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► **To cite this version:**

Diane Deroualle, Michel Toupet, Christian van Nchel, Ulla Duquesne, Charlotte Hautefort, et al.. Anchoring the Self to the Body in Bilateral Vestibular Failure. PLoS ONE, 2017, 12 (1), pp.e0170488. 10.1371/journal.pone.0170488 . hal-02121685

HAL Id: hal-02121685

<https://amu.hal.science/hal-02121685>

Submitted on 6 May 2019

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RESEARCH ARTICLE

Anchoring the Self to the Body in Bilateral Vestibular Failure

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Abstract

Recent findings suggest that vestibular information plays a significant role in anchoring the self to the body. Out-of-body experiences of neurological origin are frequently associated with vestibular sensations, and galvanic vestibular stimulation in healthy participants anchors the self to the body. Here, we provide the first objective measures of anchoring the self to the body in chronic bilateral vestibular failure (BVF). We compared 23 patients with idiopathic BVF to 23 healthy participants in a series of experiments addressing several aspects of visuo-spatial perspective taking and embodiment. In Experiment 1, participants were involved in a virtual “dot-counting task” from their own perspective or the perspective of a distant avatar, to measure implicit and explicit perspective taking, respectively. In both groups, response times increased similarly when the avatar’s and participant’s viewpoint differed, for both implicit and explicit perspective taking. In Experiment 2, participants named ambiguous letters (such as “b” or “q”) traced on their forehead that could be perceived from an internal or external perspective. The frequency of perceiving ambiguous letters from an internal perspective was similar in both groups. In Experiment 3, participants completed a questionnaire measuring the experienced self/body and self/environment “closeness”. Both groups reported a similar embodied experience. Altogether, our data show that idiopathic BVF does not change implicit and explicit perspective taking nor subjective anchoring of the self to the body. Our negative findings offer insight into the multisensory mechanisms of embodiment. Only acute peripheral vestibular disorders and neurological disorders in vestibular brain areas (characterized by strong multisensory conflicts) may evoke disembodied experiences.

OPEN ACCESS

Citation: Deroualle D, Toupet M, van Nechel C, Duquesne U, Hautefort C, Lopez C (2017) Anchoring the Self to the Body in Bilateral Vestibular Failure. PLoS ONE 12(1): e0170488. doi:10.1371/journal.pone.0170488

Editor: Michel Botbol, Université de Bretagne Occidentale, FRANCE

Received: August 12, 2016

Accepted: January 5, 2017

Published: January 20, 2017

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Data Availability Statement: All files are available from the Open Science Framework database (osf.io/uwqes).

Funding: CL’s research is supported by a grant from the VolkswagenStiftung (Grant no. 89434: “Finding Perspective: Determining the embodiment of perspectival experience”). The sponsor was not involved in the study design, collection, analysis, and interpretation of data, writing the report and in the decision to submit the manuscript for publication.

Introduction

As suggested by Merleau-Ponty’s statement “*I am not in front of my body, I am in my body, or rather I am my body*” [1], common self experience is characterized by strong anchoring of the self to the body. Pioneer [2] and current [3] psychological studies revealed that adults and

Competing Interests: The authors have declared that no competing interests exist.

children invariably locate their self within their body boundaries. Only in rare clinical conditions as well as during drug use, meditation, and sleep paralysis do individuals claim that their self is located outside their physical body (i.e., out-of-body experience) [4].

Current neuroscientific models of self-location propose that the accurate integration of visual, tactile, proprioceptive, interoceptive, motor and vestibular signals underpins the experience of an embodied self [5]. In support of these models, clinical observations show that abnormal multisensory integration in epileptic, and brain-damaged patients may evoke a loss of unity between the self and the body [6–8]. Moreover, experimentally induced conflicts between vision and touch [9–13], or between vision and motor-proprioceptive signals [14], can modify the anchoring of the self to the body in neurologically normal people. However, despite the importance of the vestibular system in encoding self-motion and orientation in space, its contribution to the sense of self has received much less attention than has vision, touch and proprioception.

The last 10 years has seen a growing amount of evidence from research involving neurological patients and healthy participants suggesting that vestibular signals contribute to anchoring the self to the body (for recent reviews, see Ref. [15–17]). First, neurological patients reporting out-of-body experiences often experience concomitant vestibular illusions, such as sensations of floating and elevation of the self [7,16]. In these patients, damaged areas most frequently overlap with key vestibular regions, including the temporo-parietal junction [11] and posterior insula [8]. Second, patients with peripheral vestibular disorders may report an abnormal self-body relationship, which is reminiscent of depersonalization disorders [18–20]. For example, patients with Menière’s disease may report experiences such as “*I feel like I’m outside of myself. I feel like I’m not in myself*”, or “*I am not actually being there or having anything to do with my body*” ([21], p. 531–532). Yet, we lack convincing evidence of full-blown disembodiment related to peripheral vestibular disorders [19,22]. Third, experiments involving healthy participants indicate the possibility of manipulating anchoring of the self to the body by using vestibular stimulation. Ferrè *et al.* [23] showed that low-intensity galvanic vestibular stimulation promoted first-person perspective taking in participants who perceived letters drawn on their forehead. This finding suggests that weak vestibular stimulation may increase the natural tendency of the vestibular system to anchor the self to the body.

If vestibular information plays a significant role in anchoring the self to the body, as suggested by the corpus of data summarized above, how do vestibular-defective patients experience self-location? Anecdotal reports have been collected over the last century [18–20], but we have no objective measures of self-body anchoring in vestibular patients according to well-controlled paradigms from cognitive neuroscience. Here, we tested the contribution of vestibular signals to anchoring the self to the body by comparing the performance of patients with chronic, idiopathic, bilateral vestibular failure (BVF) and healthy controls in three experiments addressing several aspects of embodiment. *Experiment 1* measured implicit and explicit visuo-spatial perspective taking in a virtual-reality-based “dot-counting task” [24–26]. *Experiment 2* measured implicit perspective taking in a non-visual task [23,27] and required naming letters drawn on the participant’s forehead and neck. *Experiment 3* measured the experienced closeness between the self and the body by using pictorial descriptions adapted from the Inclusion of Other in the Self (IOS) scale [28]. The rationale and hypotheses for each experiment are reported in details in the subsequent sections.

Participants with Idiopathic Bilateral Vestibular Failure

We tested a population of 23 patients with idiopathic bilateral vestibular failure (BVF) in a series of experiments (22 participants in Experiment 1, 23 in Experiment 2, and 22 in

Experiment 3). The BVF occurred at a mean of 14 ± 12 years before inclusion in the study. At the time of the tests, all patients were adapted to the vestibular loss, which had moderate functional impact on their daily life, although they reported oscillopsia and imbalance in darkness. The clinical status of these patients and their performance in cognitive, postural and oculomotor tasks are described elsewhere [29–31].

The BVF was established on the basis of standard otoneurological examinations including a bithermal caloric test (irrigation of the left and right auditory canals with water at 44°C and 30°C), the video head impulse test (vHIT) [32], and measurement of vestibulo-ocular responses during a pendular test on a rotating chair. The saccular and utricular functions were evaluated for some patients by recording cervical vestibular-evoked myogenic potentials (cVEMPs) over the sternocleidomastoid muscles [33] and ocular vestibular-evoked myogenic potentials (oVEMPs) over the inferior oblique muscles [34], respectively.

