
41 336 **the visual detection task were larger after left than right vestibular neurectomy. As previous studies have**
42 337 **related vestibular loss to poorer visuo-spatial ability and attention [27], we cannot exclude that larger**
43 338 **attentional deficits in patients with left neurectomy contributed to larger RTs for 3PP taking. However,**
44 339 **as RTs were not larger for the 1PP task and the 3D-object mental imagery task in these patients, we can**
45 340 **rule out a general effect of attentional deficits in all tasks after left neurectomy. We interpret increased**
46 341 **RTs in the visual detection task as resulting from deficits of alertness (because RTs were short, around**
47 342 **750 ms, whereas RTs were around 3000 ms for 3PP taking). Visual detection assessed more alertness**
48 343 **(reaction times) than high-level visuo-spatial cognition. Our results are consistent with data showing**
49 344 **that patients with unilateral vestibular loss performed worse than healthy controls in a processing speed**
50 345 **task [4].**

348 **Relation between clinical and behavioural data**

349 We only found a statistical trend for slower 3PP taking in patients with larger deficits at the presurgical
350 caloric test. This relation suggests that information from the lateral semicircular canals, or the normal
351 functioning of the structures processing this information, is involved in own-body mental rotation in the
352 yaw plane. The caloric test delivers low-frequency stimulation of the canals and assesses vestibular
353 pathways that are likely relevant for the cognitive functions tested here. Interestingly, stimulation of the
354 lateral canals by whole-body rotation influenced RTs for 3PP taking in a direction-dependent manner
355 [16] and caloric vestibular stimulation improved own-body mental imagery in healthy participants [28].
356 Our data are congruent with observations in patients with unilateral vestibular disorders showing that
357 lower caloric response correlated with deficits in processing speed, memory and executive function [4].
358 Finally, we found no correlation between hearing loss and performance in the cognitive tasks, congruent
359 with recent findings showing similar performance in deaf signers and hearing nonsigners engaged in
360 visuo-spatial perspective-taking, 3D object mental rotation and spatial orientation tasks [29].

362 **Limitations of the study and perspectives**

363 A limitation of the present study is the absence of detailed neuropsychological evaluation of the
364 participants, which could have accounted for some variability in our data. However, the mean age in our
365 sample was not high, controls were selected to carefully match the patients, and our statistical analyses
366 controlled for the effect of age.

367 The present study documents deficits of spatial cognition only in the acute stage of a unilateral
368 vestibular neurectomy. This was motivated by the need to better understand the domains of cognition
369 affected and spared when a vestibular tone imbalance is present, i.e. when compensatory mechanisms
370 are not fully expressed. There is evidence of brain disorganization in the acute stage of a unilateral
371 vestibular loss, both in humans [18] and animal [30] models. It is unknown if the deficits in 3PP taking
372 reported here vanish when patients have compensated from their unilateral vestibular disorder. Future
373 studies should endeavor to explore the postlesional recovery of spatial cognition deficits after unilateral
374 vestibular deafferentation and compare its time course to that of functional recovery.

375 As in most studies of this kind, a limitation of the present study is the sample size, which may
376 explain some discrepancies in the literature regarding the effects of left and right vestibular loss on
377 cognition [4, 13, 14, 26], in addition to the variety of tasks and procedures used. Studies remain to be
378 conducted in large samples of patients to determine the effects of left vs right vestibular loss on a large
379 range of spatial cognitive functions.

381 **Conclusions**

382 The present study shows that acute unilateral vestibular deafferentation impairs embodied spatial
383 cognition by disrupting visuo-spatial tasks involving mostly egocentric mental imagery (3PP taking),
384 but not object-based mental imagery. These effects were observed only in patients with left vestibular

385 loss. We believe that the present investigation helps understand the cognitive complaints of patients with
1 386 vestibular disorders. Finally, our data brings further evidence that vestibular signals contribute to several
2 387 sensorimotor bases of social cognition, including 3PP taking, and strengthens the connections between
3 388 the so far distinct fields of social neuroscience and human vestibular physiology (for a perspective, see
4 389 [23]).
5 390
6 391

11 392 **Acknowledgements**

13
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17 396 consciousness').
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22 399 **Compliance with ethical standards**

23
24 400 **Conflicts of interest.** C. Lopez serves as an associate editor of *Frontiers in Integrative Neuroscience*
25 401 and guest editor of *Frontiers in Neurology*.
26 402
27 403

