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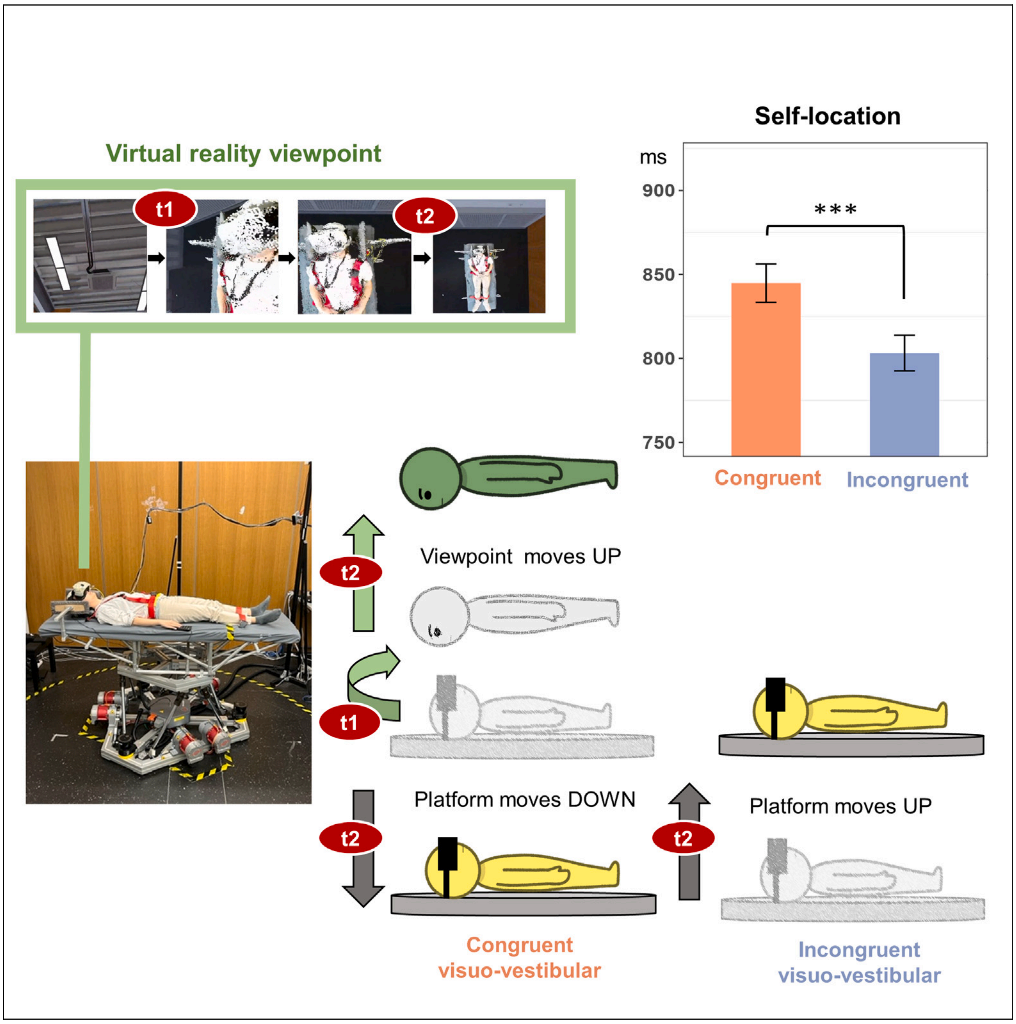

Hsin-Ping Wu,
Estelle Nakul,
Sophie Betka,
Florian Lance,
Bruno Herbelin,
Olaf Blanke

olaf.blanke@epfl.ch

Highlights

Immersive visual-vestibular stimulation can induce out-of-body-like experiences

Induced sensations involve elevated self-location, disembodiment and lightness

Effects are stronger when vestibular direction is congruent with visual self-motion

Individual visual-vestibular sensory weighting modulates disembodiment experience

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Out-of-body illusion induced by visual-vestibular stimulation

Hsin-Ping Wu,[1] Estelle Nakul,[1] Sophie Betka,[1] Florian Lance,[1] Bruno Herbelin,[1] and Olaf Blanke[1,2,3,*]

SUMMARY

Out-of-body experiences (OBEs) are characterized by the subjective feeling of being located outside one's physical body and perceiving one's own body from an elevated perspective looking downwards. OBEs have been correlated with abnormal integration of bodily signals, including visual and vestibular information. In two studies, we used mixed reality combined with a motion platform to manipulate visual and vestibular integration in healthy participants. Behavioral data and questionnaires show that congruent visual-vestibular stimulation in a self-centered reference frame induced an OBE-like illusion characterized by elevated self-location and feelings of disembodiment and lightness. The OBE-like illusion was also modulated by individuals' visual field dependency assessed by the Rod and Frame Test. These results show that the manipulation of visual-vestibular stimulation in the present study induces various aspects of OBEs and further link OBE to congruency mechanisms between visual and vestibular gravitational and self-motion cues.

INTRODUCTION

A core dimension of consciousness includes a subject of conscious experience and a recently established way to investigate this aspect of consciousness (self-consciousness) is to explore the link between the subject or self and its bodily foundations, which refers to the concept of bodily self-consciousness (BSC[1]). BSC is an implicit and pre-reflexive account of self-consciousness[2] and consists of different aspects including self-identification (the experience of being identified with a physical body), self-location (the experience of occupying and being located within a defined volume of space, usually overlapping with the body) and first-person perspective (the experience of perceiving the world from a particular viewpoint, usually centered on the body, and with a particular direction). Altered states of BSC such as out-of-body experiences (OBEs) provide opportunities to better understand the multisensory bases of BSC.[3–5] OBEs are mental states during which a person feels located outside of her body, usually in a new elevated location (e.g., in Green[6]). OBEs are often associated with visual impressions such as observing the environment from a new elevated location, as if seeing the world and one's body from that elevated location and perspective.

OBEs have also been related to the vestibular system as they are frequently associated with otolithic vestibular sensations such as self-motion, flying, weightlessness, and floating.[3,4,6,7] OBEs are usually reported with subjects in supine position,[6,8] a position known to reduce vestibular and somatosensory graviceptive cues.[8] It has also been found that vestibular patients are more likely to report OBEs[9] and OBEs occur with disruptions of activity at the temporo-parietal junction (TPJ) due to direct electrical stimulation[7] or different neurological conditions.[10–12] The TPJ is one of the core regions for vestibular processing as well as multisensory integration.[13] Collectively, these observations led to the proposal that visual and vestibular signals and the combination of such cues contribute to OBEs.[3,7,14] However, OBE studies in neurological and ontological patients are rare and such clinical studies may not inform about the multisensory mechanisms of OBEs in the healthy population.

Full body illusions (FBIs) are experimentally controlled altered states of BSC aiming to reproduce experiences close to the phenomenology of OBEs,[15,16] including altered self-location and first-person perspective (1PP). FBI paradigms rely on exposing participants to conflicting or incongruent bodily cues. In the original FBI developed by Lenggenhager and colleagues,[16] the participants were stroked on their back and wore a head-mounted display (HMD) in which they observed their body being touched on the back. The video presented through the HMD could either be synchronous, when the observed and felt touch on the back are presented at the same place at the same time, or asynchronous, when the video is presented with a delay. A similar but different setup was employed by Ehrsson,[17] where participants were stroked on their chest while watching synchronous or asynchronous stroking applied to a camera placed behind them. In this study, participants reported feeling located at the location of the camera in a synchronous visuo-tactile condition. Both Leggenhager and colleagues' and Ehrsson's experiments, as well as their follow-up studies,[18–21] demonstrated that the elicitation of changes in BSC depends on the multisensory integration of bodily signals, including visual, tactile, and proprioceptive signals (see Blanke, Slater and Serino[22] and Park and Blanke[23] for detailed

[1]Laboratory of Cognitive Neuroscience, Neuro-X Institute & Brain Mind Institute, Faculty of Life Sciences, Ecole Polytechnique Fédérale de Lausanne, Geneva, Switzerland
[2]Department of Clinical Neurosciences, University Hospital Geneva, Geneva, Switzerland
[3]Lead contact
*Correspondence: olaf.blanke@epfl.ch
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reviews). On the other hand, based on clinical observations of OBEs regarding vestibular and gravitational sensations,[3,7] several subsequent adaptations of this paradigm additionally manipulated the congruency between visual and vestibular gravitational information.[24,25] One way to manipulate vestibular gravitational information and their congruency with visual gravitational cues is to have participants lying in one position while presenting the avatar in another body position in VR (e.g., standing or prone position). In an FBI experiment with participants in supine position, self-location and 1PP direction were found to be modulated by directionally conflicting otolithic vestibular and visual gravitational cues.[15] Individual visual-vestibular weighting strategies (tested by measuring visual field dependency) were also found to influence self-location and 1PP direction changes. Using the well-established Rod and Frame Test, in which participants have to make perceptual verticality judgments in a visually biased context,[26–28] Pfeiffer and colleagues[29] were able to identify the subgroups among the participants and found that, visually dependent (field dependent [FD]) participants tended to experience a down-looking 1PP, as if they were looking downwards from above the body/avatar they saw, and relocated self-location toward this body/avatar (perceived as "below" them). In contrast, more visually independent (field independent [FI]) participants relocated their self in the upward direction and experienced an up-looking 1PP, as if they were looking from below the body/avatar they saw and relocated toward this body perceived as "above" them. These changes in experienced 1PP direction (downwards vs. upwards) were associated with activation of bilateral TPJ.[15] Another study using FBI-like paradigms combined with artificial vestibular stimulation demonstrated that, when the vestibular stimulations elicited a swinging sensation that was in synchrony with the movement of the virtual body, participants experienced a stronger sense of ownership over the observed body.[30] Collectively, these data suggest that vestibular signals and their integration with visual signals, likely involving the TPJ, contribute to OBEs as well as changes in self-location and 1PP direction during the FBI. However, no studies thus far have directly and naturally manipulated vestibular signals to induce illusions close to a full-blown OBE.

