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# Navigation strategies in patients with vestibular loss tested in a virtual reality T-Maze

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## Abstract

During navigation, humans mainly rely on egocentric and allocentric spatial strategies, two different frames of reference working together to build a coherent representation of the environment. Spatial memory deficits during navigation have been repeatedly reported in patients with vestibular disorders. However, little is known about how vestibular disorders can change the use of spatial navigation strategies. Here, we used a new reverse T-maze paradigm in virtual reality to explore whether vestibular loss specifically modifies the use of egocentric or allocentric spatial strategies in patients with unilateral ( $n = 23$ ) and bilateral ( $n = 23$ ) vestibular loss compared to healthy volunteers matched for age, sex and education level ( $n = 23$ ). Results showed that the odds of selecting and using a specific strategy in the T-maze was significantly reduced in both unilateral and bilateral vestibular loss. An exploratory analysis suggests that only right vestibular loss decreased the odds of adopting a spatial strategy, indicating a functional asymmetry of vestibular functions. When considering patients who used strategies to navigate, we observed that a bilateral vestibular loss reduced the odds to use of an allocentric strategy, whereas a unilateral vestibular loss decreased the odds to use of an egocentric strategy. Age was significantly associated with an overall lower chance to adopt a navigation strategy and, more specifically, with a decrease in the odds of using an allocentric strategy. We did not observe any sex difference in the ability to select and use a specific navigation strategy. Findings are discussed in light of previous studies on visuo-spatial abilities and studies of vestibulo-hippocampal interactions in peripheral vestibular disorders. We discuss the potential impact of the history of the disease (chronic stage in patients with a bilateral vestibulopathy vs. subacute stage in patients with a unilateral vestibular loss), of hearing impairment and non-specific attentional deficits in patients with vestibular disorders.

**Keywords:** vestibular system, labyrinth, spatial navigation, spatial strategies, egocentric, allocentric, reference frame.

## 1. Introduction

Spatial navigation refers to the ability to accurately orient oneself through the environment, which requires the integration of self-motion and environment information (i.e., gravito-inertial and proprioceptive signals, optic flow, visual, olfactory and acoustic landmarks). Vestibular signals, which provide information about own-body translations and rotations, may thus be pivotal for spatial navigation abilities (Angelaki & Cullen, 2008; Jacob et al., 2014; Yoder & Taube, 2014). Indeed, severe navigation deficits have been reported in animals models with bilateral vestibular deafferentation (Baek et al., 2010; Besnard et al., 2012; Machado et al., 2012; Russell et al., 2003). However, research in patients with vestibular disorders has provided equivocal results as to whether spatial navigation abilities are altered, depending on the clinical population and parameters recorded (reviewed in Smith, 2017). Spatial memory deficits have been reported in patients with a chronic bilateral vestibulopathy (BVP) tested in a virtual adaptation of the Morris water maze task (Brandt et al., 2005; Kremmyda et al., 2016). Others studies found no deficits in BVP patients tested with the Morris water maze task (Dobbels et al., 2020) or in other computer-based navigation and visual memory tasks (Jandl et al., 2015). More clearer deficits have been reported in BVP patients during real-space navigation in a building (Schöberl et al., 2021). The effects of unilateral vestibular loss on spatial navigation abilities are similarly equivocal: while some studies reported altered navigation abilities during triangle completion tasks in a desktop-based setting (Péruch et al., 1999, 2005) others found no consistent alteration in a virtual Morris water maze task (Hüfner et al., 2007). Clearer deficits have been reported in real-space navigation, such as when participants walked along a triangular path (Glasauer et al., 2002) or completed triangular paths (Péruch et al., 2005; Xie et al., 2017), without direct investigation of the spatial navigation strategies used by the patients.

Spatial navigation mainly relies on egocentric and allocentric frames of reference (Burgess, 2006), two operational modes working together to build a coherent representation of the environment (Chen et al., 2014; Gramann et al., 2010; Weniger et al., 2011). Egocentric representations are self-centered and based on subject-object associations. Allocentric representations are instead centered on aspects of the external environment, such as object-object or object-environment associations. While age (e.g., Rodgers et al., 2012) and sex (e.g., Astur et al., 2016) have been shown to influence the use of egocentric and allocentric frames of reference for spatial navigation, little is known about how the vestibular system contributes to these reference frames during navigation. Questionnaires given to 783 adults (aged 18–96 from the general German-speaking population) about their navigation strategies indicated that having experienced vertigo/dizziness during the last 12 months “reduced the scores of both the orientation and the route [egocentric] strategies” (Ulrich et al., 2019). However, frame-dependent strategies during navigation have not been systematically evaluated in humans suffering from vestibular loss using objective measures in well-controlled experimental paradigms.

A convenient way to objectively measure navigation strategies in rodents is the “reverse T-maze paradigm” (Machado et al., 2014; McIntyre et al., 2003), during which animals can use either a spatial strategy based on external landmarks (e.g., visual cues on the walls of or around the T-maze) or a response (egocentric) strategy to find the reward hidden in one arm of the maze. Using the reverse T-maze paradigm in rats, Machado et al. (2014) showed that bilateral vestibular loss affected hippocampal-dependent allocentric strategy (i.e.,

109 navigation relied less on visual landmarks around the T-maze) and favoured the use of striatum-dependent  
110 egocentric strategy (i.e., the ability to remember if the animal turned to the right/left in previous trials). Here,  
111 we adapted these procedures for investigations in humans and created a new reverse T-maze paradigm in  
112 virtual reality (VR) presented on a computer screen to explore whether unilateral vestibular loss and BVP  
113 specifically modify the use of egocentric or allocentric spatial strategies. Although desktop-based settings limit  
114 egocentric signals (vestibular, proprioceptive, motor signals), they provide a safe and well-controlled  
115 environment and allow patients to allocate most of their attentional resources to the navigation task, instead of  
116 to balance and eye movement controls. Navigation deficits have already been demonstrated in desktop-based  
117 settings (e.g., Péruch et al., 1999; Brandt et al., 2005), suggesting that vestibular disorders change spatial  
118 memory based only on the optic flow generated by virtual space navigation. This is supported by recent  
119 behavioural studies in healthy participants showing similar performance when egocentric information (head  
120 rotations and locomotion) was present or not during navigation in a virtual space (e.g., Huffman & Ekstrom,  
121 2019).

122 The aim of this study was to compare the ability to select and use a navigation strategy, and to compare  
123 the nature of the navigation strategy selected (egocentric vs. allocentric), in a group of patients with a chronic  
124 BVP, a group of patients tested in the subacute stage of a unilateral vestibular neurectomy, and a group of  
125 healthy participants carefully matched for age, sex and education level. We also included control tasks for  
126 visual recognition memory and visuo-spatial processing speed. As found in rodents (Machado et al., 2014),  
127 vestibular loss may favour egocentric spatial frameworks during navigation. Alternatively, vestibular loss may  
128 favour the use of visual landmarks for spatial navigation, as showed for postural control and spatial orientation  
129 (Lopez et al., 2006).

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## 2. Methods

### 2.1. Participants

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Forty-six patients with a vestibular failure took part in the study. Among them, 45 participants were right-handed and one was left-handed based on the Edinburgh Handedness Inventory (Oldfield, 1971). Twenty-three patients presented a severe BVP (*BVP group*: 11 females; mean age  $\pm$  SD:  $58.9 \pm 14.1$  years) according to the diagnostic criteria from the Bárány Society (Strupp et al., 2017). The BVP was idiopathic in all patients, which have been described elsewhere (Deroualle et al., 2017; Nakul et al., 2020). Patients were tested during the chronic stage of the BVP. Twenty-three patients had a unilateral vestibular loss (*UVL group*: 11 females;  $58.6 \pm 11.4$  years) due to an acute unilateral vestibulopathy (AUPV; vestibular neuritis and labyrinthitis,  $n = 9$ ) or a unilateral vestibular neurectomy (UVN; neuroma and Menière's disease,  $n = 14$ ). Patients with AUPV were tested 1–7 days after hospitalization ( $3.6 \pm 1.7$  days) and patients with UVN were tested 2–8 days ( $6.3 \pm 1.4$  days) after surgery, depending on their fatigue level. All patients tested in the acute or subacute phase of the UVL were included in the study only if they were able to sit upright with their head and trunk straight and motionless at the time of the test, and if they reported no severe fatigue, and experience no severe nausea, vertigo and dizziness the day of the test. Nausea and vomiting were non-inclusion criteria.