All patients had weak responses to the caloric test [mean slow phase eye velocity $<5^{\circ}/\text{s}$ [35]; left ear (mean \pm SD): $2.42 \pm 2.73^{\circ}/\text{s}$, right ear: $2.36 \pm 2.53^{\circ}/\text{s}$] and reduced responses to the vHIT [mean gain <0.7 [36]; horizontal canals: 0.38 ± 0.19 ; anterior canals: 0.34 ± 0.17 ; posterior canals: 0.34 ± 0.15]. Responses to the pendular test were also reduced [mean slow phase eye peak velocity $<20^{\circ}/\text{s}$; left rotation: $5.89 \pm 7.37^{\circ}/\text{s}$; right rotation: $4.84 \pm 5.11^{\circ}/\text{s}$]. Cervical VEMPs were present in the left ear for 9 patients (mean p13-n23 amplitude \pm SD: $33.59 \pm 42.14 \mu\text{V}$) and in the right ear for 12 patients ($41.76 \pm 44.09 \mu\text{V}$). Ocular VEMPs were present in the left ear for 5 patients ($0.68 \pm 1.34 \mu\text{V}$) and in the right ear for 6 patients ($0.97 \pm 1.61 \mu\text{V}$). In conclusion, all patients presented severe bilateral vestibular hypofunction that was not associated with neurological disorders.

Ethics statement

All participants were informed about the study and gave their written informed consent. Experimental procedures were approved by the local Ethics Committee (Comité de Protection des Personnes Sud-Méditerranée II) and followed the ethical recommendations laid down in the Declaration of Helsinki.

Experiment 1

Experiment 1 aimed at measuring the degree of anchoring the self to the body by visuo-spatial perspective taking tasks. Recent research has suggested that implicit third-person perspective taking can be evaluated by asking participants to perform visuo-spatial judgments from their own perspective while another, task-irrelevant, person is in their visual environment. Participants spontaneously adopt the viewpoint of the person in their environment. For example, participants instructed to describe the relative position of two objects more often located these objects according to the perspective of a person sitting in front of them [37–39]. This effect was further increased when the other person gazed or acted toward one of the objects.

Here, we compared implicit and explicit visuo-spatial perspective taking tasks in BVF patients and controls by using a virtual “dot-counting task” developed by Samson and colleagues and replicated by others [24–26,40–44]. In this task, participants reported whether the number of dots presented on the walls of a 3D virtual room matched a digit presented in a previous instruction. The environment involved a task-irrelevant avatar. Under conditions where the avatar could “see” a number of dots incongruent with the number of dots visible from the participants’ viewpoint, response times and error rates increased. Several studies confirmed that such effects were due to “altercentric intrusion” [24–26,40,41,43,44], that is, an implicit and unconscious simulation of the avatar’s viewpoint. An opposite effect was reported when participants were explicitly asked to simulate the avatar’s perspective (i.e., to imagine how

many dots the avatars would see). Participants were slower and made more errors when the number of balls seen from the avatar's and participant's viewpoints was incongruent. This effect, referred to as "egocentric intrusion", indicates that participants cannot totally ignore their own visuo-spatial perspective.

If vestibular signals are important to anchor the self to the body [23], BVF patients may more easily separate from their own perspective. Accordingly, they may be more prone to implicitly take the avatar's disembodied perspective (i.e., more altercentric intrusion) and less anchored to their body when required to explicitly take the avatar's perspective (i.e., less egocentric intrusion). An opposite hypothesis would be that BVF patients would be less likely to implicitly and explicitly adopt the avatar's perspective because vestibular signals are required for computing a third-person perspective [45]. Preliminary findings were presented in a conference abstract [46].

Methods

Participants. Twenty-two patients with idiopathic BVF participated in the experiment (9 females and 13 males, mean age \pm SD: 60 ± 11 years, mean duration of education after high school: 4 ± 2 years). All patients but one were right-handed, as confirmed by the Edinburgh Handedness inventory (mean laterality quotient: $91 \pm 30\%$) [47]. They had normal or corrected-to-normal vision. BVF patients were compared to 22 healthy volunteers matched on age, sex and education level (9 females and 13 males, age: 58 ± 12 years, education: 5 ± 3 years). Healthy participants were all right-handed, (laterality quotient: $94 \pm 13\%$), had normal or corrected-to-normal vision, and no history of vestibular, neurological, or psychiatric disease.

Implicit perspective taking task (IPT task). Visual stimuli consisted of a colored 3D rendering of a room with three visible walls. The left and right walls were yellow and contained from 0 to 3 blue balls aligned horizontally. In the middle of the room and at the center of the screen, an avatar was shown sitting on a cube placed on the room floor. Two sets of pictures were created: female avatars were always shown to female participants, and male avatars were always shown to male participants. The avatar faced the left or right wall of the 3D room. The spatial arrangement of the balls was manipulated to create situations where the participant and avatar could "see" the same number of balls on the walls (i.e., congruent viewpoint), or a different number of balls (i.e., incongruent viewpoint) (Fig 1). In total, for both female and male avatars and for both avatar orientations (i.e., facing the left or right wall), 10 visual stimuli were created to balance the number of trials with congruent and incongruent viewpoints (following procedures from Ref. [24]).

Visual presentation was controlled, and responses were collected by using PsychoPy2 v1.82.01 [48]. Each trial started with the presentation of a white fixation cross on a black background for 750 ms. This was followed by the presentation of the question "How many blue balls do you see?" for 1500 ms and the presentation of a number (0, 1, 2 or 3) for 1000 ms. Then, one of the visual scenes was presented. Participants were instructed to indicate as quickly and accurately as possible whether the number of balls they saw matched the number specified after the question. The response time was not limited. Participants pushed one of two buttons on a keyboard to respond: half of the participants had to press a button with their right index finger to answer "yes" or another button with their right middle index finger to answer "no"; the other participants had a reverse configuration for the response buttons. As soon as participants pressed a button, the visual scene disappeared and the next trial started. Although participants had to count the number of balls according to their first-person perspective, the presence of the avatar in the visual scene allowed for measuring implicit third-