Here, we propose to combine controlled visual and natural vestibular stimulation to investigate the multisensory brain mechanisms of OBEs. We adapted a mixed reality (MR) setup that employed scenic visual inputs and simulated elevation compatible with changes during OBEs. This setup was first developed in Song's study,[31] in which he used an OBE-like scenario consisting of a simulated visual viewpoint that progressively changed from an embodied, body-centered position to an elevated, disembodied position, including the corresponding changes from an up-looking to down-looking direction of the perspective. Song's study showed that exposure to this visual OBE-like scenario induced an elevation in self-location and OBE-like sensations (i.e., disembodiment and vestibular sensations of floating). Based on this research and to investigate the role of vestibular cues and of visual-vestibular integration in OBEs and related aspects of BSC, we introduced additional vestibular stimulation to the visual OBE-like scenario by placing supine participants on a Stewart-Gough motion platform that was programmed to displace our participants in the earth-vertical direction (i.e., upward or downward, see STAR Methods for details) simultaneously with the viewpoint elevation of the visual OBE-like scenario. In this study, we aimed at inducing OBE-like sensations and investigating visual-vestibular interaction by varying the direction congruency between visual and vestibular cues. That is, we changed the platform's moving directions by condition, while keeping the visual stimulation the same (see Figure 1), thereby manipulating the congruency between visual and vestibular stimulation. We hypothesized that the additional vestibular signals would influence participants' OBE-like sensations and that the condition with congruent visual-vestibular cues (i.e., visual-vestibular down condition, see Figure 2) would lead to higher self-location and stronger OBE-like experiences.

RESULTS

Study 1: Self-location was lowered by the incongruent visual-vestibular self-motion stimulation

The aim of Study 1 was to investigate whether visual-vestibular stimulation and the congruency of visual and vestibular cues influence OBE-like sensations and key aspects of BSC such as self-location. For this, we exposed 37 healthy participants to a custom-made 3D MR scenario that simulated several key elements of OBEs through the combination of visual-vestibular stimulation. Before the experiment started, participants wore an HMD and were immersed into an MR environment programmed to mimic the actual experimental room in 3D (see STAR Methods for details). They saw from the first-person viewpoint a 3D reconstruction of their body. Movements of their body were tracked and shown synchronously with their actual movements, in real-time, in order to immerse participants in the virtual scene and virtual body. Once the experiment began, participants lay supine on the motion platform and experienced the OBE-like scenario along with the pre-defined platform movements. The sequence of the virtual OBE-like scenario began with participants having an embodied visual viewpoint, centered on their physical eyes and looking upwards at the virtual ceiling. Then the visual viewpoint underwent a slow 180° rotation (45°/sec) to turn into a disembodied viewpoint, looking downward at their virtual body. This disembodied viewpoint was then slowly elevated (i.e., backwards translation-elevation toward the ceiling; in nose-to-back direction) so as to move away from their virtual body (Figure 1). These visual changes were chosen because they simulate the elevation and extracorporeal self-location, the view of the environment and of one's body, and the elevated disembodied viewpoint that are reported by the majority of people with OBEs.[3,4,6] The translational movement lasted for 5 s and always followed the same predefined trajectory, ending at two virtual meters (vm) above the virtual body in the MR environment. This was the visual condition (V condition) in the present experiments, which was adapted from Song's previous study.[31]

In two other conditions, in addition to visual stimulation, participants underwent a 5-s vestibular stimulation in the earth-vertical direction, with a nearly raised cosine velocity profile characterized by the amplitude of 41 cm and maximum acceleration of 13.1 cm/s^2 (see supplemental information Figure S1 for details). Vestibular stimulation was integrated, in real-time, in the MR environment and presented jointly with the visual viewpoint changes in MR. This led to two main experimental visual-vestibular conditions, namely, visual-vestibular down (hereinafter, VVD) and visual-vestibular up (hereinafter, VVU) conditions. In the VVD condition the platform moved downward while in the VVU condition the platform moved upward (see STAR Methods for details). We note that the physical movements of the platform were not presented in the

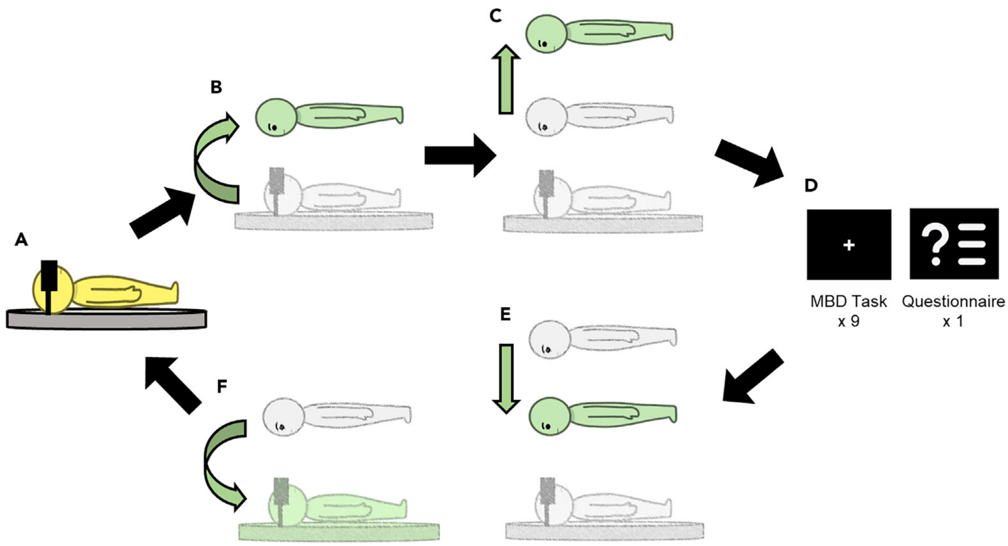

Figure 1. Schematic view of virtual reality OBE-like scenario in Study 1 and 2

Participants immersed themselves in a VR environment, where they engaged in a simulated OBE through a headset. The OBE scenario was divided into two sections: the first half (from A to C) involved the scenario of "leaving the body," while the second half (from E to A) showed "returning to the body." The sequence of events is illustrated by the black arrows, starting with (A) in which the yellow human figure represents the embodied view co-located with the physical body. The grayed-out and green human figures represent the starting positions and the destinations reached as the participants' viewpoint moved through the VR environment respectively. See Videos S1 and S2.

(A) The scenario started with an embodied view, looking up at the virtual ceiling (1PP). Participants' visual viewpoint and physical body are co-located at this stage.

(B) The viewpoint then went through a 180° rotation to become down-looking (green figure without HMD: visual viewpoint; gray figure with HMD: physical body and the observed virtual body).

(C) The viewpoint moved up to two meters above the virtual body (gray figure without HMD: starting point of the movement; green figure: ending point of the movement) and stayed at this position for 8 s.

(D) The screen gradually faded out and turned into darkness. The response session began. Participants either performed a Mental Ball Dropping task or answered questionnaire (MBD task: Mental Ball Dropping task; see STAR Methods).

(E and F) Once participants completed the task or answered the questions, the screen resumed and the visual viewpoint moved back to the embodied perspective following the opposite trajectory until restoring the initial embodied view (A).

virtual environment. That is, from the participants' viewpoint, the 3D image of the platform and their body remained static even though the platform moved in VVD and VVU conditions. Therefore, the visual stimulation (i.e., viewpoint changes in MR; see Figure 1) was identical in all experimental conditions; although only in the V condition did the platform also remain physically stationary. The identical visual inputs that we combined with downward movement (VVD) and upward movement (VVU) of the platform resulted in congruent and incongruent visual-vestibular cue combinations in the egocentric frame of reference respectively, which is illustrated in Figure 2. The platform movement, leading to physical body displacements, are shown in the lower part of Figures 2A and 2B while the identical visual viewpoint movements simulated in MR are illustrated in the upper part of Figure 2. In the VVD condition (Figure 2A), the downward movement of the platform moved the participants' body "backwards" in the egocentric frame of reference (i.e., subjectively in nose-to-back direction; as indicated by the "Physical body backward" arrow). Hence it was congruent with the visual viewpoint change in MR that also simulated a backward translation-elevation (indicated by the "Viewpoint backward" arrow). In contrast, in the VVU condition (Figure 2B), the upward movement of the platform moved the participants' body "forward" (i.e., in back-to-nose direction; as indicated by the "Body forward" arrow), incongruent with the visual viewpoint change in MR that simulated a backward movement. Therefore, by varying the moving direction of the platform, we manipulated the direction congruency between visual and vestibular self-motion cues across conditions.

To investigate the influence of visual-vestibular integration on BSC, first we implemented the Mental Ball Dropping (MBD) task, an implicit measure of self-location based on mental imagery. The MBD task was developed by Lenggenhager and colleagues[19] for a version of the FBI in participants lying in supine position, and has been widely used in different bodily illusions since then.[15,32,33] Self-location as measured by MBD response times (i.e., the estimated duration of a ball that is imagined as falling from participants' hand to the floor) has been shown to reflect a participant's perceived distance from the ground.[15,19,34] That is, a longer or shorter MBD response time compared to the baseline indicates a higher or lower self-location, respectively. The three experimental conditions (V, VVD, and VVU) were then carried out in randomized blocks. Each experimental condition (block) consisted of ten trials. In the first nine trials, participants performed the MBD task and answered questions about self-motion direction and the degree of disembodiment (Q9–Q11; see STAR Methods Table S1). On the last trial, they answered a standardized questionnaire on various aspects of BSC, including vestibular-related sensations such as sense of reduced gravity and feeling of floating, feeling of disembodiment and other BSC components (see STAR Methods Table S2).

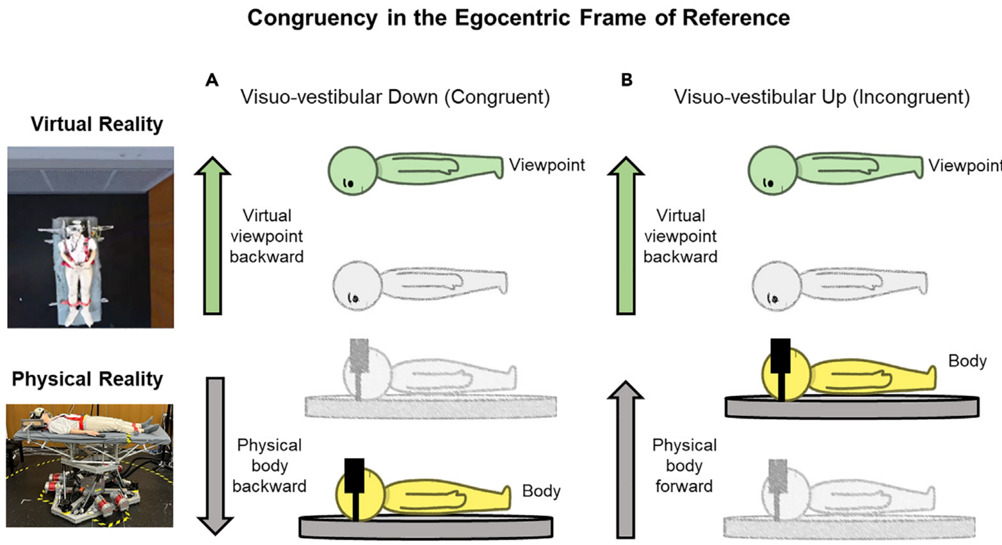

Figure 2. Congruency in the egocentric frame of reference

Visual and vestibular congruency was defined based on the moving direction, dependent on the subjective, egocentric reference frame. The grey-scaled avatars indicate the starting points of participants' visual viewpoint (without HMD) as well as the physical body (with HMD). Human figures in green and yellow indicate the reached destinations of the viewpoint and physical body respectively after the translational movements. Green and gray arrows indicate the interpreted moving direction in the subjective, egocentric frame of reference for virtual viewpoint and physical body, respectively. The translational movements of the virtual viewpoint and the physical body were achieved by the virtual reality technique and the motion platform, respectively, shown in the leftmost column.