146 Patients underwent standard otoneurological examinations, including the bithermal caloric test with  
147 water at 44°C and 30°C, and the video head impulse test. Some patients underwent cervical and/or ocular  
148 vestibular-evoked myogenic potentials recordings. Clinical data are summarized in **Table 1** and **Tables S1-S2**.  
149 Both groups of patients were compared to 23 volunteers without history of otoneurological disorder (*Control*  
150 *group*: 11 females, 58.1 ± 13.5 years). **All controls were right-handed based on the Edinburgh Handedness**  
151 **Inventory (Oldfield, 1971)**. Although controls did not receive otoneurological examination, they showed  
152 subjective visual vertical within the normal range. The three groups of participants did not differ in terms of  
153 age, sex, education level, and game experience (**Table 1**). Participants were informed about the study and gave  
154 their written informed consent. Procedures were approved by the local Ethics Committee (CPP Sud-  
155 Méditerranée II) and followed the Declaration of Helsinki.

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## 2.2. Visuo-spatial tasks

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160 The virtual environments were designed using the VRmaze RESEARCH software (InMind-Vr ®), previously  
161 reported with a learning spatial task in healthy participants (Machado et al., 2019) and displayed on a 24''  
162 computer screen (Iiyama ProLite XUB2493HSU-B1). We used a large screen non-immersive VR environment  
163 rather than 3D immersive VR, in order to prevent cybersickness, a common complaint of exposure to VR  
164 goggles (LaViola, 2000). Participants navigated through the virtual environments by using three arrows on a  
165 keyboard: “up” to move forward; “right” and “left” to rotate their viewpoint in the clockwise and counter-  
166 clockwise direction, respectively. It was not possible to navigate backwards, neither to move the viewpoint  
167 upward or downward.

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### 2.2.1. *Virtual reverse T-Maze task*

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172 Participants were instructed that they would find themselves in a virtual maze located at the centre of a room.  
173 The VR environment gave a first-person viewpoint and contained salient landmarks, i.e., coloured geometric  
174 symbols (**Figure 1a**). The T-maze was composed of two opposite arms extending from the middle one, in  
175 which participants were initially placed. Each arm ended with a wall, behind which there may or may not be a  
176 target, which participants could not see. Before the first trial, participants were instructed that only one of the  
177 two opposite arms contained a target and that they had to retrieve it. When they **reached** the target, the text  
178 “Found” was displayed on the screen and the trial was over. There was no time limit to complete a trial. Then,  
179 participants were relocated to the starting point and asked to find the target again. A total of 5 trials were  
180 administered. For the first four trials (T1–T4), the target was always located in the same arm (right or left arm,  
181 counterbalanced across patients) **in order to make it possible to create a spatial association between the target**  
182 **and the visual landmarks (allocentric reference), or between the target and the arm side with respect to the**  
183 **subjective, egocentric viewpoint**. On trial 5, referred to as the *probe* trial, the T-maze was rotated by 180°, so  
184 that visual landmarks were inverted front/back and right/left) as classically done in animal studies (Machado  
185 et al., 2014) (**Figure 1b**). In the probe trial, both arms contained a target.

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182 After they completed the probe trial, participants were asked to explain which strategy they used during  
183 this last trial. For coding the navigation strategy, we followed procedures adapted from previous T-maze  
184 studies (Astur et al. 2016):

185 - When participants answered they turned in the same right/left arm of the T-maze (with respect to their  
186 viewpoint) where they remembered they found the target previously, and thus ignored the rotation of the visual  
187 environment, we recorded an *egocentric strategy*.

188 - When participants reported they followed the visual landmarks (coloured geometrical symbols) that were  
189 rotated, we recorded an *allocentric strategy*.

190 - When participants reported to have followed no particular strategy, *No-Strategy* was recorded.

191 Verbal reports were compared to behavioural data and corrected to “No-Strategy” if incongruent, as in this  
192 case participants failed to use and report a clear navigation strategy. For example, if participants reported that  
193 they followed the rotation of visual landmarks (allocentric strategy), but the behavioural data showed that they  
194 turned on the same side where they found the target during the previous trials (egocentric strategy), we  
195 corrected to “No-Strategy”. This correction was applied in only 3 out of 69 participants (2 patients, 1 control)  
196 and it was confirmed that the overall results were not affected by this correction.

### 198 2.2.2. Control for visuo-spatial processing speed

199 Participants were virtually placed at the centre of a neutral circular area. They were instructed to locate a  
200 circular red target, which could be on their back, front, or side, and to retrieve it as quickly as possible by  
201 rotating their viewpoint and moving forward towards the target. When participants reached the target, the text  
202 “Found” appeared on the screen and participants were repositioned at the centre of the circular area. The  
203 location of the target changed in each trial in a pseudorandomized order. Eight trials were administered, for  
204 which the time to retrieve the target was recorded.

### 206 2.3. Control for visual recognition memory

207 To control that navigation strategy was not modulated by altered visual recognition memory in patients, we  
208 used a computer-based adaptation of the Doors Test (Baddeley et al., 2006) following procedures from  
209 previous studies on spatial navigation abilities (Brandt et al., 2005; Hübner et al., 2007). The test was presented  
210 on a computer screen using PsychoPy (Peirce et al., 2019) and consisted of two parts: Part A and Part B. Each  
211 part was composed of a presentation and a response phase. In the ‘presentation phase’, participants were  
212 presented with a sequence of 12 different types of doors for 3 s each. In the ‘response phase’, a same target  
213 door of the presentation phase was displayed in a 2 × 2 array together with three distractors. The whole phase  
214 was composed of 12 arrays in which participants were asked to identify the target door without time limit. In  
215 Part A, the distractors were different categories of doors than the target door (e.g., a garage door, a garden  
216 door), whereas in the more difficult Part B, the distractors were the same type of door with a few different  
217 details (e.g., different doorbells). One point was awarded for each correct response and only those participants  
218 who obtained at least a score of 8 in Part A were administered Part B.

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## 2.4. Experimental procedures

Participants were tested while comfortably sitting in front of a desk with the lights switched off in the room to minimize the influence of peripheral visual signals from the experimental room. They first received instructions about the virtual T-Maze task, after which they completed a minimum of 8 training trials with no maze to become familiar with procedures to navigate in the VR environment. During the training, participants were asked to move into a virtual open space in order to retrieve a circular red target. When the training was over, the T-Maze task started, and participants were asked to report the strategy they used. Participants then performed the control task for visuo-spatial processing speed and the Doors Test. Participants took short breaks between tasks and they were instructed to stop if they felt nauseous, dizzy or experienced any kind of discomfort. No patient had to stop the experiment due to any of these symptoms. Several pilot tests were conducted to develop a sequence of cognitive tasks in VR (including the T-Maze task) which reduced as much as possible the duration of VR exposure to avoid the occurrence of nausea, fatigue and lack of comfort. The whole experiment lasted not more than 30 minutes on average.

