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Influence of vestibular signals on bodily self-consciousness: Different sensory weighting strategies based on visual dependency

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A R T I C L E I N F O

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A B S T R A C T

Previous studies showed that the vestibular system is crucial for multisensory integration, however, its contribution to bodily self-consciousness more specifically on full-body illusions is not well understood. Thus, the current study examined the role of visuo-vestibular conflict on a full-body illusion (FBI) experiment that was induced during a supine body position. In a mixed design experiment, 56 participants underwent through a full-body illusion protocol. During the experiment, half of the participants received synchronous visuo-tactile stimulation, and the other half received asynchronous visuo-tactile stimulation, while their physical body was lying in a supine position, but the virtual body was standing. Additionally, the contribution of individual sensory weighting strategies was investigated via the Rod and Frame task (RFT), which was applied both before (pre-FBI standing and pre-FBI supine) and after the full-body illusion (post-FBI supine) protocol. Subjective reports of the participants confirmed previous findings suggesting that there was a significant increase in ownership over a virtual body during synchronous visuo-tactile stimulation. Additionally, further categorization of participants based on their visual dependency (by RFT) showed that those participants who rely more on visual information (visual field dependents) perceived the full-body illusion more strongly than non-visual field dependents during the synchronous visuo-tactile stimulation condition. Further analysis provided not only a quantitative demonstration of full-body illusion but also revealed changes in perceived self-orientation based on their field dependency. Altogether, findings of the current study make further contributions to our understanding of the vestibular system and brought new insight for individual sensory weighting strategies during a full-body illusion.

1. Introduction

Our bodies are at the centre of our daily experiences and with them, we are deeply embodied in this physical world. Interoceptive signals (Craig, 2002) and exteroceptive signals (Suzuki, Garfinkel, Critchley, & Seth, 2013) bring constant awareness of our bodies and this allows us to interact with the environment around us. All of these sensations underpin a unique experience of possessing a self, of which the physical body is the essential foundation. This basic sense of the self is defined as a type of multisensory mental state resulting from integration of bodily inputs from different senses which referred as bodily self-consciousness (BSC) (Blanke, 2012; Gallagher, 2000; Metzinger, 2007). Thus, the notion of being embodied in a physical body with multiple senses provides new lines of research for understanding bodily self-consciousness and its sensory basis (Blanke, 2012).

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Experimental studies using bodily illusions have revealed the role of multisensory integration on BSC. These previous studies not only include visuo-motor (Tsakiris, Prabhu, & Haggard, 2006) and visuo-interoceptive (Adler, Herbelin, Similowski, & Blanke, 2014; Aspell et al., 2013) integration, but also includes proprioceptive-tactile (Ehrsson, Holmes, & Passingham, 2005) modalities, and visuo-vestibular system (Ferrè, Lopez, & Haggard, 2014; Macauda et al., 2015; Pfeiffer et al., 2013; Thür, Roel Lesur, Bockisch, Lopez, & Lenggenhager, 2019). Importantly, the vestibular system differs from other sensory modalities, since the processing of vestibular signals themselves are incorporated with other sensory modalities such as vision, somatosensation, and proprioception (Buttner & Henn, 1976; Deecke, Schwarz, & Fredrickson, 1977; Dieterich et al., 2005; Guldin & Grüsser, 1998; Kotchabhakdi, Rinvik, Walberg, & Yingchareon, 1980; Lang, Büttner-Ennever, & Büttner, 1979; Lopez & Blanke, 2011; Lopez, Blanke, & Mast, 2012; Marlinski & McCrea, 2008a, 2008b; Matsuo, Takeuchi, Ikoma, & Hosogai, 1999). Because of its role in sensing body orientation, the vestibular system is considered as a critical aspect of bodily self-consciousness (Lackner & DiZio, 2005; Lopez, 2015; Pfeiffer, Serino, & Blanke, 2014; Pfeiffer et al., 2013; Thür et al., 2019).