(A) In the VVD condition, the visual viewpoint was moving backwards while the physical body was pulled backwards by the platform's downward movement, hence providing congruent visual-vestibular stimulations in the egocentric frame of reference (i.e., subjectively in nose-to-back direction; as indicated by the "Physical body backward" black arrow).

(B) In the VVU condition, the visual viewpoint moved backwards while the upward movement of the platform moved the participants' body "forward". This provided incongruent visual-vestibular stimulations in the egocentric frame of reference (i.e., subjectively in back-to-nose direction; indicated by the "Physical body forward" arrow).

Our hypothesis was that participants' self-location measured by MBD response times and OBE-related sensations would depend on the congruency between visual and vestibular stimulations. Based on previous studies on optic flow and vestibular congruency[35] and our pilot studies, we expected that congruent VVD condition would lead to stronger OBE-related sensations and higher self-location as both visual and vestibular cues suggest the same direction of self-motion. Moreover, we predicted that participants' self-motion ratings would be positively correlated with the MBD responses, meaning that the stronger they felt the movement, the higher they would re-locate themselves. Our analysis plan was to apply linear mixed effects model (LMEMs) to MBD reaction time data and cumulative link mixed models (CLMMs) to ordinal data of questionnaire ratings. Both models were specified with the fixed effect of Condition and random intercept for individual participants. This model was then compared using log likelihood ratio test (LRT) to another LMEM or CLMM that included only random intercepts of participants without any fixed effect. The LRT allowed us to estimate the significant contribution (i.e. main effect) of individual predictor of Condition. If a main effect of Condition was observed, we obtained estimated marginal means for each experimental condition and compare the conditions pairwise without adjustments. Where we carried out exploratory analyses are additionally specified.

For self-location, first, we observed that the VVD condition led to the highest MBD responses while the VVU condition the lowest (Mean (M) $\pm$ SEM: V = 841 $\pm$ 10.4, VVD = 845 $\pm$ 11.4, VVU = 803 $\pm$ 10.6). Next, the LMEM and LRT detected an effect of Condition ($\chi^2 = 31.81$, $p < 0.001$). The VVD and V conditions led to longer MBD response times compared to the VVU condition (V-VVU: $t = 3.91$, $p < 0.001$; VVD – VVU: $t = 5.48$, $p < 0.001$). This shows that participants' self-location was relocated to a higher position with congruent visual-vestibular stimulation (VVD) as well as purely visual stimulation (V condition), compared to the incongruent visual-vestibular stimulation (VVU). No significant difference was found between V and VVD conditions ($t = 1.58$, $p = 0.115$, Figure 3A; see Table S4 for detailed results). On the other hand, for subjective self-motion ratings (Q9), although we did observe a significant effect of Condition ($\chi^2 = 19.76$, $p < 0.001$), contrasting with MBD responses, ratings in the V condition (M $\pm$ SEM = 0.76 $\pm$ 0.09) were significantly higher than the other visual-vestibular conditions (V – VVD: $z = 2.85$, $p = 0.004$; V – VVU: $z = 4.35$, $p < 0.001$), with no differences between VVD and VVU conditions ($z = 1.43$, $p = 0.152$; M $\pm$ SEM: VVD = 0.42 $\pm$ 0.12; VVU = 0.23 $\pm$ 0.11). To further explore self-motion ratings, we performed additional exploratory analyses using separate Wilcoxon rank-sum tests for each condition to assess how the ratings compared to 0. It was revealed that the ratings were greater than 0 in the V and VVD conditions (V: $r = 0.43$, $p < 0.001$; VVD: $r = 0.20$, $p < 0.001$), but not in the VVU condition ($r = 0.11$, $p = 0.08$; all p values with Bonferroni correction). This result is compatible with the self-location results (MBD responses), indicating that in V and VVD conditions participants felt moving upwards and re-located to a higher position. A significant Spearman correlation was also found between self-location

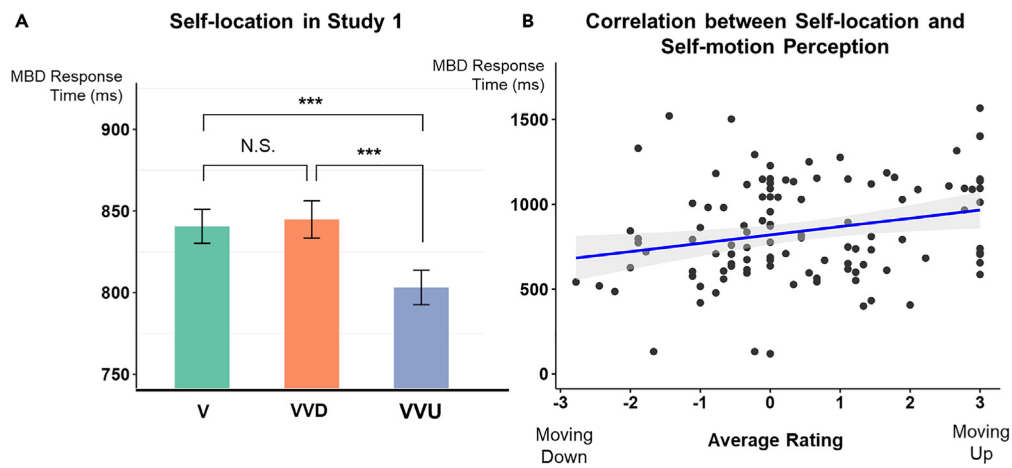

Figure 3. Self-location and correlation with self-motion perception in Study 1

Self-location measured by MBD response times, self-motion (questionnaire) and questionnaire data in Study 1. The bars represent the means and the error bars show the standard error of means (SEM). Green: V condition. Orange: VVD condition. Blue: VVU condition. (***: p-value < 0.001; N.S.: non-significance).

(A) VVU condition led to significantly lower self-location measured by MBD response times compared to both V and VVD conditions.

(B) A significant Spearman correlation between average self-motion ratings and MBD response times confirmed that the condition inducing higher self-location as measured by MBD response time also led to stronger feeling of moving up.

and self-motion perception (average MBD response times and self-motion ratings for each participant and condition; Rho = 0.23, $p = 0.015$, Figure 3B), showing that stronger feelings of upward movement were associated with higher self-location (i.e., longer MBD response times).

In addition, we implemented vestibular control tasks to control whether participants perceived the physical movements of the platform and their direction. In these tasks, the platform moved up or down (i.e., Control-Up and Control-Down conditions, with the same motion profile as implemented in VVU and VVD conditions respectively), but without any concurrent visual input. Participants performed the same MBD task and self-motion ratings in the control tasks. As expected, the mean MBD response was higher when the platform was moving up (M $\pm$ SEM: Baseline = 750 $\pm$ 14, Control-Down = 765 $\pm$ 9.89, Control-Up = 817 $\pm$ 10.3). An LMEM confirmed that participants were well able to perceive the platform movements and showed that self-location (measured by MBD response times) was higher when the platform moved up compared to when it moved down ($t = -6.08$, $p < 0.001$) as well as compared to the baseline measurement (measured at the beginning of the task; $t = -2.92$, $p = 0.003$). A CLMM on self-motion ratings further revealed that participants reported to feel moving upward more strongly for an upward movement of the platform compared to a downward movement ($z = -7.28$, $p < 0.001$; M $\pm$ SEM: Control-Up = 0.55 $\pm$ 0.1, Control-Down = -0.48 ± 0.1) and compared to the baseline ($z = -2.63$, $p = 0.009$; M $\pm$ SEM = 0.11 $\pm$ 0.07). Exploratory Wilcoxon rank-sum tests confirmed that self-motion ratings were not different from 0 in baseline ($r = 0.16$, $p = 1$), greater than 0 when moving upward ($r = 0.3$, $p < 0.001$) and below 0 when moving downward ($r = 0.24$, $p < 0.001$), corresponding to the physical moving direction. This shows that participants were able to distinguish between upward and downward movements of the platform when there were no visual inputs.

Together, these results show that combining visual and natural vestibular stimulation can induce higher self-location. Elevated self-location, along with stronger sensation of moving upwards, was induced under congruent visual-vestibular stimulation in an egocentric reference frame (VVD condition) compared to an incongruent stimulation (VVU condition). This shows the importance of the congruency of visual and vestibular self-motion cues in an egocentric frame of reference for self-location. Of note, self-location in the VVD condition did not significantly differ from that in the V condition. However, OBEs are not only characterized by changes in self-location, but also changes in other BSC feelings such as disembodiment or sensations of lightness. Subjective reports may therefore differ between the V condition versus both visual-vestibular conditions.

Disembodiment and vestibular sensations were increased by visual-vestibular stimulation

To measure such OBE-like sensations, we adapted standardized questionnaires on various aspects of BSC, including vestibular-related sensations such as sense of reduced gravity and feeling of floating, feeling of disembodiment and other BSC components (see STAR Methods). Participants answered the question about the degree of disembodiment (Q11) on the first nine trials following the MBD task and the full questionnaire on the tenth trial of each condition. Note that we particularly focus on subjective experiences concerning OBE-like sensations (i.e., five questionnaire items about disembodiment and vestibular-related feelings). Other items were implemented as control items and are not directly relevant to OBE-like phenomenology (for detailed analyses, see supplemental information).