## 2.5. Data Analysis

The navigation strategy (Allocentric vs. Egocentric) or absence of strategy (No-Strategy) reported for the probe trial was coded as a categorical variable. To analyse the predictors of the navigation strategy, we calculated several logistic regressions (SPSS 26, IBM, USA). Outcomes were either the presence of a navigation strategy (Strategy vs. No-Strategy) or the type of strategy (Allocentric vs. Egocentric). In patients with unilateral vestibular loss, we also conducted two exploratory analyses regarding (1) the type of UVL, *i.e.* patients with AUVP tested in the acute stage of the disorder vs. patients with UVL tested in the acute stage after the neurectomy but during the chronic stage of a neuroma or a Menière's disease; (2) the influence of left vs. right vestibular lesion, irrespective of the type of UVL. Depending on how participants were stratified, predictors in the logistic regression were the Group (BVP, UVL, Controls), Type of UVL (AUVP vs. UVN) and/or Side of UVL (left vs. right UVL), with the Sex and Age as covariates.

For each participant and each trial in the T-Maze, we measured the time and path length to retrieve the target. For each participant, we calculated the mean time to reach the target in the control task for visuo-spatial processing speed. As the Shapiro-Wilks test showed that most of these data were not normally distributed, we ran non-parametric procedures in SPSS 26 (IBM, USA). Within-group analyses were carried out using Friedman's tests with the trials (T1–T4) as a within-subject factor and post-hoc comparisons were performed using the Wilcoxon test with a Bonferroni correction. Between-group analyses were carried out using the Kruskal-Wallis test. Differences were considered significant for  $p < 0.05$  unless alpha level was corrected for multiple comparisons.



### 255 3. Results

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#### 257 3.1. Spatial strategies in the VR T-Maze

258 Although 65% of the controls reported having used a navigation strategy (whether allocentric or egocentric),  
259 only 35% of BVP patients and 30% of UVL patients used one (**Figure 2a**). A first logistic regression indicated  
260 that the ability to use a navigation strategy with respect to No-Strategy was significantly predicted by the  
261 Group ( $\chi^2 = 7.59, p < 0.05$ ) and Age ( $\chi^2 = 10.04, p < 0.01$ ). The odds to use a navigation strategy vs. No-  
262 Strategy were significantly reduced in BVP patients (odds ratio [OR]: 0.23; 95% confidence interval [CI]:  
263 0.06–0.89;  $p = 0.033$ ) and in UVL patients (OR: 0.19; CI: 0.05–0.73;  $p = 0.016$ ) when compared to controls  
264 (**Table 2**). In other words, the odds of controls to use a navigation strategy compared to No-Strategy were 4.4  
265 times more than that for BVP patients and 5.3 times more than that for UVL patients. Age was significantly  
266 associated with a reduction in the odds of using a strategy with respect to No-Strategy (OR: 0.93; CI:  
267 0.88–0.98;  $p = 0.005$ ). Sex was not a significant predictor ( $p = 0.893$ ) (**Table 2**).

268 **In a first exploratory analysis**, UVL patients were stratified in AUVP and UVN (**Figure S1 and Table**  
269 **S3**). A logistic regression showed that the odds to use a navigation strategy vs. No-Strategy were significantly  
270 reduced in patients with UVN ( $p = 0.008$ ) when compared to controls, whereas this was not the case in AUVP  
271 ( $p = 0.348$ ). The odds of controls to use a navigation strategy compared to No-Strategy were 11.1 times more  
272 than that for patients with UVN.

273 **In a second exploratory analysis**, patients were stratified according to the side of the vestibular loss. A  
274 logistic regression analysis indicated that only right UVL reduced significantly the odds to use a navigation  
275 strategy vs. No-Strategy when compared to controls ( $p = 0.015$ ) (**Figure S2 and Table S4**). This was not the  
276 case in patients with left UVL ( $p = 0.204$ ). The odds of controls to use a navigation strategy were 20 times  
277 more than that for patients with right UVL.

278 In a last multivariate logistic regression analysis, Group ( $\chi^2 = 18.6, p < 0.001$ ) and Age ( $\chi^2 = 16.84, p$   
279  $< 0.001$ ) were significantly associated with the odds of using specifically an egocentric or an allocentric  
280 navigation strategy when compared to No-Strategy (**Figure 2a**). **Table 3** shows that UVL patients had a  
281 significantly lower chance of using an egocentric strategy when compared to No-Strategy than controls ( $p <$   
282  $0.05$ ), whereas this was not the case of BVP patients ( $p = 0.20$ ). Conversely, BVP patients had a significantly  
283 lower chance of using an allocentric strategy when compared to No-Strategy than controls ( $p < 0.05$ ). This was  
284 not the case of UVL patients ( $p = 0.23$ ). Altogether, this indicates a reduced use of allocentric strategies in  
285 BVP patients and a reduced use of egocentric strategies in UVL patients. The analysis also indicates that Age  
286 was significantly associated with a reduced odds of using an allocentric strategy when compared to No-  
287 Strategy ( $p = 0.001$ ). By contrast, Age was not significantly associated with the odds of using an egocentric  
288 strategy rather than No-Strategy. Sex was neither related to the odds of using an egocentric or an allocentric  
289 strategy when compared to No-Strategy.

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### 3.2. Time and path length to retrieve the target

Friedman's tests showed that the time to retrieve the target significantly changed from T1 to T4, indicating improved ability to navigate in the T-Maze in all groups of participants (Controls:  $\chi^2_{(3)} = 13.07, p = 0.004$ ; BVP:  $\chi^2_{(3)} = 10.77, p = 0.013$ ; UVL:  $\chi^2_{(3)} = 21.37, p < 0.001$ ) (**Figure 2b**). Friedman's tests showed that the path length did not significantly change from T1 to T4 for Controls ( $\chi^2_{(3)} = 4.47, p = 0.215$ ) and UVL patients ( $\chi^2_{(3)} = 3.26, p = 0.353$ ), but the change was significant for BVP patients ( $\chi^2_{(3)} = 8.48, p = 0.037$ ) (**Figure 2c**). Followed up tests for the BVP group showed that the path length decreased between T1 and T4 (Wilcoxon test,  $p = 0.026$ ), and between T2 and T4 ( $p = 0.009$ ), however the differences were not statistically significant after Bonferroni correction (corrected  $\alpha = 0.0083$ ). Kruskal-Wallis tests indicated no significant effect of the Group for T1 to T4 regarding the time (all  $H_{(2)} < 5.19$  and  $p > 0.075$ ) and the path length (all  $H_{(2)} < 5.0$  and  $p > 0.082$ ). For the probe trial, there was no significant effect of the Group for the time ( $H_{(2)} = 1.54, p = 0.464$ ) and the path length ( $H_{(2)} = 1.17, p = 0.917$ ).

### 3.3. Controls for visuo-spatial processing speed and visual recognition memory

The time to retrieve the target in the control task did not differ between groups (Kruskal-Wallis test:  $H_{(2)} = 3.67, p = 0.159$ ; **Figure 2d**), indicating similar abilities to locate visual targets and to navigate the virtual environment between groups.

Participants from the three groups recollected a similar number of items in the Doors Test, indicating no significant effect of vestibular loss on visual recognition memory ( $H_{(2)} = 5.46, p = 0.065$ ; **Figure 2d**).

## 4. Discussion

### 4.1. Vestibular loss decreases the odds of using a navigation strategy

#### *General effect of vestibular loss on the odds of using a navigation strategy*

We found that patients with chronic BVP and patients with a UVL in the acute/subacute stage of a vestibular loss failed to select and use a specific strategy to orient themselves in a VR T-maze. Our finding is congruent with results from a recent survey revealing that vertigo/dizziness in the last 12 months decreases the odds that individuals report using either an egocentric or an allocentric strategy (Ulrich et al., 2019). Such a failure to select and use a proper navigation strategy is consistent with studies indicating that vestibular disorders impair performances in spatial memory tasks during navigation in VR (i.e. based only on optic flow and allocentric references, Brandt et al., 2005; Kremmyda et al., 2016; Péruch et al., 1999), as well as during novel route recombination (Schöberl et al., 2021) and triangle completion (Glasauer et al., 1994; Péruch et al., 2005) in VR and real space navigation (i.e. using egocentric references) tasks/settings. Other studies did not find significant effect of BVP and UVL on navigation performance (Dobbels et al., 2020; Jandl et al., 2015).