Here, sensing body orientation is referred to as self-orientation, which is described as the sensation of the position and the orientation of the body with respect to the world. For such processing of self-orientation, the vestibular system is considered as an essential mechanism. For instance, the fact that we can sense our body position unambiguously even with eyes closed implies the key role of other senses in self-orientation, such as vestibular (Lacquaniti et al., 2014), proprioceptive, and somatosensory systems (Bringoux, Nougier, Marin, Barraud, & Raphel, 2003). One of the main properties of this multisensory integration process is to create an internal model of gravity (Angelaki, Shaikh, Green, & Dickman, 2004; Mittelstaedt, 1983), which enables us to determine our body orientation (Barra et al., 2010; Harris, Jenkin, Jenkin, Zacher, & Dyde, 2017) and perspective taking capacity (Meirhaeghe, Bayet, Paubel, & Mélan, 2020). Since this internal model evolved on earth's gravity, any modulation disrupts the perception of self-orientation (Clément & Reschke, 2008; Erdeniz & Tükel, 2020; Meirhaeghe et al., 2020). For example, space flight studies showed that when the graviceptor signals are missing, astronauts lose their sense of verticality and experience illusion of orientation reversal (Lackner, 1992; Oman, 2003). These illusions in the perception of verticality and body orientation under microgravity environments are evidence for the multisensory nature of the internal model of gravity, and suggest that vestibular inputs have a significant influence on bodily self-consciousness (for a review see Lenggenhager & Lopez, 2015). Given the limited numbers of studies under micro gravity environments (Lackner, 1992; Oman, 2003), past research mostly focused on reorientation illusions to specify the contribution of visual orientation changes and physical body changes on perceived self-orientation (for a review see Carriot, DiZio, & Nougier, 2008). Typically, reorientation illusions aim to alter perceived self-orientation by modulating the visual information (Goodenough, Nowak, Oltman, Cox, & Sigman, 1982; Held, Dichgans, & Bauer, 1975; Sigman, Goodenough, & Flannagan, 1978; Witkin, 1949).

Regarding the influence of visual information on self-orientation perception, findings from previous studies revealed that people perceive their body as tilted when asked to judge their orientation in front of a tilted frame (Goodenough et al., 1982; Sigman et al., 1978; Witkin, 1949). Moreover, it was also shown that error in perceived self-orientation increased if participants were presented with polarized scenes such as a room with furniture and objects (see for example, Howard & Childerson, 1994). In addition to visual factors, the involvement of the vestibular system is suggested because people are influenced by reorientation illusions as their body position deviates from the normal with respect to the vertical plane (Groen, Jenkin, & Howard, 2002). In addition, regarding the role of vestibular systems involvement in self-orientation perception, previous studies showed that, compared to standing or sitting position, supine position, as well as roll body tilts, led people to make erroneous self-orientation judgements to greater extent (Howard & Hu, 2001; Witkin & Asch, 1948). These observations suggest that perceived self-orientation changes as a function of vestibular inputs by detecting body position (Howard & Hu, 2001).

These differences in illusory self-orientation based on body position were attributed to the specific contribution of vestibular, somatosensory, and proprioceptive information about gravity (for a review see Lackner & DiZio, 2005). For instance, Mittelstaedt (1999) highlights the importance of perceived body orientation of compensatory contributions of proprioceptive and somatosensory inputs in addition to the vestibular signals. More recently, Bringoux et al. (2003) suggested that the somatosensory inputs are more important than vestibular signals for the perception of body orientation while moving at slow velocities. On the other hand, artificial vestibular manipulation was found to induce illusory body rotation, indicating the primary role of the vestibular system (Day & Fitzpatrick, 2005). This might also explain why the participants are more susceptible to reorientation illusions in the supine position, indicating decreased sensitivity of vestibular receptors (Howard & Hu, 2001). Taken together, the influence of body position on reorientation illusions supports the contribution of the vestibular signals on self-orientation. For the reasons mentioned above, supine body position was used to model reduced sensory input during spaceflight analogue studies on earth (Koppelmans et al., 2013; Moore, Dilda, & MacDougall, 2011; Mulavara et al., 2018).