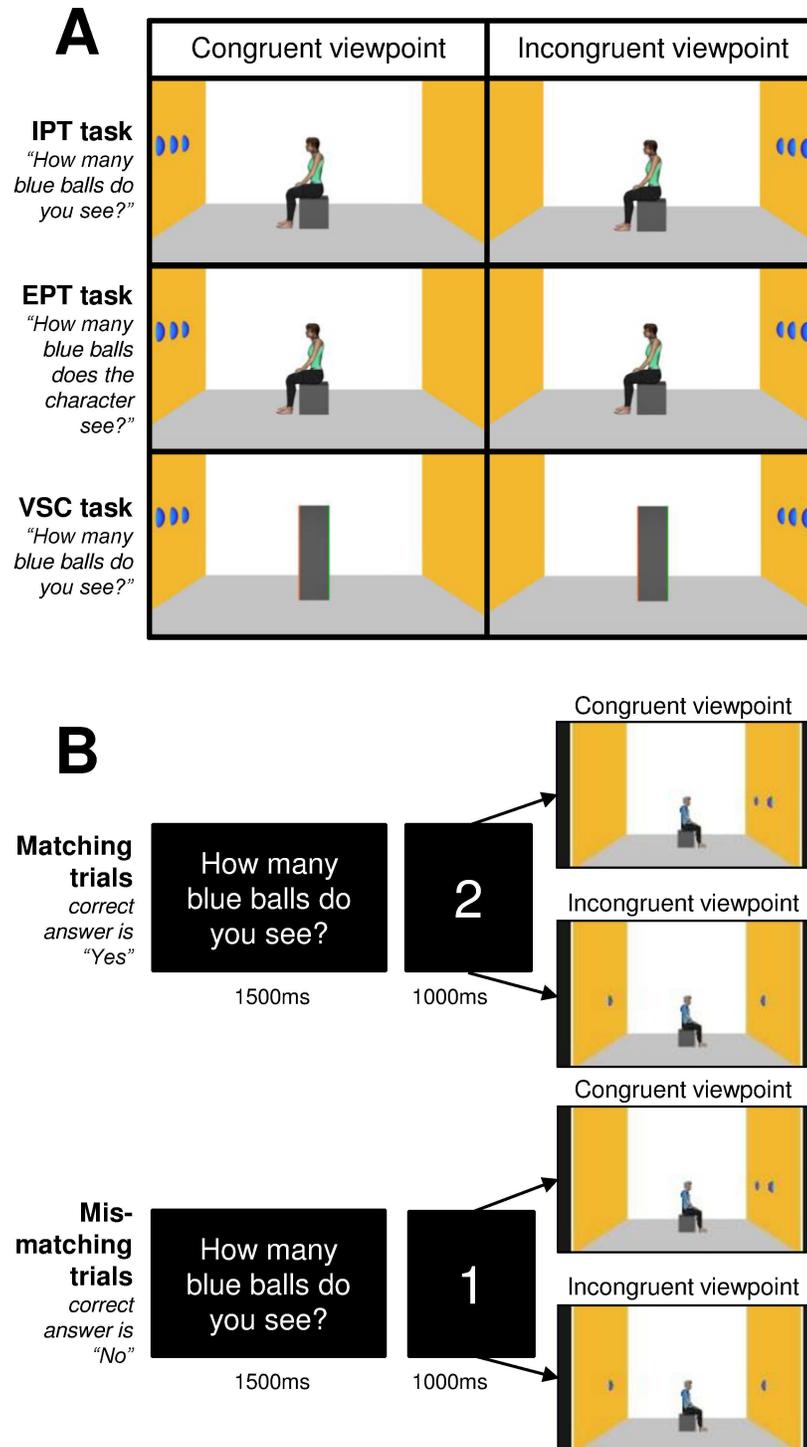


Fig 1. Methods for visuo-spatial perspective-taking tasks (Experiment 1). (A) Examples of visual stimuli used for the tasks of implicit perspective taking (IPT), explicit perspective taking (EPT) task, and visuo-spatial control (VSC) task. Visual stimuli presented a congruent or an incongruent viewpoint of the avatar with the participant's viewpoint. (B) Participants indicated whether the number of balls seen from their viewpoint (IPT and VSC tasks) matched (i.e., matching trials) or did not match (i.e., mismatching trials) the number presented in the instruction.

doi:10.1371/journal.pone.0170488.g001

person perspective taking (IPT), i.e. the extent to which the avatar's viewpoint interfered with the participant's viewpoint.

In half of the trials ("matching trials"), the number specified after the question matched the number of balls visible from the participant's viewpoint (Fig 1B). For the trials involving a congruent viewpoint, the number shown after the question corresponded to the quantity of balls visible from both the participant's and avatar's viewpoints. For the trials involving an incongruent viewpoint, the number corresponded to the quantity of balls visible only from participant's viewpoint. In the other half of the trials ("mismatching trials"), the number specified after the question differed from the quantity of balls the participant could see. For the trials involving a congruent viewpoint, the number shown after the question corresponded to one of the three quantities of balls that did not match the quantity of balls visible from the participant's and avatar's viewpoints. For the trials involving an incongruent viewpoint, the number corresponded to the quantity of balls visible only from the avatar's viewpoint. Following the procedures from Ref. [24], we created six "filler trials" corresponding to a visual scene containing no ball on the left and right walls and for which the number "0" shown after the question was the correct answer. Visual stimuli were presented as 35 × 20 cm images on a computer screen.

Explicit perspective taking task (EPT task). Visual stimuli were identical to the 10 stimuli created for the IPT task, with the same avatar at the center of the screen facing one of the walls (Fig 1A). Here, the instruction differed: participants were explicitly asked to take the avatar's viewpoint (explicit third-person perspective taking, EPT).

Each trial started with the presentation of a white fixation cross on a black background for 750 ms. This was followed by the presentation of the question "How many blue balls does the character see?" for 1500 ms and the presentation of a number (0, 1, 2 or 3) for 1000 ms. Then, one of the visual scenes was presented. Participants were instructed to indicate as quickly and accurately as possible whether the number of balls seen by the character matched the number specified after the question. Participants responded using the same two buttons on a keyboard as for the IPT task.

As for the IPT task, we included trials in which the participant and the avatar could "see" the same number of balls (i.e., congruent viewpoint) or a different number of balls (i.e., incongruent viewpoint). Half of the trials were "matching trials" and the other half were "mismatching trials" and we included six filler trials.

Visuo-spatial control task (VSC task). To control for visuo-spatial and attentional bias in the IPT and EPT tasks, participants completed a visuo-spatial control task (VSC task) involving neither implicit nor explicit perspective taking. Here, a grey rectangle (a geometric shape devoid of social meaning) replaced the avatar at the center of the screen (for similar procedures, see Ref. [24,25,49]) (Fig 1A). The control task aimed to control for (1) differences in visual processing, motor response accuracy and speed between BVF patients and controls and (2) visuo-spatial effects that may account for longer response times in incongruent trials (balls on one wall or on two opposite walls) as compared to congruent trials (balls always on the same wall).

An arbitrary "orientation" of the rectangle in the room was created by coloring the left and right sides of the rectangle in orange or green. Half of the participants were presented with the right side of the rectangle in orange and the left side in green, and other participants were presented with the opposite orientation. Spatial arrangements of the balls labeled "congruent viewpoint" in the IPT task were considered the congruent viewpoint in the control task and vice versa for trials labeled "incongruent viewpoint" in the IPT task (Fig 1A).

As for the IPT task, the VSC task involved matching trials in which the number specified after the question matched the number of balls visible from the participant's viewpoint. In the

other half of the trials (i.e., mismatching trials), the number specified after the question differed from the quantity of balls the participant could see. Six filler trials were also presented. The VSC task involved the same instructions, experimental procedures and timing of events presentation as for the IPT task.

Experimental procedures. For all three tasks, participants sat on a chair facing a screen placed on a table. Their heads were aligned with the center of the screen, which was at a viewing distance of 70 cm. A keyboard was placed on the table in front of participants.

For each task, participants completed a total of 78 trials presented in random order in 2 blocks of 39 trials. There was an equal number of matching trials ($n = 39$) and mismatching trials ($n = 39$), and an equal number of trials with congruent ($n = 36$) and incongruent ($n = 36$) viewpoints. Before the experiment, participants completed a training session consisting of a random selection of 20 trials for familiarization with the keyboard and experimental procedures.

Participants first performed the VSC task then the IPT task and the EPT task. This order was chosen because our pilot experiments [50] and other studies [25,49] showed that performing the IPT or EPT tasks first changes reaction times in a control task presenting a non-corporeal object (i.e., a rectangle or an arrow). Accordingly, since the control task was a baseline to measure the participant's ability to process space, it was always conducted first. To allow for between-group comparisons, the sequence was identical for the BVF patients and healthy controls.

Data analysis. We calculated the mean response time and percentage of correct answers for the matching trials. Data for mismatching trials and filler trials were discarded from the analysis according to previous studies [24]. Trials yielding incorrect answers were discarded from the analysis of the response times and we removed trials for which response times exceeded 2 standard deviations of the participant's grand average. We focused on response times, shown to be more sensitive than accuracy to multisensory conflicts [51–53]. For the three tasks, response times were analyzed by repeated-measures ANOVAs with Statistica, Version 12 SP3 (StatSoft Inc.), with Viewpoint (congruent vs incongruent) as a within-subject factor and with Group (BVF patients vs controls) and Gender (female vs male) as between-subject factors. Main effects and interactions were considered significant at $p < 0.05$. We also calculated a congruency effect (CE), adapted from the cross-modal CE used to investigate visual-tactile and visuo-vestibular conflicts [51–53]. For each of the three tasks, CE was calculated as the difference in response times between the incongruent and congruent viewpoints.