Results from the present study and results from virtual adaptations of the Morris water maze task are difficult to compare directly, as we focused on self-reports about navigation strategies instead of performance

329 in terms of response time, path length and heading errors as in previous navigation studies (Brandt et al., 2005;  
330 Kremmyda et al., 2016; Péruch et al., 1999). Here, we chose to focus on the navigation strategy following  
331 procedures from a classical behavioural task in rodents (Machado et al., 2014). Being able to exactly record  
332 the participant's experience and strategy (following the landmarks that have rotated in the environment, or  
333 remembering the motion with respect to the egocentric viewpoint) and to compare it with the behaviour  
334 (recording of the path in the virtual T-maze) is a clear advantage with respect to animal studies. In particular,  
335 it avoids confusion between random exploration of either arm of the T-maze and explicit, deliberate  
336 exploration of a given arm of the T-maze based on a clear spatial strategy.

337 Only 5 trials were applied in the present task, and it is possible that patients with a BVP or UVL require  
338 a larger number of trials before being able to select and report a proper navigation strategy, instead of searching  
339 randomly into one arm of the T-maze or the other. The dramatic decrease in the odds of selecting and using a  
340 navigation strategy (with respect to No-Strategy) in both groups of patients with vestibular disorders can be  
341 accounted for by specific influence of vestibular disorders on the function and structure of the brain network  
342 involved in spatial navigation (review in Smith, 2017) and/or by unspecific effects of the vestibular loss on  
343 attention, fatigue and ability to explore and remember visual landmarks (see below). The lower ability to select  
344 and use navigation strategies in patients with vestibular disorders indicates that vestibular signals about own-  
345 body rotations and translations are in general important for spatial memory and wayfinding strategies (Ulrich  
346 et al., 2019). Alternatively, it can indicate that vestibular disorders have general effects on cognition reaching  
347 beyond spatial navigation, as suggested by recent epidemiological studies (Bigelow et al., 2016; Harun et al.,  
348 2016; Semenov et al., 2016).

#### 349 *Measures taken to reduce unspecific effects of vestibular loss on fatigue and attention*

350 There is a large body of evidence showing that patients with a BVP, and to a lesser extent patients with a UVL,  
351 can complain about a lack of attention, difficulty to focus and fatigue (Bigelow et al., 2016; Popp et al., 2017).  
352 As the experiment lasted about 30 min, fatigue may have installed, especially for patients who underwent  
353 surgery and general anaesthesia several days before the T-Maze task. Several measures were taken to reduce  
354 these effects. The T-Maze task was administered first during the experiment in order to limit the effects of  
355 fatigue on navigation performance. In addition, participants were tested while sitting on a chair in front of a  
356 computer screen in order to have most of their attentional resources allocated to the navigation task, instead of  
357 to keeping balance control and stabilizing gaze (see below). Overall larger attentional deficits in patients with  
358 BVP and stronger fatigue in UVL patients who underwent surgery may have decreased the attention paid to  
359 visual landmarks. Although there was no eye movement recording in the present experiment to measure  
360 exploration of visual landmarks, there is evidence to suggest that BVP patients exhibit different visual  
361 exploration than healthy participants, including fewer object fixations during real-space navigating (Schöberl  
362 et al., 2021).

363 It is important to note that the lack of group difference in the control task for navigation speed indicates  
364 that the decrease in the likelihood to select and use a navigation strategy cannot be accounted for by a decrease  
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366 in processing speed or in the ability to navigate through the VR environment. In addition, the absence of group  
367 difference in the Doors Test rules out an influence of altered visual recognition memory on the difference in  
368 navigation strategies. Although the Doors Test did not control for visual memory in the T-Maze task directly,  
369 it provides congruent findings with previous investigations in BVP patients (Brandt et al., 2005; Kremmyda et  
370 al., 2016) and indicates that general mechanisms of visual memory and attention remained unaltered in chronic  
371 BVL and in UVL patients tested in the subacute phase of the surgery for UVN and hospitalization for AUVP.  
372 Finally, the careful matching of the groups also excludes an effect of age, education level or computer/game  
373 expertise on the reported differences in the navigation strategies.

#### 374 *Impact of hearing impairment*

375 Another factor that may partly explain differences between the groups of patients is a concomitant hearing  
376 impairment (reviewed in Smith, 2022). Recent studies suggest that cognitive dysfunctions previously reported  
377 in patients with vestibular disorders may be related to hearing loss (Dobbels et al., 2019, 2020). Dobbels et al.  
378 (2019) used a battery of cognitive tests in 64 BVP patients and 83 controls and found that the hearing status  
379 was significantly related to performance in the immediate memory (remembering a list of words) and language,  
380 but hearing loss was not significantly related to visuo-spatial functions, which are at stake in the present study.  
381 In another study using the virtual Morris water maze in BVP patients, the degree of hearing loss was  
382 significantly related to the time to reach the hidden platform, and inversely related to the time participants  
383 spent searching in the right quadrant of the water maze (Dobbels et al., 2020). There was no significant relation  
384 with the path length and the heading error. By contrast, other studies found no correlation between hearing  
385 loss in UVL patients (after neurectomy for neuroma and Menière's disease) and performance in egocentric and  
386 allocentric mental rotation (Deroualle et al. 2019), and found no difference between deaf signers and hearing  
387 nonsigners engaged in visuo-spatial perspective-taking, 3D object mental rotation and spatial orientation tasks  
388 (Secora & Emmorey, 2019). As pointed out in a recent comprehensive review of the topic (Smith, 2022),  
389 understanding the respective contributions of hearing impairment and vestibular loss on spatial cognition will  
390 require large scale prospective studies comparing navigation strategies in patients with only a vestibular loss  
391 (BVP or UVL), patients with only hearing impairment, patients with vestibular and hearing loss, and carefully  
392 matched control participants. At the moment, we cannot exclude that a sensorineural loss, including both  
393 vestibular and auditory dysfunctions, is responsible for the reported decrease in the odds of using a navigation  
394 strategy.

#### 395 396 397 4.2. Exploratory analysis of the effect of the type of unilateral vestibular loss on the odds of using 398 a navigation strategy

399 An exploratory analysis suggests that patients with UVN, but not patients with AUVP, had lower chance to  
400 select and use spatial strategies. This result should be taken with caution because of the small sample size when  
401 patients were stratified according to their type of UVL. It is important to note that the chronic/acute stage of  
402 the vestibular loss differs strongly in both subpopulations of patients. UVL patients tested in the chronic stage

403 of a neuroma or Menière's disease present a similar reduction in the odds of using a navigation strategy as  
404 patients with a chronic BVP. The vestibular loss in the patients was probably already important before the  
405 neurectomy, and vestibular compensation was probably well developed before neurectomy, as indicated by  
406 moderated subjective visual vertical deviation after the UVN (**Tables S1-S2**). By contrast, patients tested in  
407 the acute stage of AUVP do not show this reduction in the odds of using a navigation strategy, despite larger  
408 subjective visual vertical deviations (**Tables S1-S2**).