28 404 **Ethical standard.** Ethical approvals have been obtained from the local ethics committees (Comité de
29 405 Protection des Personnes Sud-Méditerranée II, 2011-A01221-40) and participants provided informed
30 406 consent in accordance with the Declaration of Helsinki.
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Figure legends

Figure 1. Visual stimuli and tasks. (A) Example of a visual scene for the 3PP taking task showing six avatars located around a circle (adapted from Ref. [16]). One avatar was facing the participants (180°), one was seen from the back (0°), two were on their right (60° and 120°), and two on their left (-60° and -120°). From one trial to another, the colour of the avatars' T-shirt could change (white, red or blue). Participants were instructed to simulate the visuo-spatial perspective of the avatar holding the ball (identified by a blue T-shirt) and from this position to toss the ball to the avatar wearing a red T-shirt. The avatar with the blue T-shirt was located either at $\pm 60^\circ$, $\pm 120^\circ$ or 180° (but never at 0° , to avoid confusion with the 1PP task), resulting in a total of 5 angles of 3PP taking. The avatar wearing the red T-shirt was located 60° or 120° to the right or left of this avatar. Participants pressed a key on a response pad (RB-830, Cedrus Corporation, San Pedro, USA) with their right middle finger to toss the ball to the right, or their right index finger to toss the ball to the left. A fixation cross was presented during 1 s before each visual scene. In the example presented, the correct response is to toss the ball to the left. (B) Example of a visual scene for the 1PP task showing five avatars located around a circle. One avatar was facing the participants (180°), two were on their right (60° and 120°), and two on their left (-60° and -120°). Participants were instructed to toss the ball to the avatar wearing a red T-shirt, which was located at $\pm 60^\circ$ or $\pm 120^\circ$ from their viewpoint (4 visual stimuli). Participants pressed a key with their right middle finger to toss the ball to the right, or their right index finger to toss the ball to the left. A fixation cross was presented during 1 s before each visual scene. The correct response here is to toss the ball to the right. (C) Example of a visual scene for the visual detection task. Visual stimuli were the same as for the 3PP taking task, except that all avatars wore a white T-shirt. Thirteen participants had to press a button with their right middle finger as soon as they detected a ball, or with their right index finger when they detected there was no ball, and vice versa for the other participants. A fixation cross was presented during 1 s before each visual scene. The correct response here is "yes", as there is a ball in the scene. (D) Example of a visual stimulus for the 3D objects mental rotation. Half of the participants pressed a button with their right middle finger if objects were identical, or with their right index finger if they were different, and vice versa for the others. The correct response here is "no", as the objects were different.

Figure 2. Influence of unilateral vestibular deafferentation on visuo-spatial perspective taking. (A) Mean response times for the 3PP taking task are plotted separately for the whole population of patients (left part), for the patients with left vestibular neurectomy (central part) and the patients with right vestibular neurectomy (right part) together with their age- and gender-matched control participants. Error bars represent the standard error of mean. * indicates statistical significance between the patients and their controls ($P < 0.05$). (B) Mean response times for the 3PP taking task are illustrated for the patients as a function of the vestibular pathology. (C) Box-and-whisker plots illustrate the percentage of

456 errors in the whole sample of participants. The top and bottom ends of the whisker represent the 95th and
1 457 5th percentiles of the distribution and the horizontal line inside the box represents the median. (D)
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3 458 Response times for the 1PP task and the visual detection task are plotted for the whole sample of patients.
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5 459 Same conventions as for Parts C.

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8 461 **Figure 3.** Influence of unilateral vestibular deafferentation on 3D objects mental rotation. (A) Mean
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10 462 response times for the mental rotation of 3D objects are plotted separately for the whole population of
11 463 patients (left part), for the patients with left vestibular neurectomy (central part) and the patients with
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13 464 right vestibular neurectomy (right part) together with their age- and gender-matched control participants.
14
15 465 Error bars represent the standard error of mean. (B) Box-and-whisker plots illustrate the percentage of
16 466 errors in the whole sample of participants. The top and bottom ends of the whisker represent the 95th and
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18 467 5th percentiles of the distribution and the horizontal line inside the box represents the median.