Results

IPT task. Results showed a main effect of Viewpoint ($F_{1,40} = 22.87$, $p < 0.0001$, $\eta^2_p = 0.36$). As predicted, the mean response time was significantly longer when participant's and avatar's viewpoints were incongruent (mean \pm SD: 1040 ± 234 ms) than congruent (995 ± 230 ms), thereby showing a typical pattern of "altercentric intrusion" (Fig 2A). There was no main effect of Group ($F_{1,40} = 1.27$, $p = 0.27$, $\eta^2_p = 0.03$) and no Viewpoint \times Group interaction ($F_{1,40} = 0.90$, $p = 0.35$, $\eta^2_p = 0.02$), showing no effect of vestibular deficits on altercentric intrusion. There was no main effect of Gender ($F_{1,40} = 1.38$, $p = 0.25$, $\eta^2_p = 0.03$), but a significant Viewpoint \times Gender interaction ($F_{1,40} = 4.43$, $p < 0.05$, $\eta^2_p = 0.10$). Although response times were longer with incongruent than congruent trials for both females (planned comparison: $F_{1,40} = 20.07$, $p < 0.0001$) and males ($F_{1,40} = 4.38$, $p < 0.05$), the statistical difference was stronger in females. In addition, the CE was numerically larger for females (70 ± 63 ms) than males (27 ± 67 ms).

EPT task. As predicted, again we found a main effect of Viewpoint ($F_{1,40} = 10.61$, $p < 0.01$, $\eta^2_p = 0.21$), with significantly longer response times when the participant's and avatar's viewpoints were incongruent (mean \pm SD: 956 ± 268 ms) than congruent (925 ± 239 ms). This

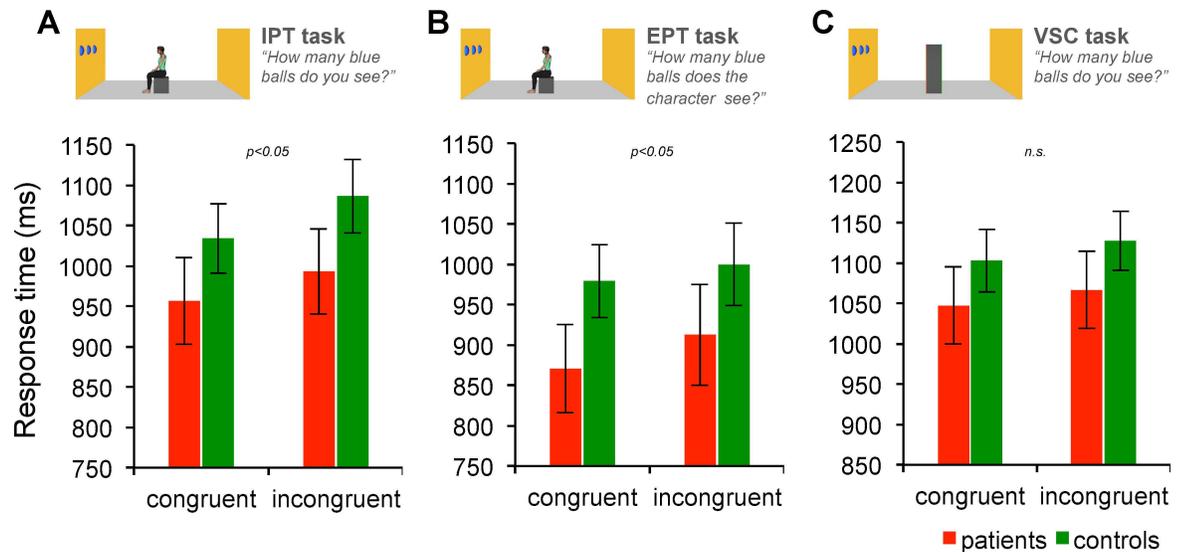


Fig 2. Results for the visuo-spatial perspective-taking tasks (Experiment 1; Response times). Histograms represent the effect of the within-subject factor Viewpoint, which was significant for the implicit perspective-taking (IPT) task ($p < 0.05$) and the explicit perspective-taking (EPT) task ($p < 0.05$), but not for the visuo-spatial control (VSC) task (n.s.: not significant). Data for patients and controls are shown separately for illustration purposes only. Vertical bars represent the standard error of the mean.

doi:10.1371/journal.pone.0170488.g002

finding indicates a typical pattern of “egocentric intrusion” (Fig 2B). We found no main effect of Group ($F_{1,40} = 1.18$, $p = 0.28$, $\eta^2_p = 0.03$) and no Viewpoint \times Group interaction ($F_{1,40} = 0.50$, $p = 0.49$, $\eta^2_p = 0.01$), which again shows no effect of vestibular deficits on altercentric intrusion, and no effect of Gender ($F_{1,40} = 0.44$, $p = 0.51$, $\eta^2_p = 0.01$).

VSC task. In contrast to IPT and EPT tasks, analysis of the response times for the VSC task depicting a non-human object revealed no effect of Viewpoint ($F_{1,40} = 2.53$, $p = 0.12$, $\eta^2_p = 0.06$). Thus, response times did not differ for incongruent (1097 ± 200 ms) and congruent (1075 ± 203 ms) viewpoints (Fig 2C). We found no significant effect of Group ($F_{1,40} = 0.66$, $p = 0.42$, $\eta^2_p = 0.02$), no Viewpoint \times Group interaction ($F_{1,40} = 0.08$, $p = 0.77$, $\eta^2_p < 0.01$) and no effect of Gender ($F_{1,40} = 0.52$, $p = 0.47$, $\eta^2_p = 0.01$).

Congruency effects. We compared the CE between groups for both perspective taking tasks and VSC tasks (Fig 3). Although the CE for the IPT task was numerically lower for the BVF patients (37 ± 78 ms) than controls (53 ± 57 ms), which suggests reduced altercentric intrusion for patients, the difference was not statistically significant ($F_{1,42} = 0.63$, $p = 0.43$, $\eta^2_p = 0.02$). An opposite trend was found for the EPT task, with numerically higher CE for patients (42 ± 72 ms) than controls (21 ± 61 ms), which suggests increased egocentric intrusion for patients, but the difference was not statistically significant ($F_{1,42} = 1.06$, $p = 0.31$, $\eta^2_p = 0.01$). Post-hoc analyses revealed that CEs were significantly different from zero for the perspective taking tasks (except for controls in the EPT task) but never for the VSC task.