409 We speculate that the decrease in the odds of using a navigation strategy is not an immediate effect of  
410 the UVL but reflects the chronic stage of a vestibular loss. While a vestibular neurectomy after a chronic  
411 Menière's disease or neuroma creates a total and enduring deafferentation affecting spatial perception and  
412 cognition durably (Borel et al., 2008; Devèze et al., 2015; Lopez et al., 2007; Vibert & Häusler, 2000), AUVP  
413 may preserve part of the vestibular function, patients may recover within a couple of days (Halmagyi et al.,  
414 2010; McGarvie et al., 2020), and its impact on cognition may depend on the disease severity. There is indeed  
415 evidence to suggest that both hippocampal functions and structure depend on vestibular reflexivity and the  
416 degree of clinical impairment (Göttlich et al., 2016; Jacob et al., 2020; Kamil et al., 2018; Seo et al., 2016).

417 Another important difference between the groups is that UVN patients, but not AUVP and BVP  
418 patients, were evaluated shortly after a surgery under general anaesthesia. General anaesthesia may have  
419 influenced performance because of its well-known effects on cognition (Belrose & Noppens, 2019). A recent  
420 study isolated the specific effect of general anaesthesia on cognition. Cognitive abilities, such as spatial  
421 memory and attention, recovered within 3 hours of return of consciousness after general anaesthesia (Mashour  
422 et al., 2021). This study was conducted in healthy participants and the effect of anaesthesia on cognition in  
423 patients with a chronic UVL may be different. Animal studies showed that anaesthesia can modify the time  
424 course of vestibular compensation (reviewed in Gliddon et al., 2004) and anaesthesia may even reduce pre-  
425 existing compensation in patients with Menière's disease and neuroma. Although the influence of anaesthesia  
426 cannot be excluded in the present study, our control cognitive tasks revealed no significant difference in visual  
427 processing speed and visual recognition memory between UVN patients and the two other groups.

#### 428 429 4.3. Exploratory analysis of the effect of the side of unilateral vestibular loss on the odds of using 430 a navigation strategy

431 Our exploratory analysis suggests that only right UVL decreased the probability to select and use spatial  
432 strategies. This result should be taken with caution because of the small sample size when patients were  
433 stratified according to their lesion side, and because of the different sizes of the two groups. The limited sample  
434 size in the present study, as well as in previous studies, may account partly for the equivocal results reported  
435 in the literature comparing the effects of left vs. right vestibular disorders on perception and cognition. In line  
436 with the present findings, Hübner et al. (2007) showed a trend to perform worse in a VR navigation task only  
437 in patients with right UVL. This result and our results are in line with neuroimaging studies highlighting a  
438 dominance of the right cerebral hemisphere in right-handed participants (Dieterich et al., 2003, 2017; Dieterich  
439 & Brandt, 2018). Importantly, the neural network involved in visuo-spatial attention has been located mainly

440 in the right cerebral hemisphere (Dieterich & Karnath, 2006), and right UVL (in right-handed participants)  
441 may disorganize the functions of this visuo-spatial attention network. In contrast with the present findings,  
442 studies have assessed no differences between right and left UVL with respect to cognitive performance (Ayar  
443 et al., 2020; Popp et al., 2017), or found that only left UVL altered the perceived straight ahead (Saj et al.,  
444 2013) and own-body mental imagery (Deroualle et al., 2019). How the side of the vestibular loss influences  
445 cognition requires further investigations in much larger samples of participants, especially with respect to  
446 spatial navigation abilities.

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#### 448 4.4. Effect of BVP and UVL on egocentric vs. allocentric navigation strategies

449 To the best of our knowledge, this is the first systematic comparison of spatial strategies during navigation in  
450 humans with unilateral and bilateral vestibular loss.

451 Our results indicate that a chronic BVP dramatically decreased the odds of using an allocentric  
452 navigation strategy. Our findings in humans are fully compatible with observations in rats with a bilateral  
453 vestibular loss also tested in a reverse T-maze (Machado et al., 2014): bilateral vestibular loss affected  
454 hippocampal-dependent allocentric strategy and favoured the use of striatum-dependent egocentric strategy.  
455 Allocentric coding has been associated with activation of the hippocampus and/or the entorhinal cortex during  
456 visually guided navigation in VR (Bohbot et al., 2012; Guderian et al., 2015; Jacobs et al., 2013; Maguire,  
457 1998; Sherrill et al., 2013). Interestingly, there is evidence to suggest that the volume of the hippocampus is  
458 reduced in patients with a total and chronic BVP (patients with neurofibromatosis 2; Brandt et al., 2005) and  
459 in patients with a partial BVP (Kremmyda et al., 2016) when compared to healthy controls. This hippocampal  
460 atrophy remains controversial as it was not confirmed in other groups of patients with chronic and partial BVP  
461 (Cutfield et al., 2014; Göttlich et al., 2016). Furthermore, BVP patients showed lower activation in the right  
462 anterior hippocampus and bilateral insula during real navigation, which correlated with higher error rates on  
463 recombined novel routes (Schöberl et al., 2021). In the same study, patients with a complete BVP showed  
464 higher activations in the caudate nucleus when compared to patients with incomplete lesion (Schöberl et al.,  
465 2021). Another fMRI study, using a computer-based spatial navigation task, indicated that cerebellar activity  
466 was higher in BVP patients when compared to controls (Jandl et al., 2015), especially in a cerebellar region  
467 known to be involved in sequence-based navigation (Iglói et al., 2015). Altogether, these results suggest that  
468 BVP increases the odds of shifting from an allocentric strategy to a striatum-dependent (i.e., egocentric)  
469 navigation strategy.

470 On the contrary, we found that UVL decreased the odds of using an egocentric navigation strategy.  
471 The vestibular system has been proposed to be strongly connected to a multisensory fronto-parieto-temporal  
472 network in the right cerebral hemisphere underlying visuo-spatial processing and attention in an egocentric  
473 frame of reference (Bottini et al., 2001; Fink et al., 2003; Saj et al., 2014). As summarized in Dieterich &  
474 Karnath (2006), data from patients with stroke and neuroimaging studies show a right hemisphere dominance  
475 and common areas for both visuo-spatial neglect and vestibular information processing. There is evidence to  
476 suggest distortions of the egocentric reference frame in patients with unilateral vestibular disorders tested either

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477 in the chronic stage after a total vestibular neurectomy (Saj et al., 2013), or in the chronic stage of a partial  
478 unilateral vestibulopathy (Saj et al., 2021), as patients present with deviations of the subjective straight ahead.  
479 A study from our group in patients with UVL, operated on for schwannoma and Menière’s disease as in the  
480 present study, indicates deficits for spatial imagery in an egocentric reference frame, whereas spatial imagery  
481 in an allocentric reference frame was unaffected (Deroualle et al. 2019). Similarly, studies in healthy  
482 participants indicate that caloric, galvanic and magnetic vestibular stimulation can change egocentric space  
483 perception (Hamann et al., 2009; Lindner et al., 2021; Pavlidou et al., 2018). In addition to interfering with the  
484 brain network underlying egocentric representations, UVL can affect the function and structure of the  
485 visuospatial attention network (Corbetta et al., 2008), such as altered responses in the intraparietal sulcus  
486 (Helmchen et al., 2014), or gray matter volume reduction in the right superior temporal gyrus (zu Eulenburg  
487 et al., 2010) and supramarginal gyrus (Hüfner et al., 2009). Consistently, recent measures of visuospatial  
488 attention in microgravity showed enhanced stimulus-driven attentional capture to the detriment of endogenous  
489 attention (Salatino et al., 2021). A neuroimaging study after short-term acute exposure to microgravity showed  
490 a decreased functional connectivity at the right temporo-parietal junction/angular gyrus (Van Ombergen et al.,  
491 2017), a core area within the right attentional network and deemed crucial for self and own-body consciousness  
492 (Ionta et al., 2011). Acute exposure to microgravity creates mismatches between visual, proprioceptive and  
493 vestibular inputs (Van Ombergen et al., 2017), which can disorganize networks supporting visuospatial  
494 processing and attention in a body-centred reference frame. We speculate that similar disorganization may  
495 occur in UVL patients tested in the acute or subacute stage of a neurectomy or AUVP.