Crucially, an influence of body position on verticality perception was also shown, suggesting the same underlying mechanisms of perception of self-orientation. More specifically, perception of verticality and self-orientation requires the process of sensory weighting and integration of vestibular, somatosensory, and visual signals providing information about gravity, body position, and visual environment, respectively (Lopez, Mercier, Halje, & Blanke, 2011). In general, the perception of verticality was investigated by asking participants to orient a line with respect to their inner representation of gravitational direction. A well-known experimental paradigm to study the perception of verticality is the rod and frame task (RFT) (Witkin & Asch, 1948). In RFT, people are asked to orient a tilted line embedded in a tilted frame into the vertical position relative to gravity. The degree of perceived verticality deviates as a function of participants' reliance on different sensory signals, such as vision. Participants with greater deviations are classified as visual field-dependent, implying increased weighting of visual signals, and those with smaller deviations are classified as visual field-independent, indicating increased weighting of vestibular or somatosensory signals (Lopez, Lacour, Magnan, & Borel, 2006; Pfeiffer et al., 2013; Witkin & Asch, 1948). Independent of visual field dependency, roll body tilt and supine position were also found to increase the amount of deviation in verticality judgements (Goodenough, Oltman, Sigman, & Cox, 1981; Guerraz, Poquin, & Ohlmann, 1998; Lichtenstein & Saucer, 1974; Templeton, 1973; Van Beuzekom & Van Gisbergen, 2000). These differences are likely explained by reduced vestibular signals in the supine position, since the body is not aligned with gravity (Lopez & Blanke, 2010). Supporting the role of vestibular signals and body orientation, Lopez, Lacour, Léonard, Magnan, and Borel (2008) found that patients with unilateral vestibular deficiency, and thus, impairment in verticality perception and postural control, improved the accuracy of verticality judgements in standing position after surgical treatment. Further evidence that supine body position is related to decreased vestibular signals is provided in Saj, Honoré, Davroux, Coello, and Rousseaux (2005), who studied patients with spatial neglect. They revealed that spatial neglect patients made more accurate verticality judgements in supine position than when seated. Since the spatial neglect is associated with asymmetrical otolith signals from the inner ears (Pizzamiglio, Vallar, & Doricchi, 1997), it was proposed that the improvement in verticality judgements were related to more symmetrical otolith signals due to decreased sensitivity in the supine position (Lopez et al., 2008).

Extending the findings from verticality perception, neuropsychological studies that examine the phenomenon of out-of-body experiences (OBEs) provided further insight for the contribution of vestibular system on BSC (Blanke, Ortigue, Landis, & Seeck, 2002). During OBEs, people experience themselves localized in the illusory body in an elevated position, followed by the sensation of floating or flying (Blanke & Mohr, 2005). Importantly, around 73% of healthy individuals (Green, 1968) and 80% of neurological patients (Blanke & Mohr, 2005) reported that OBEs occurred while in supine position. Thus, it is proposed that OBEs occur due to the modification of the weighting of sensory signals, depending on the body position (Lopez & Blanke, 2010). That is, supine position decreases vestibular, motor, and somatosensory signals, thus, the weighting of vision enhances, resulting in a visually dependent form of bodily self. In line with these, full-body illusions support the influence of body position and vestibular signals, suggesting that inducing full-body illusion in supine position affects the accuracy of vestibular sensations, triggering the experience of floating as well as changes in self-location (Ionta, Gassert, & Blanke, 2011; Lenggenhager, Mouthon, & Blanke, 2009).