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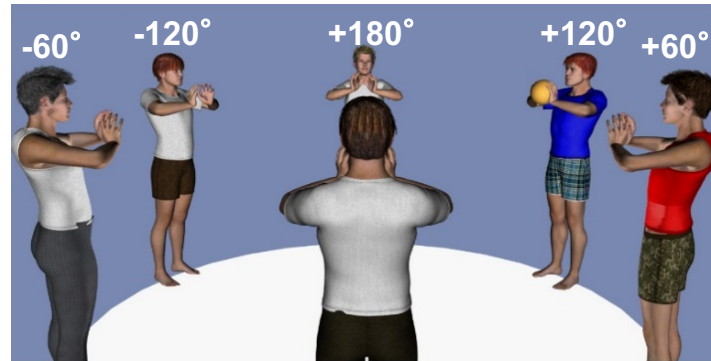
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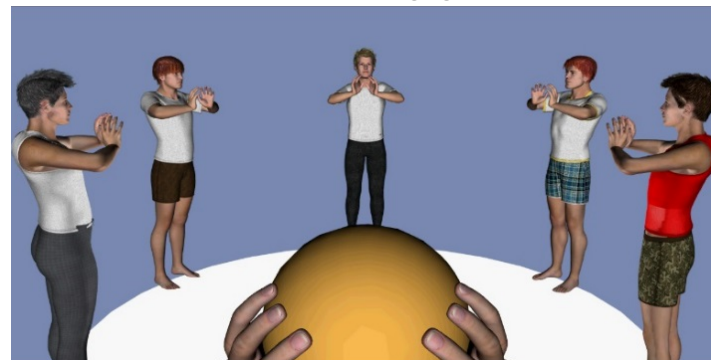
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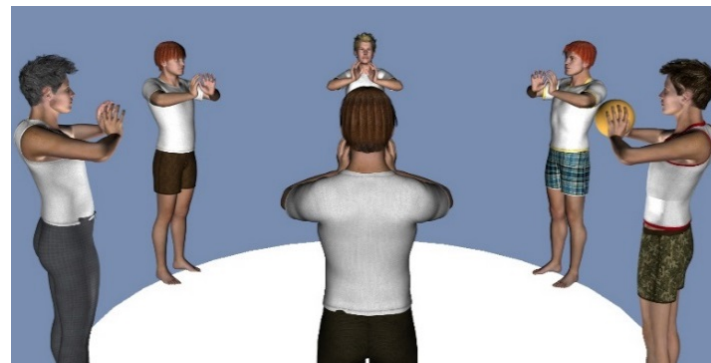
A Virtual ball-tossing game: 3PP