Experiment 2

Experiment 2 was designed to measure implicit perspective taking in BVF patients using a tactile task instead of a visuo-spatial task, as in Experiment 1 and in previous studies [54–56]. We adapted a tactile perception task referred to in the literature as a “graphaesthesia” task. The task consists of drawing ambiguous letters (such as d, b, p and q) on the participant’s forehead directly with the experimenter’s finger [57], a cotton bud [23], or a mechanical device [58]. Participants may perceive letters drawn on their forehead from an egocentric, first-person

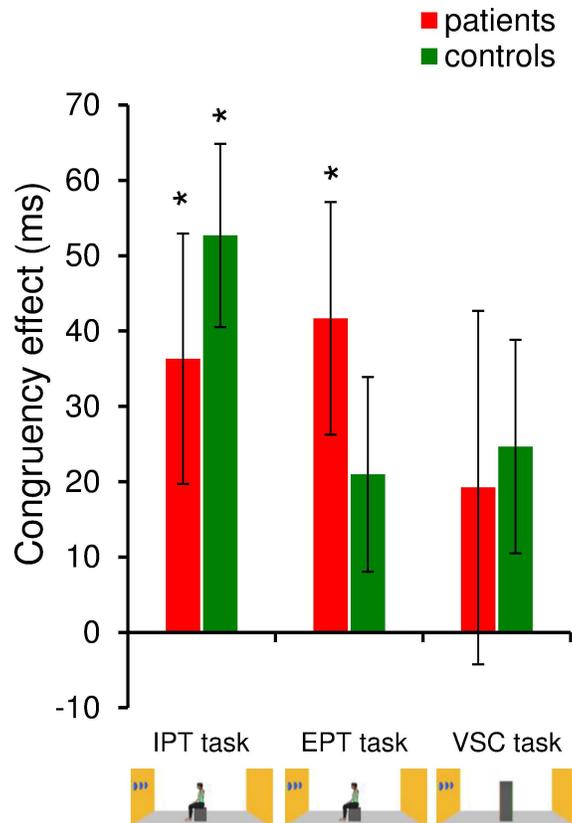


Fig 3. Results for the visuo-spatial perspective-taking tasks (Experiment 1; Congruency effects). Histograms represent the average congruency effect (incongruent viewpoint minus congruent viewpoint) calculated for the implicit perspective-taking (IPT) task, explicit perspective-taking (EPT) task, and visuo-spatial control (VSC) task for patients and controls. * indicates significant differences with respect to zero (t-test). Vertical bars represent the standard error of the mean.

doi:10.1371/journal.pone.0170488.g003

perspective (e.g., they perceive the letter “d” after the letter “b” is drawn on their forehead) or from a disembodied, third-person perspective (e.g., they perceive the letter “d” after the letter “d” is drawn) (reviewed in [59]). An early study by Natsoulas and Dubanoski [27] revealed that 70% of participants experienced ambiguous letters drawn on their forehead according to a first-person perspective. Interestingly, this proportion changed depending on the site of stimulation and the spatial orientation of stimulated body parts [27,60–62]. For example, only 13% of participants used a first-person perspective when letters were drawn on the back of their head, whereas about 50% of participants used a first-person perspective for letters drawn on the side of their head [27]. Altogether, these data indicate that interpreting tactile patterns on the skin varies across participants and may reflect sensory and cognitive styles, such as those involved in visual field dependence/independence. Accordingly, the graphaesthesia task constitutes a valid measure of implicit perspective taking [23,60].

Two opposite predictions can be made regarding the consequences of BVF in the graphaesthesia task: (1) If vestibular signals are involved in simulating another person’s perspective, as suggested by healthy participant research [45], the lack of vestibular information in BVF patients may promote tactile perception according to a first-person perspective. (2) Conversely, if vestibular signals anchor the self to the body, as suggested by the effect of galvanic vestibular stimulation in healthy participants [23], BVF patients without vestibular signals may more easily take a disembodied viewpoint.

Methods

Participants. Twenty-three BVF patients (9 females and 14 males, mean age \pm SD: 61 ± 11 years, 22 right-handed and 1 left-handed, Edinburgh Handedness inventory [47]: $90 \pm 30\%$, duration of education: 4 ± 2 years) and 23 healthy volunteers (mean age: 59 ± 12 years, all right-handed, Edinburgh Handedness inventory: $93 \pm 15\%$, duration of education: 6 ± 3 years) participated.

Tactile stimuli and experimental procedures. Procedures for this graphaesthesia task were adapted from those used by Ferrè *et al.* [23] and by Natsoulas and Dubanoski [27]. Before the experiment, participants were verbally instructed that the experimenter would draw letters on their forehead or their neck (on the back of the head below the hairline) by using a cotton bud (Fig 4A). Participants were informed that only one of those letters—d, b, p, q, n, v, w and o—would be drawn on their skin, and they were instructed to report as spontaneously as possible the letter they experienced (Fig 4B). The experimenter traced the letters by using a cotton bud in a single continuous motion on the skin. To increase the difficulty of the task and to not cue participants to select a strategy based on the direction of the writing, all letters were drawn with the motion starting from one or the other end of each letter, so that letters were traced according to a canonical or non-canonical direction of writing. Thus, participants first had to create a representation of the global shape of the letter before giving an answer, because the direction of the writing was uninformative.

Participants were comfortably seated on a chair and were instructed to close their eyes throughout the recording session. In one session, the experimenter sat in front of the participant and drew the letters on the central part of the participant's forehead. In the other session, the experimenter sat at the back of the participant and drew the letters on the participant's neck. Each session comprised 48 trials, including 32 presentations of ambiguous letters (8 presentations of d, b, p and q) and 16 presentations of non-ambiguous letters (4 presentations of n, v, w and o). Letters with their direction of drawing were presented on a computer screen to the experimenter in a randomized order by using PsychoPy2 (v1.82.01) [48]. The experimenter used a

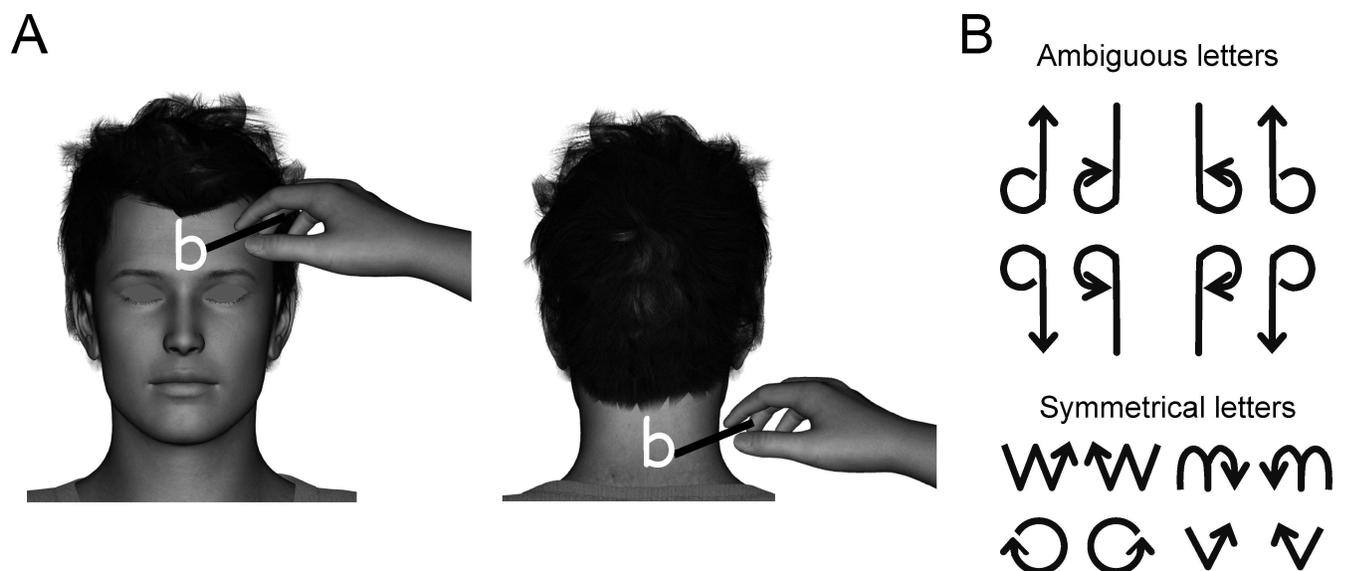


Fig 4. Methods for the graphaesthesia task (Experiment 2). (A) The experimenter drew letters on the participants' forehead and neck by using a cotton bud while participants kept their eyes closed. (B) Letters included ambiguous, non-symmetrical letters (b, d, p, q) and non-ambiguous, symmetrical letters (w, n, o, v) that were all drawn in the canonical direction of writing or in the reverse direction, starting from the opposite end of the letter. All letters were drawn by using a single and continuous hand motion.

doi:10.1371/journal.pone.0170488.g004

keyboard to manually enter participants' verbal responses, which were saved by using PsychoPy and processed offline.