496 The different patterns observed in patients with BVP and UVL can be accounted for by other factors  
497 than the extent of the vestibular loss. One crucial difference is that BVP patients were tested in the chronic  
498 stage of their vestibular loss, whereas UVL patients were tested in the acute/subacute stage of the vestibular  
499 loss. Accordingly, the brain mechanisms that are in place at the time of the cognitive tests in patients with  
500 chronic BVP and in patients with acute UVL may be very different.

#### 501 502 4.5. Effect of age on navigation strategies

503 Age was significantly associated with an overall lower chance to adopt a navigation strategy and a decrease in  
504 the odds of using an allocentric strategy. These results are consistent with previous studies that pointed out an  
505 association between the age-related decline of the vestibular function and spatial orientation accuracy (Anson  
506 et al., 2021). Moreover, other studies highlighted the use of an allocentric frame of reference in younger  
507 compared to older adults during navigation (Bohbot et al., 2012; Li & King, 2019) and the increased odds of  
508 using an egocentric than an allocentric spatial strategy in older adults (Irving et al., 2018; Rodgers et al., 2012).  
509 For example, individuals tested in a homing task requiring to combine self-motion signals and visual landmarks  
510 revealed that “older adults did not place as much influence on visual information as would have been optimal”  
511 for accurate spatial representations (Bates & Wolbers, 2014). However, studies of real-space navigation  
512 revealed that older participants make more saccades and search saccades when navigating (Irving et al., 2018).  
513 Many factors can explain the effect of age on navigation strategies and performance, including decline in the

514 visual, proprioceptive and vestibular sensory systems, or changes in the entorhinal-hippocampal network  
515 (reviewed in Lester et al., 2017). **Functional neuroimaging revealed that activity in the hippocampus decreases**  
516 **with age whereas activity in the cerebellum and right putamen increases with age, in line with a shift from**  
517 **predominantly allocentric to egocentric navigation strategies (Irving et al., 2018).**

#### 518 519 4.6. Effect of sex on navigation strategies

520 We did not observe any sex difference in the ability to select and use of specific navigation strategy. This  
521 results seems in contrast with results from a recent survey in healthy participants (Ulrich et al., 2019), results  
522 from navigation tasks (Astur et al., 2016; Mueller et al., 2008) and data from neuroimaging suggesting that  
523 men and women use different strategies and activate different brain areas during navigation (Grön et al., 2000;  
524 Irving et al., 2018). However, our results are consistent with other studies that did not observe any sex-related  
525 difference in the use of navigation strategies **in virtual radial mazes and T-mazes** (Levy et al., 2005; Schmitzer-  
526 Torbert, 2007). **Our results are also consistent with a lack of differences in navigation performance and visual**  
527 **exploration parameters reported in a recent study using real-space navigation (Irving et al., 2018).** Many  
528 reasons could explain these differences. For example, as highlighted by Astur and colleagues, previous  
529 administered tasks may influence strategy selection of the subsequent spatial tasks (Astur et al., 2016).  
530 Contrary to previous works (Astur et al., 2016; Levy et al., 2005), the current study administered no other  
531 spatial tasks before the T-Maze, preventing any bias toward egocentric or allocentric strategies. A second  
532 possible issue concerns the different male and female reliance on visual information for navigation. As  
533 previously demonstrated, females generally spend more time looking at surrounding landmarks and show  
534 impaired performance when no landmarks are available (Andersen et al., 2012; Sandstrom et al., 1998), while  
535 males typically show an advantage in time performance as they are more prone to use additional information  
536 from the environment, such as room geometry or Euclidian coordinates. Although this is not correlated to the  
537 use of a spontaneous spatial strategy during navigation (Andersen et al., 2012), most of the previous findings  
538 that revealed an effect of sex resulted from the analysis of the time and accuracy to navigate (Grön et al., 2000;  
539 Mueller et al., 2008) and not from a direct comparison of behavioural data and verbal reports. Indeed, a third  
540 point concerns the methodology used to determine the strategies. In contrast with other studies (Astur et al.,  
541 2016; Levy et al., 2005), participants of the present study were asked to explain which strategy they used  
542 during the probe trial, making it possible to correct the behavioural data if inconsistent and to record the No-  
543 Strategy option. The evidence on sex-related differences for spatial strategies are therefore equivocal. Further  
544 researches are needed to address the influence of sex in adopting a specific spatial strategy during navigation.

#### 545 546 4.7. Time and path length to retrieve the target in the virtual T-maze

547 **The data indicate that overall, there was no difference between groups regarding the time and the path length**  
548 **to retrieve the target in the T-maze. This indicates that the ability to navigate through a virtual maze using a**  
549 **keyboard was equivalent across groups and that differences in performances were mostly related to differential**  
550 **use of spatial navigation strategies. We note a significant effect of the trial on the path length only in patients**



551 with BVL, suggesting that these patients improve their ability to navigate in the VR-maze over the trials  
552 repetition. Such an effect might be related to the fact that BVL patients showed delayed spatial learning when  
553 required to find a hidden platform in the VR Morris water maze (Kremmyda et al., 2016), and present the  
554 strongest cognitive impairments among patients with a vestibular loss, including deficits of visuo-spatial  
555 attention, speed processing and executive functions (Popp et al., 2017).

#### 556 557 4.8. The virtual reversed T-maze task to measure navigation strategies in patients with vestibular 558 disorders and healthy controls

559 We used a large screen, VR environment in sitting participants rather than a 3D immersive environment or  
560 real-space navigation. The approach, which is common in cognitive neuroscience, has several advantages.  
561 First, it aimed at reducing cybersickness, which is common during immersion in VR (LaViola, 2000). Second,  
562 a desktop-based setting allows to better control the sensory stimuli between groups of participants. Third, it  
563 avoids the confounding factors related to the different abilities of controls, BVP and UVL patients to perform  
564 head rotations and to stabilize images on the retina when exploring the environment. Fourth, as patients with  
565 vestibular disorders can have attentional deficits, performing the task while sitting in front of a computer screen  
566 ensures that most of the attentional resources are allocated to the navigation task, instead of to balance control.

567 Several authors suggested that navigation in desktop-based settings loses ecological validity compared  
568 to real-space navigation and immersive VR using goggles (e.g., see review in Taube et al., 2013). Navigating  
569 in a 3D environment is much more complex than in a 2D environment (Brandt et al., 2017), especially with  
570 respect to the multisensory processing of vestibular and proprioceptive inputs, as well as auditory and olfactory  
571 stimuli (Schöberl et al., 2020). Desktop based-settings impoverish sensory feedback from motion-sensitive  
572 systems (vestibular, motor, proprioception) as there is no locomotion. The lack of sensory feedback related to  
573 locomotion and exploration may have decreased the use of egocentric navigation strategies in all groups of  
574 participants tested in the virtual T-maze task. However, recent behavioural and neuroimaging studies in healthy  
575 participants suggest that there is a modality-independent brain network underlying spatial memory and that  
576 removing egocentric signals does not change navigation performance (Huffman & Ekstrom, 2019). In line  
577 with this idea, early studies in patients with vestibular disorders found no difference between real-space and  
578 VR navigation (Péruch et al., 1999).

579 The fact that in our study participants were tested sitting on a chair while looking straight to the screen  
580 in front of them may have impacted performance with respect to real navigation. This posture decreases the  
581 difficulty of the task for patients with BVP and UVL when compared to real navigation because the cognitive  
582 load related to balance control (Bessot et al., 2012; Redfern et al., 2004) is reduced in this non-challenging  
583 posture. It is therefore possible that this setting decreases the deficits in spatial cognition when compared to  
584 the disorders that patients may experience in their daily life when navigating in real space, especially when  
585 they are involved in multiple tasks. In our setting, the main sensory feedback about self-motion in the VR  
586 environment comes from the optic flow on the screen and there is evidence to suggest that vestibular disorders  
587 change the ability to encode navigation based on optic flow only (Péruch et al., 1999).