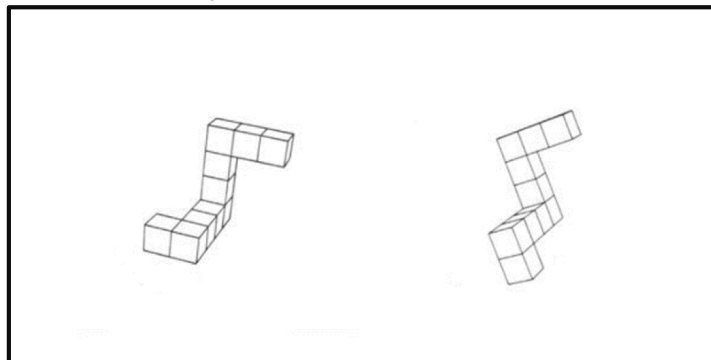
B Virtual ball-tossing game: 1PP

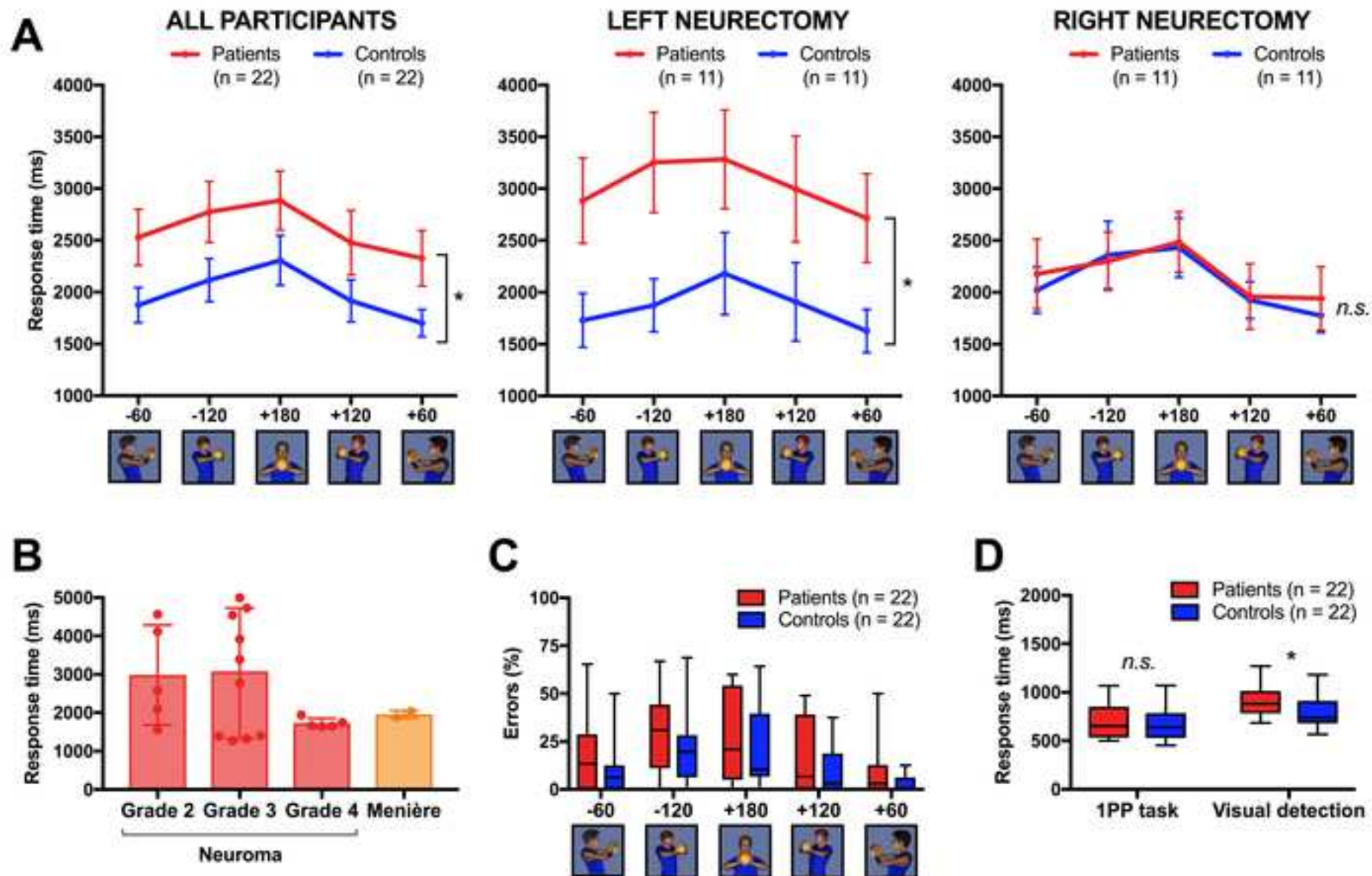


C Visual detection task: 1PP



D 3D objects mental rotation task





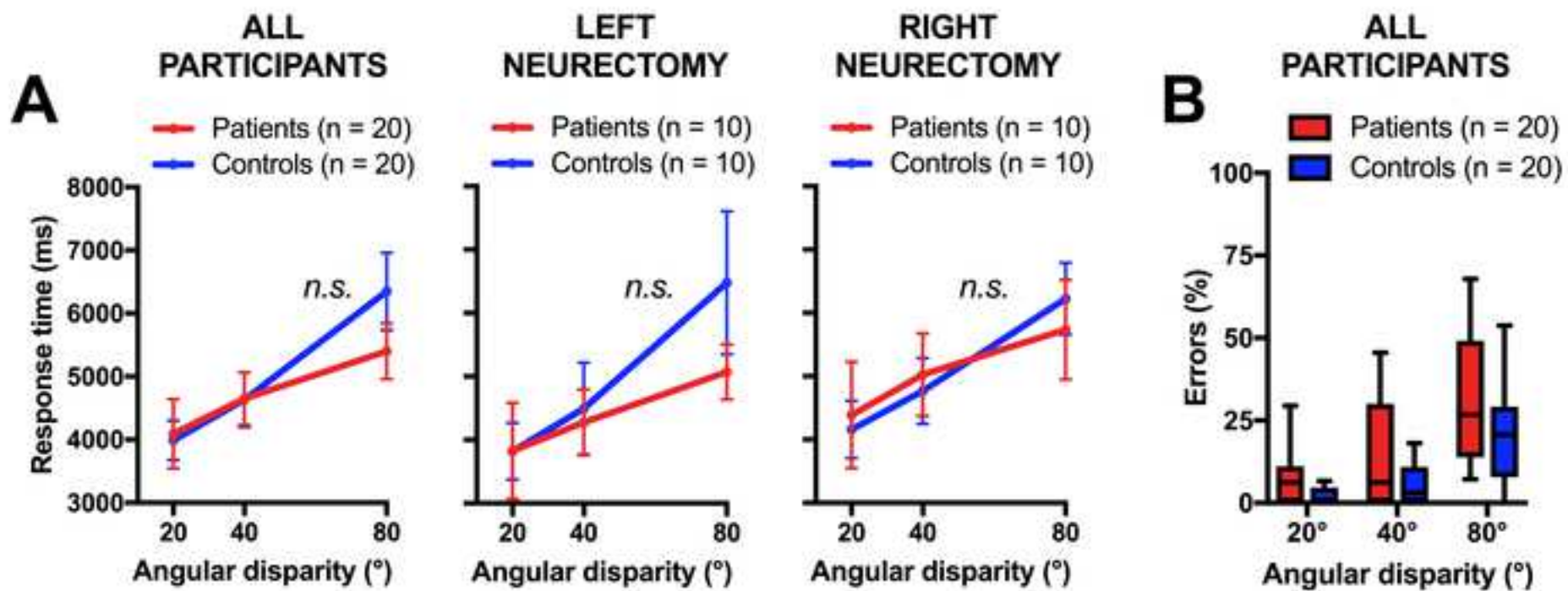


Table 1

	Age (years)	Gender	Diagnosis	Examination at D-1				Examination at D+7			
				CVS (% deficit)	VOR (gain)	VHIT (gain) ^a	SVV (°) ^b	CVS (% deficit)	VOR (gain)	VHIT (gain) ^a	SVV (°) ^b
Left neurectomy	49.9 ± 11.6	7 women 5 men	4 grade 2 6 grade 3 2 grade 4	66.2 ± 39.8	0.36 ± 0.14	0.45 ± 0.36	-2.3 ± 2.4	95.6 ± 11.7	0.43 ± 0.21	0.38 ± 0.41	-7.1 ± 4.0
Right neurectomy	53.0 ± 14.0	6 women 5 men	3 grade 2 3 grade 3 3 grade 4 2 MD	41.9 ± 34.3	0.44 ± 0.22	0.69 ± 0.36	0.1 ± 1.0	80.0 ± 25.2	0.41 ± 0.22	0.25 ± 0.28	-6.2 ± 4.2
	<i>P</i> = 0.57 ^c	<i>P</i> = 0.86 ^d	<i>P</i> = 0.63 ^e	<i>P</i> = 0.19 ^c	<i>P</i> = 0.35 ^c	<i>P</i> = 0.18 ^c	<i>P</i> = 0.01 ^c	<i>P</i> = 0.16 ^c	<i>P</i> = 0.90 ^c	<i>P</i> = 0.56 ^c	<i>P</i> = 0.63 ^c

Table 1. Comparison of clinical data in patients with left and right vestibular neurectomy. Means ± standard deviations are reported before (D-1) and after (D+7) surgery for each group of patients. MD: Menière's disease, CVS: caloric vestibular stimulation, VOR: vestibulo-ocular reflex, VHIT: video head impulse test, SVV: subjective visual vertical.

^a Gain for the lateral semicircular canal on the side of the disease

^b Negative signs indicate that the subjective visual vertical was tilted to the side of the disease (ipsilesional tilt)