Disembodiment is a key sensation in an OBE. Various feelings linked with disembodiment were measured by three questionnaire items (Q1: feeling outside of the body; Q6: being separated from the physical body measured specific subjective feelings; Q11: degree of disembodiment measured a more general feeling of disembodiment) (see Tables S1 and S2 in STAR Methods). For the Q11 disembodiment question, CLMM and LRT revealed a significant effect of Condition ($\chi^2 = 12.5$, $p = 0.002$). Participants gave significantly higher ratings for the VVD

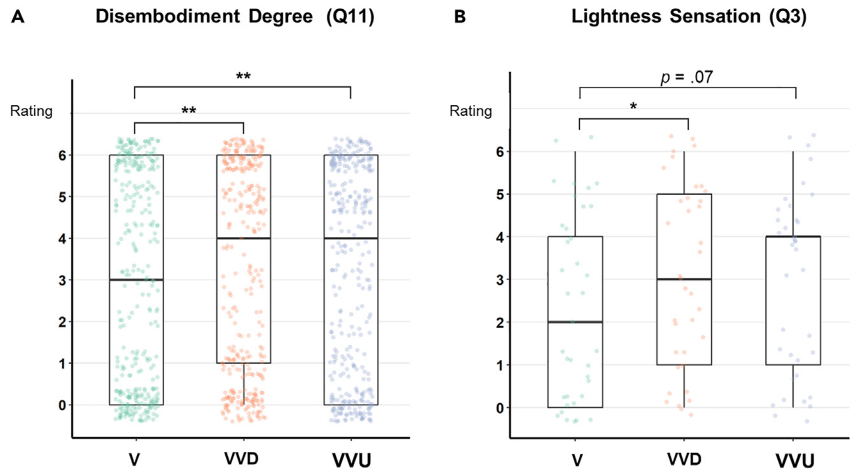

Figure 4. Questionnaire data of OBE-related sensations in Study 1

The box plots show the median and interquartile range of the ratings for the corresponding questionnaire items. Each point represents a single response from one participant. Green: V condition. Orange: VVD. Blue: VVU. (*: p-value < 0.05; **: p-value < 0.01).

(A) Disembodiment: "*I felt as if I was [inside | outside] my physical body.*" A rating of 0 indicated feeling completely inside (no disembodiment feeling) and 6 indicated feeling completely outside (strong disembodiment feeling). VVD and VVU were found to result in higher ratings for this question compared to V condition.

(B) Lightness sensation (i.e., reduced sense of gravity): "*I felt as if I became lighter.*" For this item, significantly higher ratings were found in visual-vestibular D compared to V condition.

($M \pm SEM = 3.18 \pm 0.14$) compared to V condition ($M \pm SEM = 2.94 \pm 0.14$; $z = 2.97$, $p = 0.003$) and for the VVU ($M \pm SEM = 3.22 \pm 0.14$) compared to V condition ($z = 3.16$, $p = 0.002$). No difference was found between the VVU and the VVD conditions ($z = -0.18$, $p = 0.86$). We did not find a significant effect of Condition for Q1 and Q6 (Q1 – OBE-like feeling $M \pm SEM$: V = 3.19 ± 0.42, VVD = 3.57 ± 0.41, VVU = 3.78 ± 0.38; Q6 – Separation feeling $M \pm SEM$: V = 3.32 ± 0.40, VVD = 3.49 ± 0.40, VVU = 3.59 ± 0.37; no significant difference was found between conditions and all p values were > 0.05). These results show that visual-vestibular stimulation (VVD and VVU) induced a higher general feeling of disembodiment compared to only visual stimulation (V condition) but did not affect more specific feelings such as feeling outside the body or being separated from the physical body (Figure 4A). Notably, for self-identification and body ownership, which are major components of BSC,[22,36] we did not find significant differences between V, VVD and VVU conditions (Q5: feeling that the observed body was own body; see supplemental information Table S11 for detailed results). This suggests that adding vestibular stimulation to the current visual OBE-like scenario did not differently influence participants' self-identification with the seen body. It may be argued that vestibular information and visual-vestibular integration may be more important for dis/embodiment and self-location than for self-identification and body ownership. This is in line with proposals that dis/embodiment and body ownership are distinct aspects of BSC with different sensory brain mechanisms.[24,29,37] More work is needed on the contributions of vestibular signals to self-identification, as past work has shown variable results.

In addition to the feeling of disembodiment, OBEs have also been associated with a variety of vestibular sensations, and in particular, lightness and floating sensations have often been reported in the OBE literature.[6,38] These sensations were measured in the current study by Q3 (i.e., feeling as if I became lighter) and Q4 (i.e., feeling as if floating), respectively. We expected the visual-vestibular conditions (VVD and VVU) to result in stronger sensations of lightness and floating compared to the V condition. The CLMM analysis on ratings for lightness sensation (Q3) indeed showed that participants had significantly higher ratings in the VVD ($M \pm SEM = 3.08 \pm 0.36$) compared to V condition ($M \pm SEM = 2.12 \pm 0.35$; $z = 2.32$, $p = 0.02$; Figure 4B), but there was no significant difference between VVU ($M \pm SEM = 2.95 \pm 0.34$) and V condition ($z = 1.84$, $p = 0.07$), or between VVU and VVD conditions ($z = 0.53$, $p = 0.60$). Ratings for floating sensations (Q4) were not modulated by vestibular stimulation (see Tables S7–S17 for the statistical results of the full questionnaire). These results suggest that visual-vestibular stimulation (in VVD and VVU) induces stronger feelings of disembodiment and lightness, compared to purely visual stimulation (V condition). This reveals the importance of visual-vestibular signals in experimentally induced OBEs and in the sense of gravity (changes in lightness sensation).

To summarize, Study 1 shows that the directional congruency of the visual-vestibular stimulation modulated the extent to which self-location was relocated to a higher position (MBD responses times). The direction-congruent visual-vestibular stimulation in the egocentric frame of reference, i.e., VVD condition (see Figure 2), led to a higher self-location compared to the direction-incongruent visual-vestibular stimulation, i.e., VVU condition. Moreover, the magnitude of these experimentally induced elevations in self-location correlated with stronger self-motion ratings. The elevation of self-location after the VVD condition was comparable to the V condition. However, subjective ratings show that visual-vestibular stimulation, in particular the VVD condition, induced stronger sensations of disembodiment and an altered sense of gravity, compared to purely visual stimulation. Accordingly, we argue that only the congruent visual-vestibular stimulation (VVD condition) led to an OBE-like illusion, including both elevated self-location and increased sensations of disembodiment and lightness.

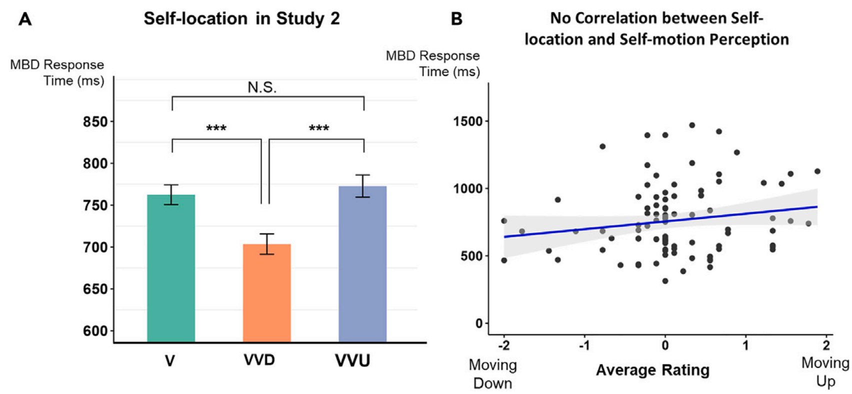

Figure 5. Self-location and the absence of correlation with self-motion in Study 2

The data are represented as mean ± SEM. Green: V condition. Orange: VVD. Blue: VVU. (***: p-value < .001; N.S.: Non-significance).

(A) Self-location measured by MBD response time. V and VVU conditions resulted in higher self-location, indicated by longer MBD response time, compared to VVD.

(B) No correlation between subjective reports of self-motion and the MBD response times was found, suggesting that, without scene background, participants felt more uncertain about their moving direction.

Study 2: Changes in self-location followed vestibular self-motion cues when lacking visual-gravitational information

Previous observations showed that spontaneous OBEs do not always contain detailed reports of visual scenes[6,39] and earlier experimental data demonstrated that altered BSC sensations such as body ownership and self-location can be induced without any visual cues from the environment.[15,29,33] In Study 2 (sample size n = 24), we further investigated the role of visual-vestibular stimulation in the induction of OBEs by removing the scenic background from the visual stimulation (see supplemental information) while keeping vestibular stimulation and tasks identical to Study 1. The absence of any visual background related to the scene reduced cues about visual orientation with respect to the virtual environment. This allowed for multiple interpretations of the visual cues regarding the viewpoint rotation and elevation. A participant could perceive the scene in at least three different ways as follows. (1) The participant felt herself to be moving and the virtual body remained static. (2) The virtual body felt to be moving away from participant's viewpoint (i.e., the participant saw her body to move away and to get smaller) while the participant felt herself to remain static. (3) The participant felt both the observed body and herself to be moving. Accordingly, we expected that they would rely more strongly on vestibular cues and hence re-locate their self-location depending on the vestibular rather than visual cues. That is, changes in self-location would follow the direction of physical movement. Moreover, to test whether individual visual-vestibular weighting strategies influenced our results, we used the Rod and Frame Test (RFT) to separate participants into two groups. The RFT requires participants to perform visual vertical judgments within a biasing visual context:[28] they have to align a tilted rod with the vertical (direction of gravity), regardless of the frame (a solid square that could be tilted by 5, 10, or 15° to the right or to the left). The magnitude of errors (i.e., deviation from 0°) provides a measure of individual visual-vestibular sensory weighting strategies.[27,40] Previously, Pfeiffer and colleagues[29] reported that individuals' field dependency is associated with their experienced 1PP direction and their self-location responses in an FBI experiment. Specifically, when in a physical supine position, people who rely more on the visual information (i.e., visual FD) showed more frequently a down-looking perspective, which was further associated with higher self-location, whereas people who rely more on the vestibular signals (i.e., visual FI) reported more frequently an up-looking perspective. Based on this observation, we hypothesized that the participants in the FD group would report the experience of down-looking perspective more frequently, which could be further associated with higher self-location. In Study 2, the RFT was carried out before participants performed the main experiment. The data of each participant's responses after removing outliers are shown in Figure 7. The data were then analyzed using hierarchical clustering, which classified participants into visual FD group and visual FI group (see STAR Methods for procedure and Figure 8 for results). The FD group was more biased by the tilted frame and rely more on visual information for verticality judgments, whereas the FI group was less biased and arguably relies less on visual signals. Based on RFT classification an additional factor "Group" was added as a between-subject predictor to the statistical models.