588 We chose to have no time limit for maze exploration to match procedures from the T-Maze in rodents  
589 with a BVL (Machado et al., 2014). There are several advantages of having no time limit to retrieve the target,  
590 including a time that participants judge necessary to navigate without experiencing nausea from fast motion in  
591 the VR, or a time necessary to explore the visual environment and to pay attention to the visual cues in the VR  
592 T-maze. Having no time limit to search for the target in the T-Maze may favour the use of navigation strategy  
593 based on the visual exploration of landmarks in all groups of participants.

594 Finally, the presentation of the task on a screen, instead of in head-mounted VR goggles, allowed  
595 participants to see visual cues in their peripheral visual field. The number of visual stimuli in the room was  
596 kept to a minimum, tests were performed in a dim room, and participants were asked to keep their heads still  
597 in front of a large screen, minimizing the influence of the peripheral visual cues on navigation strategies.

#### 599 4.9. Main limitations of the study

600 As detailed above, a predominant limitation of the study is that navigation strategies were collected in patients  
601 with a very different history of vestibular disorders: patients with a BVP had a chronic condition, UVL patients  
602 with a Menière's disease or a neuroma had a chronic condition but were tested during the acute stage of a  
603 vestibular neurectomy, whereas patients with AUVP (neuritis) were tested in the acute stage of their disease.  
604 Taken together, the results indicate that BVP and UVL patients show a decrease in the odds of using a  
605 navigation strategy, but comparisons between groups will require confirmation in larger groups of participants  
606 all tested in the chronic stage of their disease. The impact of hearing impairment on spatial memory and  
607 cognition in general will also need to be taken into account more systematically in future studies. Finally, the  
608 vestibular function was not measured in the control group. This prevented us from carrying out a  
609 comprehensive analysis of the connection between the vestibular system reflexivity and behavioural  
610 performance.

#### 612 4.10. Conclusions

613 In conclusion, findings of the present study shed light on the specific contributions of vestibular inputs on the  
614 frame-dependent spatial coding. Overall, an impairment of vestibular system has been showed to prevent  
615 adopting spatial strategies during virtual navigation. When considering patients who used strategies to orient  
616 themselves in the VR environment, we showed that a bilateral vestibular damage decreases the use of  
617 allocentric strategy, while a unilateral impairment decreases the use of an egocentric strategy. Further studies  
618 are needed to confirm these results using **real-space** navigation tasks and using functional neuroimaging, and  
619 to determine **whether and** to what extent these deficits impair the patients' daily life.

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#### 624 Conflicts of interest

625 S. Besnard and M.L. Machado have or had financial relationships with InMind-VR and have been involved in  
626 the development of the VRMaze software.

627 **Figure Legends**

628  
629 **Figure 1.** (A) Example of visual landmarks as seen from the first-person perspective at the starting point in  
630 the T-maze. (B) Top view of the virtual T-maze in the first four trials (T1–T4) and in the probe trial after the  
631 T-maze was rotated by 180°.

632  
633 **Figure 2.** (A) Percentage of participants that reported No-Strategy or a specific spatial strategy (egocentric or  
634 allocentric) to retrieve the target in the probe trial of the T-Maze task. (B) Box-and-whisker plots showing the  
635 time and the path length (C) to retrieve the target in first four trials of the T-Maze task. Means are shown as +.  
636 The solid line inside the box is the median and boxes cover the interquartile range (5–95). (D) Box-and-whisker  
637 plots showing the number of correct items recalled in the Doors Test and the time to find the target in the  
638 control task for visuo-spatial processing speed. BVP = Bilateral vestibulopathy; UVL = Unilateral vestibular  
639 loss.