Data analysis. To measure the degree of anchoring the self to the body, we calculated the proportion of ambiguous letters (d, b, p and q) that were experienced from a first-person perspective (e.g., when participants reported the letter "q" after the experimenter drew the letter "p" on their skin) [23]. The ability to correctly represent the pattern of letters drawn on the skin was calculated as the proportion of correct identification of symmetrical letters (n, v, w and o). Data were analyzed by using repeated-measures ANOVAs with the Site of stimulation (forehead vs neck) as a within-subject factor and with the Group (BVF patients vs controls) and Gender (female vs male) as between-subject factors.

Results

Analysis of the proportion of ambiguous letters experienced from a first-person perspective revealed a significant main effect of the Site of stimulation ($F_{1,42} = 68.96$, $p < 0.001$, $\eta^2_p = 0.62$). Fig 5 shows that letters were more often experienced from a first-person perspective when drawn on the forehead (mean percentage of trials \pm SD: $60 \pm 31\%$) and almost never from a first-person perspective when drawn on the neck ($10 \pm 18\%$). We found no main effect of Group ($F_{1,42} = 0.40$, $p = 0.53$, $\eta^2_p = 0.01$) and no significant Site of stimulation \times Group interaction ($F_{1,42} = 0.01$, $p = 0.93$, $\eta^2_p < 0.001$). There was a significant main effect of Gender (Fig 5): letters were more often experienced from a first-person perspective for females ($40 \pm 15\%$) than males ($30 \pm 15\%$; $F_{1,42} = 5.20$, $p < 0.05$, $\eta^2_p = 0.11$).

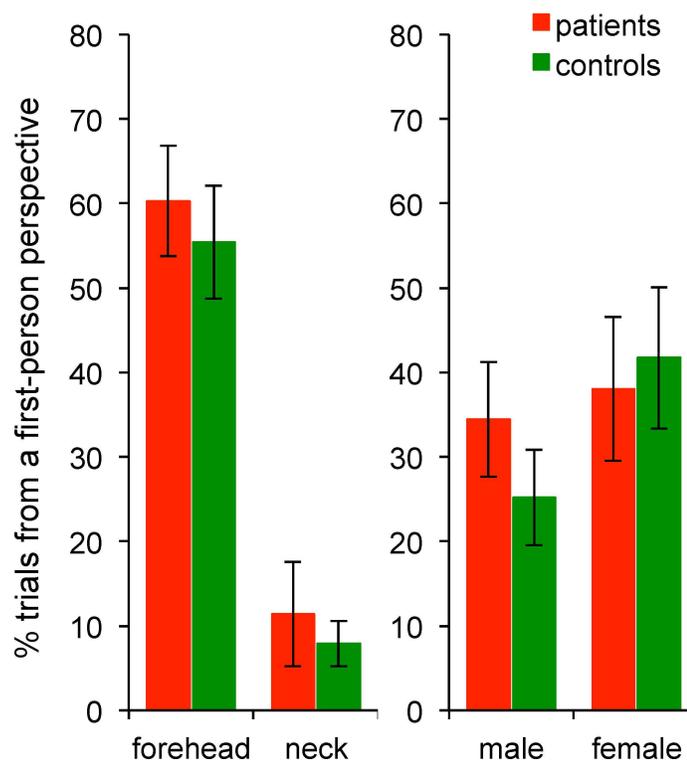


Fig 5. Results from the graphaesthesia task (Experiment 2). Histograms on the left represent the main effect of the within-subject factor Site of stimulation and histograms on the right represent the main effect of the between-subject factor Group. Data from patients and controls are shown separately for illustration purposes only. Histograms represent the mean of the percentage of trials perceived from a first-person perspective and vertical bars represent the standard error of the mean.

doi:10.1371/journal.pone.0170488.g005

Analysis of the proportion of correct identification of symmetrical letters revealed a similar performance for both Groups ($F_{1,42} = 0.01$, $p = 0.94$, $\eta^2_p = 0.001$) and Genders ($F_{1,42} = 0.1$, $p = 0.75$, $\eta^2_p = 0.002$). Participants discriminated letters better when drawn on their forehead than on their neck as revealed by a main effect of Site of stimulation ($F_{1,42} = 7.62$, $p < 0.01$, $\eta^2_p = 0.15$). There was no significant interaction.

Experiment 3

Anecdotal reports in the clinical literature suggest that acute vestibular disorders may impair bodily self-consciousness, for example, evoking sensations that the body feels enlarged, strange, or unreal [18,19]. The subjective content of these symptoms is evocative of depersonalization disorders [21]. Studies involving the depersonalization-derealization questionnaire from Cox and Swinson [63] reported a higher incidence of depersonalization in patients with vestibular disorders than healthy participants and greater incidence of depersonalization in bilateral than unilateral vestibular disorders [64–67]. The Cox and Swinson questionnaire [63] includes items tapping self/body and self/environment relationships, such as “*feeling detached or separated from [the] body*” and “*feeling of detachment or separation from surroundings*” that vestibular patients report significantly more often [64]. Yet, it is notable that there is only few descriptions of complete out-of-body experiences in vestibular disorders [18,19,21,68]. Here, we measured the experienced self/body and self/environment “closeness” in idiopathic BVF patients by using questionnaires.

Methods

Participants. Twenty-two BVF patients (8 females and 14 males, mean age \pm SD: 61 ± 11 years, 21 right-handed and 1 left-handed, Edinburgh Handedness inventory [47]: $90 \pm 30\%$, duration of education: 4 ± 2 years) and 22 healthy volunteers (mean age \pm SD: 59 ± 12 years, 22 right-handed: $93 \pm 13\%$, duration of education: 6 ± 3 years), who also took part in Experiment 2 filled out a questionnaire.

Subjective reports. Participants completed a four-item questionnaire about the perceived closeness between their self and body (Item 1), self and immediate body environment (Item 2), body and immediate body environment (Item 3), and self and others (Item 4). They were asked to answer in terms of their average perception over the last year. Participants had to select one of seven pictorial descriptions (Fig 6) of the degree of closeness between their self and body, for example, whereby two distinct circles represent clear separation between the self and the body (score = 1) and two overlapping circles represent high closeness between their self and body (score = 7). This simple, pictorial description of closeness was adapted from the “Inclusion of Other in the Self” (IOS) scale developed by Aron *et al.* [28] to measure interpersonal closeness.

Results

For each questionnaire item, the degree of closeness reported was converted into a score ranging from 1 to 7 (Fig 6). Scores for the BVF patients and controls were compared by a non-parametric statistical procedure based on the Mann-Whitney U test (i.e., nonparametric alternative to the *t*-test for independent samples). Patients and controls reported a similar degree of closeness between their self and body ($U = 235$, $Z = -0.16$, $p = 0.87$), self and immediate body environment ($U = 170$, $Z = 1.69$, $p = 0.09$), body and immediate body environment ($U = 217$, $Z = 0.59$, $p = 0.56$), and self and others ($U = 226$, $Z = 0.36$, $p = 0.72$). Finally, a separate analysis revealed no modulation of the scores by Gender as a between-subject factor (all $U > 183$, $Z < 0.99$ and $p > 0.32$).

Discussion

Three experiments revealed that severe bilateral vestibular hypofunction does not change the anchoring of the self to the body. Although negative findings are difficult to interpret, they should be reported more systematically in behavioral and clinical neuroscience [69,70]. Hereafter we discuss our results with respect to current multisensory models of embodiment and compare results from each experiment with earlier studies, while pointing out the limitations of the present study.