For self-location responses (MBD response times), we observed a higher response mean in VVU condition and a lower response mean in VVD condition (M ± SEM: V = 762.51 ± 11.74, VVD = 703.48 ± 12.13, VVU = 772.88 ± 13.18). A significant effect of Condition ($\chi^2 = 58.72$, $p < 0.001$) was detected by the LMEM and LRT, showing that the VVD condition led to lower self-location compared to VVU ($t = 5.4$, $p < 0.001$) and V conditions ($t = 3.8$, $p < 0.001$). Contrary to Study 1, where we found VVU led to lower self-location compared to V and VVD conditions, in Study 2, when participants could not rely on visual gravitational cues and had reduced visual motion cues, self-location indeed depended on the direction of vestibular stimulation in the two visual-vestibular conditions. That is, participants re-located their self-location to a lower position when the platform moved down and higher when the platform moved up (Figure 5A). No effect of Group ($\chi^2 = 0.88$, $p = 0.348$) nor an interaction of Condition and Group ($\chi^2 = 3.6$, $p = 0.308$) was found. For self-motion sensations (Q9 ratings), the CLMM and LRT revealed no significant main effect of Condition ($\chi^2 = 1.87$, $p = 0.6$), Group ($\chi^2 = 0.14$, $p = 0.71$) or interaction ($\chi^2 = 2.07$, $p = 0.558$; M ± SEM: V = 0.14 ±

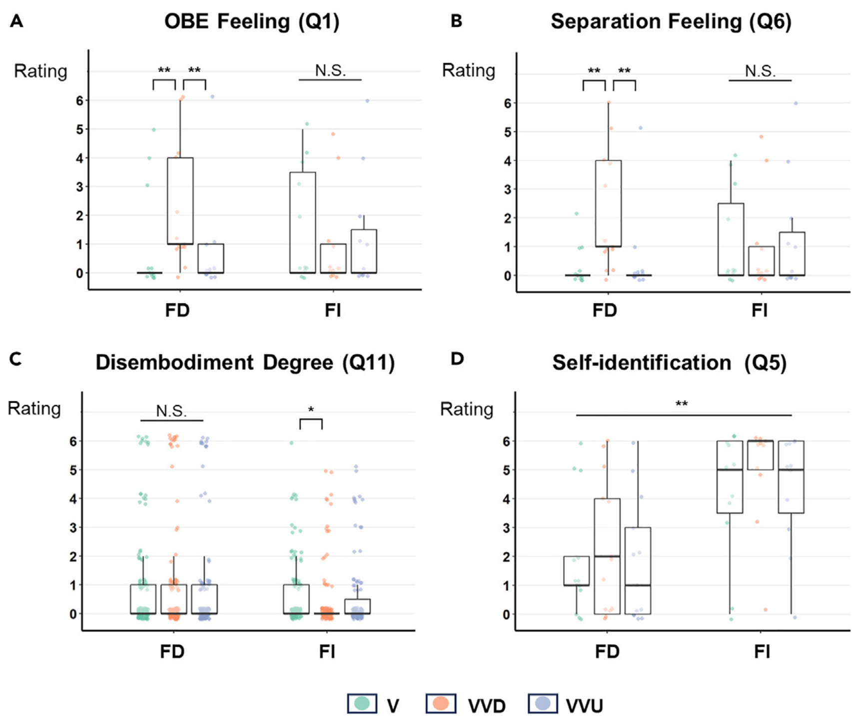

Figure 6. Significant difference in disembodiment ratings between conditions in Study 2

The box plots show the median and interquartile range of the ratings for the corresponding questionnaire items. Each point represents a single response from one participant. Green: V condition. Orange: VVD. Blue: VVU. (*: p-value < 0.05; **: p-value < 0.01; N.S.: Non-significance).

(A) and (B) Individuals in the FD group had stronger OBE-like feeling (i.e., being outside of the body) and separation feeling (i.e., being separated from their body) in the VVD compared to other conditions.

(C) The FI group showed significantly lower ratings for the disembodiment degree (Q11) in VVD compared to V condition, whereas no difference was found between conditions in the FD group. (D) The FD group rated significantly lower for self-identification across all experimental conditions compared to the FI group.

0.08; VVD = 0.01 $\pm$ 0.12; VVU = 0.2 $\pm$ 0.11). The correlation between self-location (average MBD response times) and self-motion that we observed in Study 1 was absent in Study 2 (Rho = 0.01, $p = 0.34$, Figure 5B). To further explore this null result, we carried out an additional exploratory analysis on self-motion ratings for each experimental condition to assess whether participants were able to perceive the direction of vestibular stimulation. Separate Wilcoxon signed rank tests for each condition were applied to the average self-motion ratings per participant, revealing that the medians of the ratings were not different from 0 in all the experimental conditions (V: $r = 0.13$, $p = 0.35$; VVD: $r = 0.06$, $p = 1$; VVU: $r = 0.33$, $p = 0.42$). These results suggest that without the visual-gravitational information provided by the scene background (as in Study 1), participants felt more uncertain about their self-motion direction, and that they no longer inferred their self-location based on visual-vestibular inputs, but relied more on the vestibular input alone.

These results extend those of Study 1 showing that the removal of the visual scene background in Study 2 changed the visual cue reliability[41] and led participants to rely more on the vestibular rather than the visual cues. The changes in self-location more closely reflected the vestibular cues (provided by the motion platform), instead of taking both visual and vestibular cues into account and the VVD condition resulted in a lower self-location, although participants in Study 2 were unable to explicitly report their self-motion direction.

Feeling of disembodiment was increased by visual-vestibular stimulation in visual field dependent group

In Study 2, we investigated disembodiment with the same three items as in Study 1 and found that the feelings of being outside of body (Q1) and of separation (Q6) showed a significant interaction of Condition and Group (Q1 – OBE-like feeling: $\chi^2 = 7.94$, $p = 0.047$, M $\pm$ SEM: FD-V = 0.92 $\pm$ 0.5, FD-VVD = 2.15 $\pm$ 0.59, FD-VVU = 0.69 $\pm$ 0.46, FI-V = 1.64 $\pm$ 0.61, FI-VVD = 1 $\pm$ 0.54, FI-VVU = 1.27 $\pm$ 0.60; Q6 – Separation feeling: $\chi^2 = 8.57$, $p = 0.036$, M $\pm$ SEM: FD-V = 0.31 $\pm$ 0.17, FD-VVD = 2.08 $\pm$ 0.57, FD-VVU = 0.46 $\pm$ 0.39, FI-V = 1.18 $\pm$ 0.52, FI-VVD = 1 $\pm$ 0.54, FI-VVU = 1.27 $\pm$ 0.60); there was no main effect of Condition or Group (for detailed results, see supplemental information). As shown in Figures 6A and 6B, the VVD condition led to significantly higher ratings for OBE-like feeling and separation feeling compared to the V condition (OBE-like feeling: $z = 2.66$, $p = 0.008$; Separation feeling: $z = 2.97$, $p = 0.003$) as well as to the VVU condition (OBE-like feeling: $z = 2.62$, $p = 0.009$; Separation feeling: $z = 3.04$, $p = 0.002$). These effects were only present in the FD group and absent in the FI group (see supplemental information).

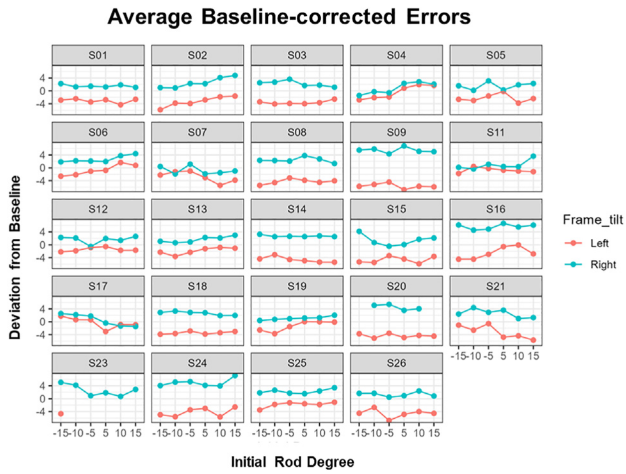

Figure 7. Average baseline-corrected errors in left- and right-tilted frame conditions

Each cell shows the RFT data from one participant coded as S01 to S26. Participants' responses on the trials with vertical frame served as baselines and were subtracted from the errors produced on trials with left-tilted frame and right-tilted frame. The resulting baseline-corrected errors are shown here in pink (left-tilted trials) and cyan (right-tilted trials), with the dots representing the mean values for each initial degree of rod tilt.

While the VVD condition in the FD group resulted in stronger OBE-like and separation feelings, an exploratory analysis of the ratings of disembodiment degree revealed that the same condition led to lower ratings in the FI group (i.e., Q11: feeling how much outside the body; Condition: $\chi^2 = 7.99$, $p = 0.046$, Group: $\chi^2 = 0.37$, $p = 0.54$, Interaction: $\chi^2 = 4.81$, $p = 0.186$, M $\pm$ SEM: FD-V = 0.93 $\pm$ 0.16, FD-VVD = 0.97 $\pm$ 0.17, FD-VVU = 0.87 $\pm$ 0.17, FI-V = 0.74 $\pm$ 0.13, FI-VVD = 0.51 $\pm$ 0.12, FI-VVU = 0.6 $\pm$ 0.13) compared to the V condition ($z = -2.46$, $p = 0.042$; see Figure 6C). This shows that for the same condition (i.e., VVD), the FD group had stronger disembodied and separated feelings while the FI group felt weaker disembodied compared to when there was only visual stimulation (V condition). We also found a significant effect of Group for self-identification ratings, but no effect of Condition or interaction (Group effect: $\chi^2 = 7.45$, $p = 0.006$; Condition effect: $\chi^2 = 4.2$, $p = 0.24$; Interaction: $\chi^2 = 2.51$, $p = 0.474$), with the FD group showing lower ratings on this item compared to the FI group (M $\pm$ SEM: FD = 0.95 $\pm$ 0.08, FI = 0.72 $\pm$ 0.06; $z = -2.75$, $p = 0.006$). This suggests that in Study 2 self-identification with the virtual body depended on individual visual field dependency. Altogether, the results of the three disembodiment ratings (i.e., OBE-like feeling, separation feeling, and the degree of disembodiment) suggest that, adding vestibular cues of downward movement to a visual scenario without any scene background with visual-gravitational cues induced sensations of disembodiment in the FD group, but decreased disembodiment in the FI group. The stronger modulations in the FD group might be associated with their lower self-identification scores. No difference was found between conditions or groups for questions related to vestibular sensations (i.e., lightness and floating sensations) and experienced 1PP direction (i.e., Q12 and Q13 regarding down- or up-looking and the perceived relative location to the virtual body; see Tables S24–S38 for the statistical results of the full questionnaire).