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**A**

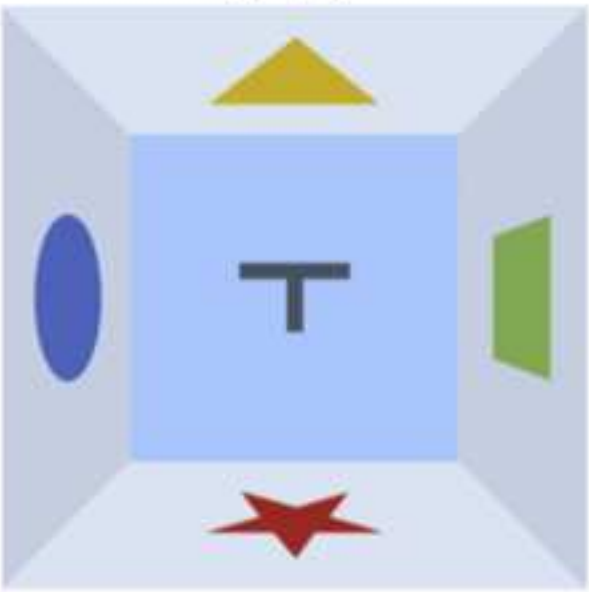
*Starting point in the T-Maze*

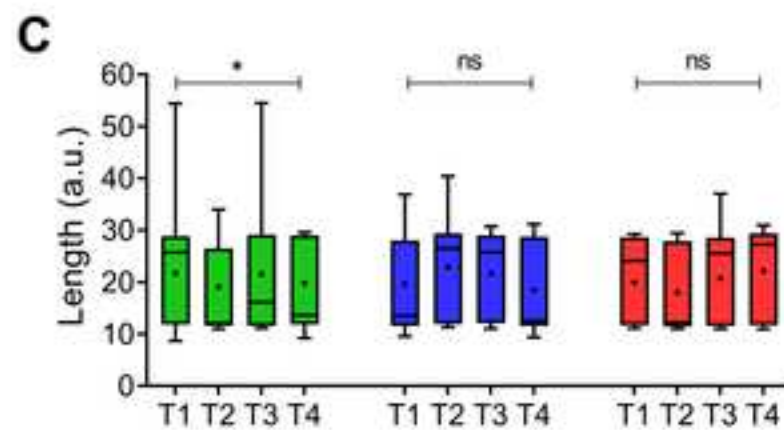
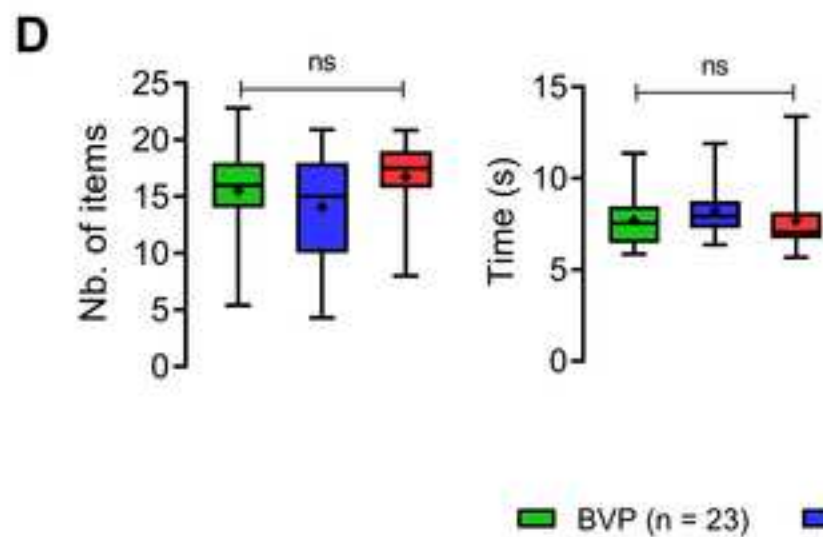
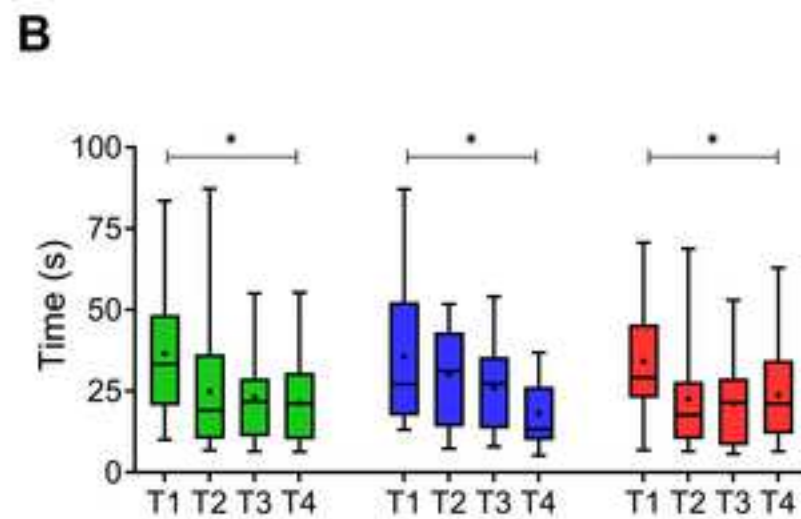
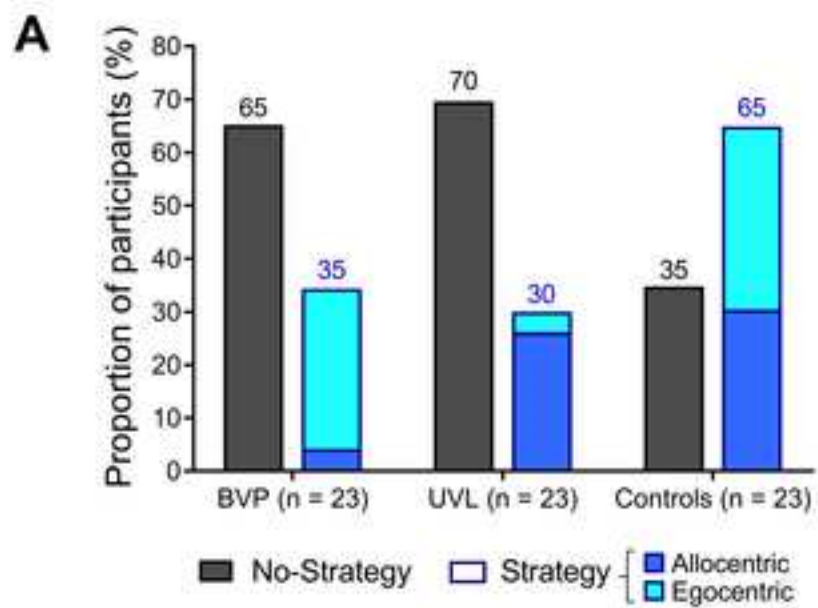


**B**

*T1-T4*

*Probe trial*





	<b>BVP</b> ( <i>n</i> = 23)	<b>UVL</b> ( <i>n</i> = 23)	<b>Controls</b> ( <i>n</i> = 23)
<b>Age (years)</b>	59.3 ± 14.2	58.7 ± 11.4	58.1 ± 13.3
<b>Females/Males</b>	14/9	14/9	14/9
<b>Handedness</b> (laterality quotient, %)	22 right-handed: 85.7 ± 14.0% 1 left-handed: -58%	23 right-handed: 85.6 ± 14.6%	23 right-handed: 89.4 ± 10.2%
<b>Highest education level (%)</b>			
<i>Level 1</i>	21.4%	13.04%	0%
<i>Level 2</i>	0%	17.3%	8.6%
<i>Level 3</i>	7.1%	30.4%	21.7%
<i>Level 4</i>	42.8%	13.04%	30.4%
<i>Level 5</i>	28.5%	26.08%	39.1%
<b>Employment status (%)</b>			
<i>Employed</i>	65.2%	56.5 %	65.2%
<i>Student</i>	0%	0%	4.3%
<i>Retired</i>	34.7%	43.4%	30.4%
<i>Unemployed</i>	0%	0%	0%
<b>Marital status (%)</b>			
<i>Single</i>	0%	0%	13.04%
<i>Married/couple</i>	82.6%	78.2%	82.6%
<i>Divorced/widowed</i>	17.3%	17.3%	4.3%
<b>Game experience</b>			
<i>Keyboard expertise</i>	5	5	5
<i>3D videogames skills</i>	0	0	0
<i>2D videogames skills</i>	0	0	0
<i>Videogaming (childhood)</i>	0	0	0
<i>Videogaming (last year)</i>	0	0	0
<b>SVV (°)</b>	2.3 ± 1.9	Left UVL: -3.6 ± 4.6 Right UVL: 4.0 ± 6.6	1.3 ± 1.6

*BVL = Bilateral vestibulopathy; UVL = Unilateral vestibular loss; SVV = Subjective visual vertical.*

**Table 1. Demographic data of patients with vestibular disorders and healthy participants.** Mean ± SD is reported for age and SVV, median is reported for Game Experience, percentage of participants is reported for education level, employment and marital status. Education level is based on the French education system: *Level 1* (before high school), *Level 2* (accomplished high school), *Level 3* (two years after high school), *Level 4* (Bachelor's degree), *Level 5* (Master's degree, Engineering degree, PhD, MD). Game experience score was rated using a six-point Likert scale (1: *never*, 2: *sometimes*, 3: *every month*, 4: *every week*, 5: *almost every day*, 6: *every day*). Negative signs indicate counterclockwise tilt of the SVV; positive signs indicate clockwise tilt of the SVV.

	Strategy vs. No-Strategy		
	$\beta$	Odds ratio (95% CI)	$p$
Intercept	4.96		<b>0.003</b>
Age	-0.07	0.93 (0.88–0.98)	<b>0.005</b>
Group			
<i>BVP</i>	-1.46	0.23 (0.06–0.89)	<b>0.033</b>
<i>UVL</i>	-1.66	0.19 (0.05–0.73)	<b>0.016</b>
<i>Controls</i>	Ref	Ref	
Sex			
<i>Female</i>	0.08	1.08 (0.36–3.27)	0.89
<i>Male</i>	Ref	Ref	

**Table 2.** Results from the logistic regression.  $R^2 = 0.22$  (Cox–Snell), 0.29 (Nagelkerke). Model fitting:  $\chi^2(4) = 16.83, p = 0.002$ .

	Egocentric strategy vs. No-Strategy			Allocentric strategy vs. No-Strategy		
	$\beta$	Odds ratio (95% CI)	$p$	$\beta$	Odds ratio (95% CI)	$p$
Intercept	1.96		0.33	7.34		<b>0.002</b>
Age	-0.04	0.97 (0.91–1.02)	0.23	-0.13	0.88 (0.82–0.95)	<b>0.001</b>
Group						
<i>BVP</i>	-0.92	0.40 (0.10–1.60)	0.20	-3.63	0.03 (0.00–0.46)	<b>0.013</b>
<i>UVL</i>	-2.87	0.06 (0.01–0.55)	<b>0.013</b>	-1.03	0.36 (0.07–1.89)	0.23
<i>Controls</i>	Ref	Ref		Ref	Ref	
Sex						
<i>Female</i>	0.48	1.62 (0.43–6.09)	0.48	-0.26	0.77 (0.17–3.59)	0.74
<i>Male</i>	Ref	Ref		Ref	Ref	

**Table 3.** Results from the multinomial logistic regression.  $R^2 = 0.39$  (Cox–Snell), 0.45 (Nagelkerke).

Model fitting:  $\chi^2(8) = 33.79$ ,  $p < 0.0001$ .