^c Independent-samples t-tests

^d Chi-square

^e Chi-square for the grade of neuroma

		Left neurectomy	Right neurectomy	Statistics
Age (years)		49.9 ± 11.6	53.0 ± 14.0	<i>P</i> = 0.57 ^a
Gender		7 women, 5 men	6 women, 5 men	<i>P</i> = 0.86 ^b
Diagnosis and acoustic neuroma grade (Koos classification)		4 grade 2 6 grade 3 2 grade 4	3 grade 2 3 grade 3 3 grade 4 2 Menière's disease	<i>P</i> = 0.63 ^c
Unilateral vestibular neurectomy		2 partial, 10 total	2 partial, 9 total	<i>P</i> = 0.92 ^b
Examination at D-1	CVS (% deficit)	66.2 ± 37.8	39.9 ± 31.1	<i>P</i> = 0.10 ^a
	VOR (gain)	0.38 ± 0.14	0.44 ± 0.22	<i>P</i> = 0.52 ^a
	vHIT ipsi. (gain)			
	Anterior canal	0.81 ± 0.15	0.88 ± 0.24	<i>P</i> = 0.49 ^a
	Lateral canal	0.45 ± 0.36	0.69 ± 0.36	<i>P</i> = 0.18 ^a
	Posterior canal	0.59 ± 0.37	0.63 ± 0.36	<i>P</i> = 0.84 ^a
	vHIT contra. (gain)			
	Anterior canal	0.95 ± 0.09	0.93 ± 0.07	<i>P</i> = 0.50 ^a
	Lateral canal	0.88 ± 0.10	0.90 ± 0.11	<i>P</i> = 0.56 ^a
	Posterior canal	0.73 ± 0.32	0.90 ± 0.11	<i>P</i> = 0.16 ^a
	Posture (mm/s) ^d			
	Eyes open	7.2 ± 3.3	12.3 ± 5.5	<i>P</i> = 0.015^a
	Eyes closed	9.2 ± 4.0	15.4 ± 11.0	<i>P</i> = 0.09 ^a
	SVV (°) ^e	-1.9 ± 2.6	-0.5 ± 1.9	<i>P</i> = 0.15 ^a
Pure tone average (dB)				
Ipsi.	1 Cop. (58.7 ± 26.0) ^f	2 Cop. (56.2 ± 35.6) ^f	<i>P</i> = 0.87 ^a	
Contra.	19.6 ± 9.0	18.9 ± 14.4	<i>P</i> = 0.88 ^a	
Examination at D+7	CVS (% deficit)	96.4 ± 9.8	80.0 ± 25.2	<i>P</i> = 0.14 ^a
	VOR (gain)	0.42 ± 0.20	0.41 ± 0.20	<i>P</i> = 0.89 ^a
	vHIT ipsi. (gain)			
	Anterior canal	0.57 ± 0.31	0.60 ± 0.26	<i>P</i> = 0.87 ^a
	Lateral canal	0.41 ± 0.37	0.26 ± 0.27	<i>P</i> = 0.46 ^a
	Posterior canal	0.60 ± 0.42	0.52 ± 0.26	<i>P</i> = 0.74 ^a
	vHIT contra. (gain)			
	Anterior canal	0.99 ± 0.03	0.88 ± 0.13	<i>P</i> = 0.10 ^a
	Lateral canal	0.89 ± 0.06	0.88 ± 0.11	<i>P</i> = 0.86 ^a
	Posterior canal	0.93 ± 0.11	0.84 ± 0.15	<i>P</i> = 0.31 ^a
	Posture (mm/s) ^d			
	Eyes open	7.4 ± 3.7	13.8 ± 12.5	<i>P</i> = 0.11 ^a
	Eyes closed	11.2 ± 6.6	19.9 ± 11.6	<i>P</i> = 0.038^a
	SVV (°) ^e	-7.1 ± 4.0	-6.2 ± 4.2	<i>P</i> = 0.63 ^a
Pure tone average (dB)				
Ipsi.	10 Cop. (12.5) ^f	5 Cop. (49.0 ± 21.3) ^f	<i>P</i> = 0.038^g	
Contra.	17.8 ± 9.6	19.9 ± 13.8	<i>P</i> = 0.69 ^a	
Rotational vertigo	4 positive, 6 negative	1 positive, 7 negative	<i>P</i> = 0.20 ^b	
Spont. nystagmus (°/s)				
Horizontal	4.5 ± 5.2	5.5 ± 7.5	<i>P</i> = 0.75 ^a	
Vertical	0.7 ± 0.7	1.7 ± 2.8	<i>P</i> = 0.30 ^a	
Body tilt	5 positive, 5 negative	3 positive, 5 negative	<i>P</i> = 0.60 ^b	
Past pointing	4 positive, 6 negative	3 positive, 5 negative	<i>P</i> = 0.91 ^b	

Table 1. Comparison of clinical data in patients with left and right vestibular neurectomy. Means ± standard deviations are reported before (D-1) and after (D+7) surgery for each group of patients. CVS: caloric vestibular stimulation, VOR:

^a Independent-samples t-tests

^b Chi-square

^c Chi-square for the grade of neuroma

^d Average velocity of the center of foot pressure measured on a posturography platform with a stable support surface

^e Negatives signs indicate an ipsilesional tilt of the subjective visual vertical

^f The number of patients with copiosis (Cop.) is indicated; the mean hearing loss in the other patients without copiosis is indicated in brackets

^g Chi-square for the number of patients with copiosis

vestibulo-ocular reflex, VHIT: video head impulse test, SVV: subjective visual vertical, ipsi.: ipsilesional ear, contra.: contralesional ear, Cop.: cophosis.