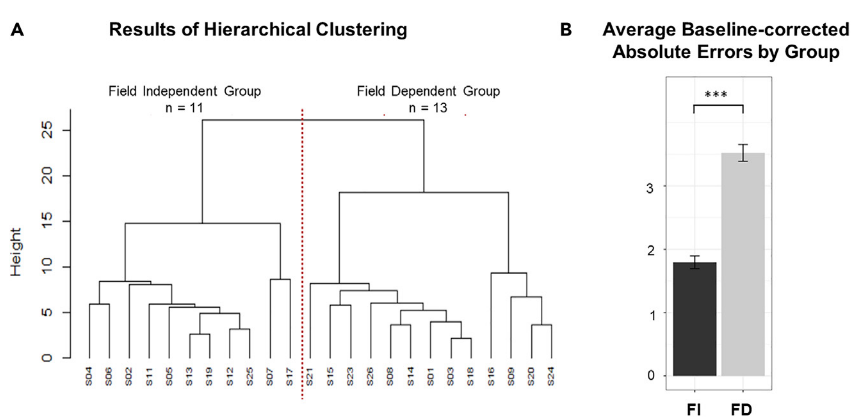

Figure 8. Hierarchical clustering classified the participants into two groups

(A) The dendrogram showed the results of hierarchical clustering with Ward method on the baseline-corrected RFT data.

(B) A Wilcoxon rank-sum test confirmed that one group showed significantly higher errors than the other group. Data are represented as mean $\pm$ SEM. By definition, the group showing larger errors was identified as visual field dependent (FD) and the other group as visual field independent (FI).

Overall, Study 2 shows that, in the absence of visual scene-related background and visual gravitational information, participants re-located their self-location depending on the direction of vestibular cues when these cues were available (i.e., in VVD and VVU conditions). Therefore, removing visual gravitational cues cancels the effect of visual-vestibular congruency on self-location observed in Study 1, highlighting the importance of visual gravitational cues and their integration with vestibular cues for BSC. We also found that participants who tend to rely more on visual cues, i.e., the FD group, had a stronger disembodiment feeling in the VVD condition. These results suggest that the increase of the most critical subjective aspect of OBE-like illusions, i.e., the sense of disembodiment, is related to individuals' visual-vestibular weighting strategies. Together, findings from both studies show that congruent visual-vestibular stimulation in a self-centered reference frame (VVD condition) leads to strongest OBE-like experience characterized by sensations of disembodiment in both Study 1 and Study 2, and resulted in higher elevated self-location as well as feelings of lightness when visual gravitational cues were present (in Study 1).

DISCUSSION

The data from Study 1 and Study 2 show that the congruency between visual and vestibular gravitational and self-motion signals is crucial for OBE-like sensations and for BSC more generally. By applying visual and natural vestibular stimulation in participants lying supine, we managed to induce an OBE-like illusion, characterized by elevated self-location, increased sense of disembodiment and vestibular sensations such as feelings of lightness. These results extend previous findings on the contributions of visual-vestibular integration to OBEs and BSC.[10,37]

Previous research combining FBI-like paradigms with vestibular signals demonstrated that congruent visual-vestibular stimulation induces illusory ownership over the observed body or mannequin,[30,42,43] and that self-identification and body ownership of the virtual body decreased in the condition with visual-gravitational conflicts.[25] In the current project, instead of manipulating body ownership, we induced elevation in self-location as reported during OBE using an OBE-like visual scenario and manipulated the congruency between visual and vestibular cues. In Study 1, participants re-located their self-location to a higher position when visual and vestibular stimulations were direction-congruent (VVD condition) compared to a condition when they were direction-incongruent (VVU condition) in a self-centered reference frame. Prior studies have shown that vestibular self-motion cues presented concurrently with radial optic flow alter the sensitivity to the visual cues, with direction-congruent vestibular cues decreasing or increasing the perceptual motion thresholds[35,44] (but see Holten and MacNeilage[45] for contrasting results). Here we report that the congruency between visual and vestibular cues modulates self-location, which we further associated with the magnitude of changes in self-motion perception. These results provide more experimental evidence to theoretical proposals suggesting that the congruency between visual and vestibular cues plays an important role in multisensory integration underlying BSC[10,22] and that alteration of the integration of such cues may lead to OBEs.[3,46]

Several experiments have shown that changes in self-location (i.e., elevated self-location) depend on visual-gravitational cues that are present in addition to the visuo-somatosensory cues in the FBI.[15,24] Extending these findings, here we additionally induced a sense of disembodiment (in Study 1 and 2) as well as feelings of lightness (in Study 1), measured by questionnaire ratings. Critically, we showed that, although purely visual stimulation (V condition) was effective in elevating self-location, the key OBE-related element of disembodiment and the frequent sensation of lightness were only induced in the same visual-vestibular condition that led to elevated self-location: the congruent VVD condition, highlighting again the importance of visual-vestibular congruency. These results are also concordant with OBE reports from neurological patients,[3,4] vestibular patients[9] and from the healthy population.[6] Thus, the large majority of OBEs are characterized the experience of an elevated, extra-corporeal visuo-spatial perspective as well as flying sensations that have been linked to altered vestibular processing, resulting from interference with multisensory and vestibular mechanisms at the cortical level or the peripheral vestibular system.[13] Our data are in line with these OBE data based on interviews and self-reports, showing that vestibular signals, especially when direction-congruent with the visual signals, contribute to OBE.

We note that congruent visual-vestibular stimulation increased disembodiment independently of the presence of visual gravitational information, suggesting that disembodiment is less related to the visual gravitational signals but more related to visual-vestibular weighting sensory strategies and self-motion processing, which is possible as these two types of information have distinct underlying mechanisms and neural correlates within vestibular network.[13,47] Moreover, questionnaire data from Study 2 show that the feeling of being outside one's own body and separated from the physical body did depend on individuals' visual-vestibular sensory weighting strategies, which extends previous work by Pfeiffer and colleagues[29] on the role of individual differences in integrating visual and vestibular cues and of vestibular, in particular otolithic vestibular, signals in inducing OBEs. However, contrasting with Pfeiffer and colleagues' findings, participants' self-location and experienced 1PP direction in Study 2 were not modulated by individuals' visual field dependency. Such discrepancy might result from the over-weighting of vestibular and other bodily signals in the current study. The absence of visual-gravitational information in Study 2 might lead both visual FD and FI groups to rely more on the vestibular signals, and hence diminished group differences. Moreover, since participants were lying supine on the bed, the somatosensory cues of the bed touching their back were constantly present, which could potentially prevent the 1PP direction changes. Taking into account previous research showing that the visual-vestibular weighting could be modulated by illusory body ownership,[48] future experiments could test different levels of visual and vestibular cue reliabilities by varying visual elements while altering BSC, and should aim for a better control of other bodily signals such as tactile cues while preserving the potential effects of visual-gravitational cues on subjective OBE-related feeling (e.g., disembodiment and lightness sensations).

There were no significant differences between V, VVD, and VVU conditions concerning self-identification ratings in both studies This seems in contrast with previous FBI findings and may indicate that the effect of visual-vestibular stimulation on bodily illusions is weaker than the classical visuo-tactile stimulation.[43] However, caution must be taken when interpreting and comparing stimulations including vestibular cues with visuo-tactile stimulations. Manipulations of visual-vestibular directional congruency (as in the present work) differ in many ways from visuo-tactile stimulations that have been tested in FBI-like paradigms. Both congruent and incongruent visual-vestibular conditions in our work here were temporally synchronous since the vestibular stimulation always started and ended at the same time with the visual viewpoint movement. It is the difference in motion direction that distinguishes VVD and VVU conditions. In other words, any differences between the present and previous results (using visuo-tactile stimulation on body ownership or self-identification) may not just stem from the involved modalities, but also from the kind of in/congruence. In addition, the effects of visuo-vestibular on self-identification are mixed in the literature, with varying methods leading to different results: Macauda and colleagues[42] using body lateral movements, Pfeiffer and colleagues' two studies[24,29] using visuo-graviceptive stimulation and Preuss and Ehrsson[30] using galvanic vestibular stimulation (GVS), all resulted in different degrees of self-identification with the observed body. This further complicates the comparisons. Future work controlling for the different aspects and testing visuo-tactile and visuo-vestibular effects in the same participants is needed.

It is also important to note that, although the sense of body ownership and self-identification is suggested in literature to be affected during an OBE, subjects spontaneously rather report changes in self-location and first-person, describing their altered state typically as an association with a non-physical body (e.g., "parasomatic experience" in Green[6]) or as an illusory body reduplication[37,49,50] at an extracorporeal location, rather than feeling of disownership for the observed body. As a result, we did not expect to see nor aimed to induce a significant effect on self-identification ratings. Nonetheless, in Study 2, we found that the FD group reported lower self-identification ratings compared to the FI group, across all conditions. Such individual difference might contribute to the FD group's stronger feeling of disembodiment in VVD condition as mentioned above. Furthermore, the observation that individuals who are more sensitive to and rely on vestibular inputs had stronger self-identification with the virtual body is in line with past research suggesting vestibular role in own body cognition and the sense of embodiment.[14,51,52] Future studies should further explore the altered state of self-identification and body ownership in respect of illusory body reduplication and investigate their potential relationships with individual visual-vestibular sensory weighting differences.

Overall, we show that it is possible to induce an OBE-like illusion characterized by elevated self-location and increased OBE-related feelings using our visual-vestibular paradigm. The results of the two studies converge to suggest the importance of congruency between visual and vestibular cues in modulating both self-location and the feeling of disembodiment. Follow-up studies should focus on modulating experienced 1PP direction using visual-vestibular cues and to further explore the role of individual visual field dependency in determining 1PP in OBE-like illusions.