Multisensory mechanisms of embodiment

The negative findings from this study shed light on the multisensory mechanisms of embodiment. Current neuroscientific models of embodiment propose that the common experience of

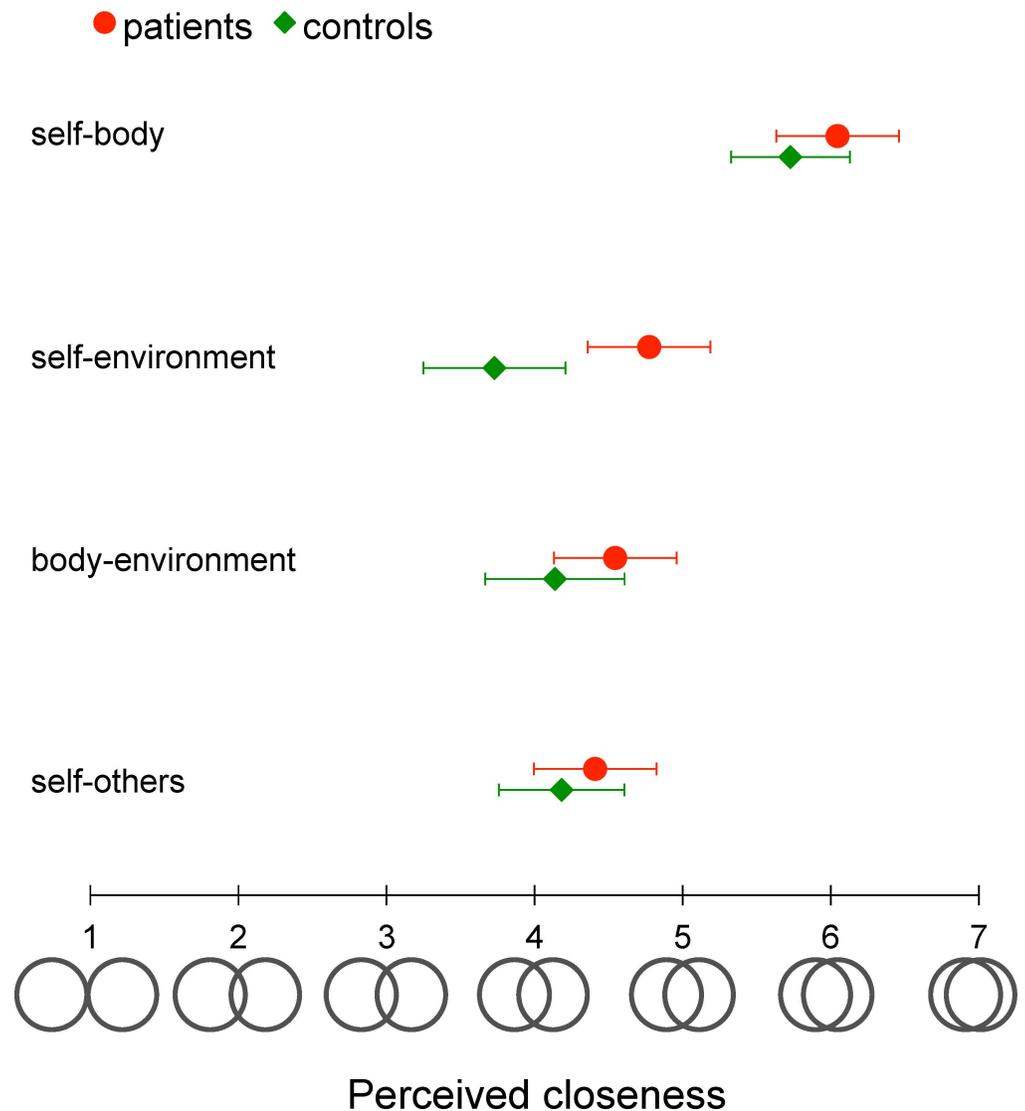


Fig 6. Subjective measures of self-body anchoring (Experiment 3). Pictorial descriptions used to measure the closeness between the self, body, environment and others. Seven pairs of circles shown at the bottom of the figure were presented to participants, who had to indicate which one better represented the perceived degree of “closeness” between two items, such as the self and body. Colored symbols represent the mean of self-reports from patients and controls and horizontal bars represent the standard error of the mean.

doi:10.1371/journal.pone.0170488.g006

an embodied self relies on normal integration of sensory signals, including vestibular signals [5,16]. These models also predict that a multisensory conflict can evoke the experience that the self is disconnected from the body [5,22].

BVF patients were tested when most of their functional deficits were moderated and they usually did not complain about vertigo and dizziness. Because vestibular information is missing in these patients, it does not contradict nor confirm visual and somatosensory signals during body motions. Accordingly, there should be no sensory mismatch and perceptual incoherence due to bilateral vestibular failure. By contrast, in patients with acute peripheral vestibular disorders, the central nervous system receives signals from the inner ear about self-motion and self-orientation that are incongruent with visual and somatosensory signals, thereby creating sensory mismatch and perceptual incoherence. We propose that abnormal forms of anchoring the self to the body may arise from perceptual incoherence in acute vestibular disorders but not from long-lasting vestibular deafferentation. Indeed, disorders of the bodily self have been reported in clinical conditions such as Menière's disease [21], recurrent vertigo attacks [68] and epileptic vertigo [71], which are characterized by episodes of strong perceptual incoherence. By contrast, we found no objective measure in the clinical literature showing that bilateral vestibular loss may evoke strong disembodied self-location.

The normal embodiment we found in BVF patients also suggests that the mechanisms underpinning the experience of an embodied self and first-person perspective are robust. Neurologically normal individuals rarely spontaneously report disembodied experiences, unless they experience multisensory conflicts. For example, Pfeiffer *et al.* [12] used visuo-tactile conflicts in healthy participants and could manipulate the direction of their first-person perspectives. Yet, the origin of the first-person perspective invariably remained bound to self-location. In addition, low-intensity galvanic vestibular stimulation promoted a first-person perspective in healthy participants during the graphaesthesia task [23]. This suggests that weak vestibular stimulation may increase the natural tendency of the vestibular system to anchoring the self to the body. In conclusion, we propose that when vestibular information does not conflict with visual and somatosensory signals, as in healthy participants and BVF patients, visuo-spatial processing from a first-person perspective may be unaffected.

We cannot exclude that our negative findings are due to some patients having a severe bilateral vestibular hypofunction rather than a total bilateral vestibular loss. If vestibular signals anchor the self to the body, even a weak residual vestibular function may be enough to maintain a coherent experience of an embodied self. Yet, additional analyses (not presented here) revealed that patients with and without cervical VEMPs had similar performances in the three experiments. Finally, because vestibular signals have been involved in both anchoring the self to the body (egocentric viewpoint) [23] and in simulating another person's viewpoint (allocentric viewpoint) [45], an alternative explanation for our negative findings could be that these effects tend to cancel each other out. It is unknown from the literature whether vestibular signals are more important for anchoring the self to the body or changing the viewpoint.