Limitations of the study

The current study tested the effects of visual-vestibular congruency on various aspects of BSC and on OBE-like phenomenology. To do so, we choose to combine natural vestibular stimulation, i.e., moving participants' body on a motion platform, with different visual and visual-vestibular stimulations, based on VR. One limitation of this method is that participants lying supine on the platform still received somatosensory cues due to platform movements (e.g., they could feel the push or pull on their back). This is unavoidable during any natural vestibular stimulation since the related bodily signals are always present when participants undergo whole-body movements. A vestibular control task (Study 1) solved this confound as participants received the same somatosensory cues during the vestibular control task, but did not respond or relocated self-location in the same way as in the OBE-like scenario. Moreover, other artificial vestibular stimulation techniques (that we could have used instead and that have been used in the past) also stimulate other sensory cues (e.g., somatosensory for GVS, auditory for sound-induced vestibular stimulation) while not being able to selectively stimulate otoliths and to provide the same level of precise temporal and spatial information as natural vestibular signals. We also note that despite the importance of inducing OBE-related phenomena experimentally in order to understand the mechanisms of OBEs, the intensity of induced changes is small compared to full-blown OBEs. Future work needs to induce stronger experimentally induced OBE phenomena, potentially working with participants who have previously reported spontaneous OBEs. Another limitation is that we did not reliably modulate participants' experienced 1PP direction in the current study. This is not trivial, as also previous studies[29] or had difficulties reporting intra-subject changes in 1PP direction or only reported inter-subject differences in 1PP.[15] Follow-up studies need to optimize the visual and vestibular stimulations, potentially inducing clearer changes in experienced 1PP direction that goes beyond the visual viewpoint change and better matches spontaneous OBEs.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2023.108547.

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AUTHOR CONTRIBUTIONS

Conceptualization and methodology: H.P.W., E.N., S.B., B.H., and O.B. Data curation, formal analysis, investigation: H.P.W., E.N., and S.B. Funding acquisition, project administration, resources, supervision: S.B., B.H., and O.B. Software: F.L. and H.P.W. Visualization, writing – original draft: H.P.W. and E.N. Writing – review & editing: H.P.W., E.N., S.B., B.H., and O.B.

DECLARATION OF INTERESTS

O.B. and B.H. are inventors on patent US17/288,598 (Title: Method and system for creating an out-of-body experience) held by the Swiss Federal Institute (EPFL).

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw and analyzed data	This paper and supplemental information	This paper and supplemental information
Software and algorithms		
R version 4.2.0	https://www.R-project.org	https://www.R-project.org/
ExVR – Open virtual psychology toolkit	In-house software	https://github.com/BlankeLab/ExVR
ExPyVR – Behavioral science experimentation engine in Python	In-house software	http://lnco.epfl.ch/expyvr
Unity 3D	https://unity.com	https://unity.com

RESOURCE AVAILABILITY

Lead contact

Requests for information and resources should be sent to the lead contact, Prof. Olaf Blanke (olaf.blanke@epfl.ch).

Materials availability

This study did not generate any new unique reagents.

Data and code availability

- The study has not been preregistered.
- All data reported in this paper will be shared by the lead contact upon request.
- This paper does not report original code.
- Any additional information required to re-analyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Participants

Forty-three participants were recruited in Study 1. One participant did not complete the experiment due to cybersickness. Four participants were excluded because of technical issues. One participant was removed as an outlier. The final data set included thirty-seven participants (23 females, mean age $\pm$ std = 25.43 $\pm$ 4.85 years). Twenty-six participants participated in Study 2. One participant stopped the experiment for cybersickness. Another participant was excluded for not following the instructions. Hence, data from twenty-four participants (14 females, mean age $\pm$ std = 26.33 $\pm$ 5.33 years) were analyzed. The study protocol was approved by the CCER (Commission Cantonale d'Ethique de la Recherche, project ID: 2021-00358) and was conducted according to the Declaration of Helsinki. Information regarding participants' ancestry, race or ethnicity was not collected and hence not available. All participants provided informed consent before the experiment started. They were compensated for their participation time at a rate of 20 CHF/hr.

METHOD DETAILS

Mixed reality

The visual stimuli and scenario to create an OBE-like experience were adapted from Song.[31] The visual scenario was created using Unity 3D (Unity Technologies, USA) and an in-house software ExVR (https://github.com/BlankeLab/ExVR). Participants were immersed in a virtual replica of the experimental room using a head-mounted display (HMD; Odyssey, Samsung, 110 degrees field of view, 1440 x 1600 px per eye). The data of eight depth cameras (Kinect V2, Microsoft) surrounding and pointing towards the participants was assembled to reconstruct a photorealistic 3D representation of the participant's body image. The reconstructed virtual body was presented in the VR scene through the HMD in real-time.[53] The virtual body had the same appearance as the participants. It was collocated with participants' real bodies and moved in synchrony with their actual movements. Hence, in this mixed reality (MR), participants experienced as if they were in the virtual scene and seeing their body as part of it.

The virtual scenario presented to participants during the trials is shown in Figure 1. Participants virtually experienced "leaving out of the body" (procedures indicated by the black arrows in Figure 1) and then "moving back to the body" (indicated by the white arrows) in the mixed reality in both experiments. In Study 1, each trial began from an embodied perspective. Participants were in supine position both physically and virtually, looking upwards at the ceiling. Their visual viewpoint was then rotated by 180°, making them look down at the upper part of their 3D body, as if going "out" of their virtual body. The visual viewpoint then moved up along a predefined trajectory to two meters above the virtual body. This higher viewpoint allowed participants to observe their entire virtual body, adopting a disembodied perspective. In Study 2, the scenario was similar to Study 1 except that the virtual room and the bed were removed and replaced by a black background. Only their virtual body was presented in the HMD. Participants could see it thanks to the same rotation and movement of their viewpoint to reach the same higher position as in Study 1. In both experiments, participants' visual viewpoints went through rotational and translational stages of movements and stayed at two meters height for eight seconds. The scene then faded into darkness and participants had to perform the behavioral task and/or answer the questionnaire (Videos S1 and S2; also see Experimental Procedure and Behavioral Measure sections below). After they gave responses, participants' viewpoint moved back to the embodied perspective following the opposite sequence of events (Figure 1, white arrows). For more details on the visual stimuli and scenario, see Videos S1 and S2.

Motion platform

Vestibular stimuli were provided through whole body translations in the naso-occipital axis in participants lying supine using a Stewart-Gough motion platform (Sonceboz Robotics SA) placed in the center of the experimental room. This motion platform is a six-axis parallel robot with six kinematic chains linking an upper platform to the base. It can perform movements in six degrees of freedom (both translational and rotational movements in three directions). In both experiments, the platform moved up and down following a precomputed profile with a nearly cosine-shaped velocity (see supplemental information). The whole-body translation lasted five seconds to cover a distance of 410 mm, with a maximum velocity of 16.4 cm/s and maximum acceleration of 13.1 cm/s^2 (see Figure S1 in supplemental information). This profile was adjusted after pilot studies to provide perceptible acceleration without discomfort.

In both studies, the vestibular stimulation was synchronized with the visual stimulation presented in the HMD. During the first rotational stage of viewpoint movement, the platform remained stationary. Then, the platform moved either up or down depending on the conditions, always at the same time as the participant's viewpoint was undergoing a translational movement towards the virtual ceiling (see shaded part in Figure 1). Note that when the participant's viewpoint moved back and closer to the virtual body (i.e., Figure 1, shaded part following white arrows), the platform was also moving back to the starting position.

Mental Ball Dropping task

In both studies, self-location was measured using the Mental Ball Dropping (MBD) task. This task is based on mental imagery and has been widely used in full-body illusion experiments[15,19,29,32] to quantify changes in self-location (see Indovina, Maffei, Bosco, Zago, Macaluso & Lacquaniti[54] for the theoretical model). In this task, a black screen is presented in the HMD and participants are asked to close their eyes. They were instructed to imagine holding a ball in their non-dominant hand and dropping it from their current location to the ground. Participants indicated when they imagined dropping the ball by pressing a button on a keypad with their dominant hand. When the ball reached the floor in their imagination, they had to release the pressure on the button. Past research has shown that participants' MBD response times correspond to their self-location relative to the ground.[15,19,34] That is, a longer or shorter MBD response times compared to the baseline indicates a higher or lower self-location respectively.

Bodily self-consciousness questionnaire

Changes in feeling of disembodiment, self-motion perception and other OBE-related aspects were measured using questionnaires. Most of the questionnaire items (Q1 - Q7) were designed based on the OBE phenomenology reports documented in Green[6] and the previous study in our lab by Song.[31] We added four (in Study 1) and six (in Study 2) more items concerning dizziness, self-motion, and other aspects related to BSC and OBE. The questionnaire included eleven items in Study 1 and thirteen items in Study 2. Ten questions were designed to capture changes in a range of BSC and OBE-related aspects, including the senses of disembodiment (Q1, Q6, and Q11), visuo-spatial location (Q2), vestibular-related sensations (Q3 and Q4), body ownership (Q5), self-motion perception (Q9) and changes in 1PP direction (Q12 and Q13). Q7 and Q10 were control questions for altered feelings of bodily consciousness and self-motion perception, respectively. Q8 was a control for cybersickness throughout the experiment. Note that, we implemented three different questions regarding the disembodiment feeling according to Green's case reports[6] and Song's finding that different aspects contributing to disembodiment sensations might involve different factors.

A group of questionnaire items (Q9-Q13, listed in Table S1 in supplemental information) was presented on each trial after the MBD task. Other items (Q1-Q8, listed in Table S2) were presented only once in the last repetition (i.e. the 10th trial) in each condition. Note that for the perceived directions of movements (Q9 and Q10), experienced viewpoint (Q12) and relative location (Q13) were indicated by the sign of the ratings. More positive ratings indicated stronger feeling of moving up while negative values indicated that of moving down. Ratings of 0 (i.e. handle posited in the middle of the scroll bar) meant no feeling of movement or feeling of uncertainty. For each item in Table S2, participants used a keypad to indicate how much they agreed or disagreed with the statement on a 7-point Likert scale presented in the HMD. Figure S2 in supplemental information shows the examples of how they were presented in VR.

Rod and frame test

In Study 2, all participants completed the Rod and Frame Task (RFT) to evaluate their visual dependency before being immersed in mixed reality. The RFT requires to perform visual vertical judgments by aligning a mobile rod appearing within a tilted square frame[28] and provides a measure of individual visuo-vestibular sensory weighting strategies. An in-house software ExPyVR (http://lnco.epfl.ch/expyvr) was used to present the stimuli and record participants' responses. Participants performed the task wearing an HMD (Oculus, Development Kit 1, Oculus VR) with their head vertical and their chin on a chin rest. A white dotted line (the rod) was presented inside a solid white square (the frame). The frame could be either vertical, right-tilted at 20 degrees or left-tiled at 20 degrees while the rod could be tilted at 5, 10, or 15 degrees in either direction (see Figure 4). Participants were asked to adjust the rod to make it as vertical as possible (i.e., align with the direction of gravity). Four trials were implemented for each combination (a frame angle paired with one rod angle), resulting in a total number of seventy-two randomized trials.