The negative findings we report here may also be due to the nature of the task. In Experiments 1 and 2, we used implicit perspective taking tasks. Participants did not explicitly evaluate their self-location and self-identification with an avatar in their environment, as done in experiments using visuo-tactile stimulation [9–14,72,73]. In these experiments, participants received a tactile stimulation on their back or chest while they observed in a head-mounted display an avatar being stroked at the same time on the same body region [9–11,13]. Participants self-identified with the avatar and localized themselves closer to it (i.e., disembodied self-location; for reviews see Ref. [5,74]). Variants of these illusions evoked sensations of body translation, lightness and levitation [11–13], which are reminiscent of otolithic vestibular sensations. By contrast, when tested with variants of the illusions that do not alter self-location,

participants do not report vestibular sensations [72,73]. These data suggest a relation between disembodied self-location and vestibular information processing. It is likely that if BVF patients (or patients with unilateral vestibular disorders) were tested using paradigms of visuo-tactile stimulation, their self-location and self-identification would differ from that of healthy controls as they strongly rely on visual information for self-orientation [75]. This hypothesis seems supported by a recent case study by Kaliuzhna *et al.* [68]. A patient with a unilateral vestibular disorder, who already had out-of-body experiences, reported during synchronous visuo-tactile stimulation a stronger sensation that he was floating in the air than control participants. The anchoring of the self to the body should now be investigated in large samples of BVF patients and patients with unilateral vestibular disorders using experimental inductions of out-of-body—like experiences, in order to fully understand the vestibular contributions to embodiment.

Comparison with previous findings

Implicit visuo-spatial perspective taking. As predicted, our data revealed a typical pattern of altercentric intrusion: participants spontaneously adopted the perspective of the avatar to the detriment of visuo-spatial processing from their own perspective (i.e., longer reaction times for incongruent viewpoint). The data also revealed an egocentric intrusion effect, whereby participants did not ignore their own perspective when required to simulate the viewpoint of a distant avatar [24–26,42]. Finally, our data indicate that altercentric and egocentric intrusion effects exist in participants older (mean age 66 years old) than previously tested healthy populations (e.g., mean age was 21 in Ref. [24]; 22 in Ref. [25]; 22 in Ref. [26]).

There is now convincing evidence that altercentric intrusion cannot be accounted for by unspecific attentional and visuo-spatial bias (see Ref. [42]). In contrast with most studies of implicit perspective taking, Santiesteban *et al.* [49] proposed that the mere presence of an avatar gazing to one side of a virtual room redirects spatial attention to this side of the room, thereby accounting for the altercentric intrusion effect. For these authors, altercentric intrusion reflects automatic attentional orienting rather than perspective taking. Because of time constraints in Experiment 1 and the effect of the order of task presentation (see [Methods](#)), we could not add another control task presenting an arrow instead of an avatar. Yet, some evidence suggests that when the avatar is replaced by an arrow pointing to one side of the virtual room (which also draws the participant's attention to this direction), the incongruence of the viewpoint is weaker than when an avatar is presented [25,50]. These data indicate that the presence of the avatar does more than merely draw the participant's attention to one side of the virtual room.

Implicit non-visual perspective taking (graphaesthesia task). Our results showed that participants implicitly used different perspectives when letters were drawn on their forehead or the back of their head. In many trials (58%), participants used a first-person perspective when ambiguous letters were traced on the forehead but mainly an external, third-person perspective when traced on their back. In addition, 63% of the patients and 63% of the controls preferentially used a first-person perspective to interpret letters drawn on their forehead. This percentage dropped to only 4% for patients and 0% for controls when letters were drawn on the back of their neck. Such percentages are congruent with data from Natsoulas and Dubanoski [27], showing that 70% of the participants preferentially used a first-person perspective for letters drawn on their forehead, whereas 13% used this strategy for letters drawn on the back of their head. Overall, our results agree with previous studies for letters drawn manually by an experimenter [23,27] or automatically with a mechanical device [58]. We note that the fact that an experimenter, instead of a mechanical device drawing letters on the participant's

skin may have increased the likelihood that participants used a third-person perspective. This proposition agrees with implicit perspective taking when a conspecific is located in the participant's immediate visual environment [24,37].

Another finding of our study was a main effect of the Gender, in that female participants more often used a first-person perspective than did males, which shows an overall stronger anchoring of the self to their body. Gender effects in perspective-taking tasks are controversial, but we have some evidence that females simulate another person's visuo-spatial perspective [76,77] or perform own-body mental transformation tasks [78] differently from males. In particular, females had longer response times during perspective-taking tasks and were more prone to conflicts between their own body posture and that of a seen individual [76]. Such effects may relate to different cognitive strategies and brain mechanisms used by females and males for mental imagery of objects and bodies, as suggested by early functional neuroimaging studies [79,80].

Subjective reports. The IOS scale measuring the perceived closeness between the self and the body did not reveal differences between BVF patients and controls. This result seems to contrast with the greater occurrence of depersonalization-derealization symptoms in vestibular patients than healthy volunteers [64,65,67]. Jauregui-Renaud *et al.* [65] found greater depersonalization-derealization scores for BVF patients than unilateral vestibular-defective patients. Yet, previous studies used a global score of depersonalization-derealization derived from questionnaire items assessing various aspects of the patient's perception [63]. As a result, whether responses to questionnaire items specifically investigating the anchoring of the self to the body differ for BVF patients and controls remain unknown.

Limits of the study and future directions

The present findings must be considered with caution because many factors can influence perspective taking and the sample size was limited. Although we controlled for age, gender and education level, which all influence perspective taking [81,76,78], cultural factors [77], personality traits [25,53,78] or anxiety [82] can also play a significant role and may have introduced variability in the data. In addition, we did not perform a power analysis before we included participants; we were constrained by the number of patients with severe BVF, which is a rare condition. Yet, a power analysis for repeated-measures ANOVAs ran *a posteriori* showed that the sample size was not underestimated for Experiments 1 and 2 (G*Power [83]: $f = 0.3$, $\alpha = 0.05$, power = 0.8). By contrast, the number of participants was underestimated for Experiment 3, for which a sample size of $n = 27$ per group (instead of $n = 22$) was required (based on a power analysis for Mann-Whitney tests using G*Power [83]: $d = 0.8$; $\alpha = 0.05$, power = 0.8).

As noted above, embodiment may be distorted in BVF patients tested with paradigms designed to evoke 'out-of-the body' self-locations [9,10,73] and this should be the topic of future investigations. It might also be interesting to evaluate the consequence of acute unilateral vestibular failure (UVF) on anchoring the self to the body. This would allow to compare the consequence of left vs. right UVF as there is an ipsilateral dominance of the vestibulo-thalamo-cortical pathways, and an overall right hemisphere dominance for vestibular information processing in right-handed participants [84,85]. Left and right UVF impact differently visuo-spatial tasks, with a stronger impact of left UVF on the perceived straight-ahead [86], and a stronger impact of right UVF on visual vertical perception [87]. Interestingly, out-of-body experiences have been related to the right temporo-parietal junction [7,11], an important region of the cortical vestibular network [88,89]. Due to the ipsilateral predominance of the vestibulo-thalamo-cortical pathways, patients with right UVF may be more prone to disembodied self-location. This hypothesis should be tested using implicit perspective tasks, such as

those used in the present study, and using multisensory conflicts designed to evoke out-of-body—like experiences [9,10,73].

Acknowledgments

Christophe Lopez's research is supported by a grant from the VolkswagenStiftung (Grant no. 89434: "Finding Perspective: Determining the embodiment of perspectival experience"). The sponsor was not involved in the study design, collection, analysis, and interpretation of data, writing the report and in the decision to submit the manuscript for publication. We thank Maxime Guyon and Anne Cassoulet for helping with data collection.

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Formal analysis: DD CL.

Funding acquisition: CL.

Investigation: DD CL UD CH CV MT.

Methodology: DD CL UD CH CV MT.

Project administration: MT CL.

Resources: MT CL.

Software: DD CL.

Supervision: CL MT.

Validation: DD CL UD CH CV MT.

Visualization: DD CL UD CH CV MT.

Writing – original draft: CL DD MT CV.

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