Data collection procedure

Before the experiment started, all participants received written and verbal explanation of the general purpose of the study and provided their written informed consent. A questionnaire was used to assess participants' eligibility for the participation. In Study 1, the experiment started with a two-stage training session of the MBD task and the immersion phase. In Study 2, participants first performed the Rod and Frame test and then proceeded to the same training and immersion phase as in Study 1. In the first stage of the training, participants used a real ball and were asked to release the ball from different heights in both standing and supine positions. They had to press down a button on a keypad using their non-dominant hand when the dropped the ball, and then released the pressure on the button when the ball hit the floor. They were explicitly asked to remember their current location and how long it took for the ball to reach the ground. This procedure allowed participants to practice estimating the collision time of a falling ball from different locations. The immersion session started following the first training session. Participants put on the HMD and were presented with the mixed reality: they saw their virtual body moving synchronously with their real body in the virtual room. They were instructed to move their arms, look around and point to the objects in the virtual room to facilitate the immersion in the virtual environment. Then they lay on the platform in supine position with the safety harness attached and their head resting comfortably on a pillow. Participants then went through the second training session in which they performed the MBD task without a ball and answered four questions (Q4, Q9, Q10, Q11) using the keypad without platform movements. Based on their responses, the experimenter ensured that they understood the task and questions, remembered the height of their current location and were able to respond properly with the keypad.

Participants were then exposed to the experimental proper. They first performed three trials of the MBD task and answered the full set of the questionnaire to provide pre-test baseline responses. Following the pre-test session, a familiarization phase began in which participants experienced a modified version of the OBE-like scenario, which involved the same procedure of viewpoint rotation and elevation (see Figure 1 and Videos S1 and S2) and simultaneous upward movement of the platform. However, instead of visually staying at two meters above the virtual body and doing the tasks, participants experienced several successive visual and vestibular synchronized stimulations. Their visual viewpoint continued to move within a range from 0.67 to 2 meters above the virtual body. After going through the sequence of movements, the visual viewpoint rotated 180 degrees to move back to the embodied position. During this familiarization, the platform was moving up and down correspondingly (i.e., when the viewpoint moved down, the platform moved down as well). The whole familiarization phase lasted about one minute. This familiarization phase was to avoid participants feeling startled in the beginning of the real experiment, and for the experimenter to ensure that the body image was presented properly in their visual field.

After the familiarization phase, participants went through all the three (Visuo-vestibular Up, Visuo-vestibular Down and Visual only in Study 1) or four conditions (with the additional Movement Control condition in Study 2) presented in blocks in a randomized order. Each condition proceeded as follows: At the beginning before the visual scenario started, participants performed three repetitions of the MBD task and answered all the questionnaire items to provide baseline measures for this condition. These baseline measures were used to ensure that participants felt they were back to their initial position before being exposed again to the scenario, and to offset the potential order effect (i.e., participants tended to rate higher or lower over time) in case it was detected. Nonetheless, since no order effect was detected (see Table S3), in the follow-up statistical analysis we directly compared the MBD response times measured in each experimental condition. In each condition, participants experienced four seconds of viewpoint rotation followed by a five-second translational elevation of the viewpoint. During the viewpoint elevation, the platform moved up or down or stayed stationary depending on the condition (see Figure 1, procedures following black arrows). Eight seconds after their viewpoint reached the target position, the screen turned black and a fixation cross appeared for 500 ms to indicate the start of the task, which contained three trials of the MBD task in a row (each cued by an auditory beep) followed by a subset of the questionnaire, including questions of self-motion, disembodiment degree (both Study 1 and Study 2) and experienced perspective directions (Study 2 only). Items are presented in Table S1. Once participants completed the MBD task and answered the questionnaire, the screen faded in and the scenario resumed. Participants' visual viewpoint went back from two meters high to the initial, embodied position following the reversed trajectory (Figure 1, white arrows). Each condition consisted of ten repetitions. The first nine repetitions were identical as described. In the tenth repetition participants did not perform the MBD task but only answered the rest of the questionnaire regarding out-of-body feeling, vestibular sensations and other control questions (see Table S2). One minute of break was implemented between conditions.

Experimental conditions

Participants were exposed to three main conditions in both Study 1 and 2. Within each experiment, visual stimuli were always the same in all three conditions (see Figure 1). In the visual condition (hereinafter, V condition), only visual stimulation was delivered (the motion platform did not move). In the two other conditions (visuo-vestibular up and visuo-vestibular down; hereinafter, VVU and VVD, respectively), vestibular stimulation was presented simultaneously with the translational movement of the visual viewpoint (shaded part in Figure 1). It lasted five seconds and stopped when the platform and the visual viewpoint reached the determined position. Of note, the visual stimulation of the translational elevating movement could be interpreted as a negative, front-to-back translation in the naso-occipital axis as participants were looking downwards in the virtual environment. As a result, the vestibular stimulation presented in the two visuo-vestibular conditions could be perceived as congruent (VVD) or incongruent (VVU) with the visual cues (Figure 2).

To confirm that participants could detect and the vestibular stimulation and distinguish the direction, we implemented different vestibular control blocks in the studies. In Study 1, the vestibular control task aimed at testing whether participants were able to detect the platform movements and distinguish the moving directions. In this task, participants experienced vestibular stimulation without any visual stimulation (i.e., they were lying supine on the platform, moving up and down while viewing a black screen). The motion profiles implemented in the vestibular control task were the same as in the main experiment and the order of upward and downward movements were randomized (for the details of the procedure, see supplemental information Methods S1). We first measured baseline responses for MBD response times and the questionnaire ratings before the control task started and when the platform was at its initial position. During the task, for each movement, participants were asked to perform the MBD task followed by answering to two questions regarding the moving direction (see Q9 and Q10 in Table S1). Half of the participants performed the vestibular control task before the main experiment while the other half did it after. The relevant statistical analyses for the questionnaire data collected in this task are presented in Tables S18 and S19 in supplemental information. In Study 2, the vestibular control was different and aimed at testing whether participants were able to detect the platform movements in contrast to only vibrations of the platform in movement. In this additional condition, Movement Control, the platform was performing small repeated vertical movements with a maximal amplitude of 1 cm to mimic the vibrations of the upward or downward translations occurred in the two experimental conditions (i.e. VVD and VVU, see Methods S2). Note that participants performed the MBD task and answered the questionnaire as in the other three main conditions. All the statistical analysis and the output tables related to the Movement Control condition are presented in Tables S20–S38 in supplemental information.

QUANTIFICATION AND STATISTICAL ANALYSIS

Mental Ball Dropping responses times processing

For both Study 1 and Study 2, we first identified and removed outliers using Interquartile Range (IQR) method applied to the whole MBD response time data set. The IQR was defined as the difference between the first quartile (Q1) and the third quartile (Q3). We removed the responses outside the lower fence (Q1 – 1.5*IQR) and upper fence (Q3 + 1.5*IQR). We opted for this method as it is a commonly used and well-established method for outlier identification.[55] Also, compared to other frequently used methods that remove data outside 2 standard deviations from the mean, which was used in previous MBD tasks (such as in Pfeiffer and colleagues' study[29]), the IQR method is more resistant to extreme values. One participant in Study 1 was excluded from the data set because more than 90% of his trials was removed. This procedure resulted in a sample size of 37 in Study 1 and 24 in Study 2. The percentages of outliers were 4.4% and 4.7% respectively. The sample size of Study 1 was based on Song's study[31] and our pilot studies. The sample size of Study 2 was determined by the effect size observed in Study 1 using a simulation method.[56] Before we did the main statistical analysis, we first checked the order effect (i.e., whether the MBD response times increased or decreased over time, see Tables S3 and S20) using a linear mixed effects model.

Bodily self-consciousness questionnaire processing

The outlier participants identified in MBD response analyses were first removed from the questionnaire data set. Then, we separated the data by the questionnaire items for further analyses. As a preliminary check, for questionnaire data in both studies, we first performed a cumulative link mixed model (CLMM) to compare the ratings of the BSC-related questions (Q1-Q8, and Q11) and the self-motion questions with the respective control questions, Q7 – *I felt as if I had more than three bodies* and Q10 - *I felt as if my body was moving to the [left / right]*. The analysis was to confirm that participants did respond according to their experiences. The results are reported in Tables S5, S6, S22, and S23.

Rod and Frame Test data processing

The Rod and Frame Task (RFT) data in Study 2 was analyzed following Lopez and colleagues' study.[27] First, we applied the IQR (Inter-Quartile-Range) method to remove identified outliers and removed the trials on which participants did not perform the task properly (e.g. pressing the confirm button by accident). Average deviation (error) under each tilt degree of frame and rod was then computed. The errors under the vertical frame condition were subtracted from the errors in the right- and left-tilted frame conditions, which resulted in the baseline-corrected deviations in two tilted frame conditions as presented in Figure 7. These baseline-corrected responses were then registered into a hierarchical classification using Ward's aggregation method.[27,57] The resulting hierarchical tree separated the participants into two groups (Figure 8A). A Wilcoxon rank sum test was performed to make sure that the two groups had significantly different average absolute errors ($r = 0.525$, $p < .001$;

see Figure 8B). The group with higher absolute errors, by definition, was referred as visual field dependent (FD) group while the group with lower absolute errors was referred as visual field independent (FI) group.

Statistical data analysis

All data analyses were performed on R (version 4.2.0) and RStudio (https://www.R-project.org/) with lme4, ordinal and emmeans packages for (general) linear mixed models, cumulative link mixed models and the relevant post-hoc comparisons respectively.

The MBD response time data were then analyzed with linear mixed effects models. Ordinal responses for the questionnaire were analyzed using cumulative link mixed effects models (CLMM). In all the mixed models applied for Study 1, we specified the condition as a fixed effect and included random intercepts for individual participants. For the mixed effects model used for the data of Study 2, we additionally included another between-subject predictor of “Group” indicating each participant’s visual field dependency (see Rod and Frame Test Data Processing section). To obtain the fixed effects in the mixed models, we performed likelihood ratio tests (LRT) to compare the compact model with the alternative model in which the effect of interest was additionally specified. In all of the mixed models in both studies, V condition served as a reference condition for both experiments. Post-hoc comparisons between experimental conditions were performed without multiple comparison adjustment in the case when a significant main effect or interaction was detected. Significance levels were all set at p = .05. All statistical results were presented in tables in Section 2 of supplemental information.