In that vein, Pfeiffer et al. (2013) revealed a positive association between individual differences in the weighting strategies of different sensory signals with the alterations in self-location and first-person perspective (1PP). In their study, they induced full-body illusion, and additionally provided visuo-vestibular conflict by manipulating the visual cues about gravity while the participants were in supine position. Visual field-dependent (FD) participants put themselves in the position of the virtual body and transferred their perspective into the imagined position, whereas visual field-independent (FI) participants experienced their self-location and perspective at the location of their physical body. This influence of visual field dependency is also corroborated by a study involving the rubber hand illusion, showing that FD participants experience greater proprioceptive drift towards the rubber hand compared to FI participants (David, Fiori, & Aglioti, 2014). Another study created a full-body illusion with conflicting visuo-graviceptive information, by presenting the virtual body in tilted orientation (Thür et al., 2019). It was also shown that only visual field-dependent participants changed their perception about body orientation in the tilted condition. It is notable that this change in perception was specific to synchronous visuo-tactile stimulation, indicating the importance of the weighting of different sensory signals. However, graviceptive signals are not only important for perceived self-location but also contributes to the sense of ownership. In a study by Macauda et al. (2015), the influence of conflicting visuo-vestibular information on full-body illusion was investigated in a relatively different setup. In their study, they found no influence of visuo-vestibular conflict on subjective expressions of body ownership but reported that visuo-vestibular congruency led to a decrease in skin temperature, which is considered as an indicator of the feeling of ownership (Salomon, Lim, Pfeiffer, Gassert, & Blanke, 2013; but also see de Haan et al., 2017). This result is compatible with previous studies showing reduced skin temperature during the illusory feeling of ownership of a rubber hand (Moseley et al., 2008; Tsakiris, Tajadura-Jimènez, & Costantini, 2011) or a virtual body (Salomon et al., 2013). Supporting the findings mentioned above, a more recent study by Preuss and Ehrsson (2019) revealed that the congruency between visual and vestibular signals is sufficient for participants to feel illusory ownership.

The aim of the present study is to investigate the influence of visuo-vestibular conflict during full-body illusion and to compare the influence of individual sensory weighting strategies on bodily self-consciousness. In order to achieve that goal, the full-body illusion from 1PP was induced in a supine position while the virtual body was standing upright so that participants were provided with visuo-vestibular conflict. This experimental setup allowed testing for the influence of full body illusion during additional visuo-vestibular conflict in supine position. The synchronous visual stimulus on the virtual body and tactile stimulus on the physical body were applied to create full-body illusion while asynchronous visuo-tactile stimuli were used as a control condition. During the experiment, a virtual version of RFT (Odin, Faletto-Passy, Assaban, & Pérennou, 2018) was performed three times: (i) Participants performed RFT in standing (pre-FBI standing), (ii) supine (pre-FBI supine) positions before the FBI and (iii) once after the FBI in supine position (post-FBI supine). Here, RFT in the pre-FBI standing condition was used to separate participants into two groups, as FD and FI, in order to differentiate individual sensory weighting strategies. Furthermore, comparison of performance during the pre-FBI supine condition and the post-FBI supine condition enabled us to evaluate the influence of full-body illusion on perceived self-orientation. We argue that the synchronous visuo-tactile stimulation during full-body illusion can compensate the errors in RFT. To this end, we developed the following three hypotheses: Firstly, the subjective reports will show an increased feeling of ownership for the virtual body and an altered sense of self-location after synchronous visuo-tactile stimuli compared to asynchronous visuo-tactile stimuli. Secondly, as mentioned earlier, there will be greater verticality errors in the pre-FBI supine condition compared to the post-FBI supine condition after synchronous visuo-tactile stimuli, which might be considered as illusory change in perceived self-orientation. Finally, we hypothesized that FD participants will feel a stronger sense of ownership of the virtual body and make fewer errors in their verticality judgments after synchronous visuo-tactile stimulation, but not for the asynchronous visuo-tactile stimulation.

2. Materials and methods

2.1. Participants

Before the experiment in order to calculate the predictive power (sample size) we looked at the effect size of the previous studies similar to our experiment (Pfeiffer et al., 2013; Thür et al., 2019). Based on those studies, we conducted a priori sample size calculation using Shiny software (https://shiny.rstudio.com/) that works with R function (Lakens & Caldwell, 2019). For 2 × 2 ANOVA, 2000 simulations were performed with 24 participants in each group (a total of 48 participants), the results provided the statistical power based on $p < .05$ as *partial* $\eta^2 = 0.69$. For 2 × 2 × 2 ANOVA, 2000 simulations were performed with a total of 48 participants (equal sample sizes of 12 in each group) by controlling multiple comparisons with Holm procedure. Based on those a priori analysis we decided to use at least fifty participants. Fifty-six right-handed volunteers (24 male, 32 female) from İzmir University of Economics between the ages of 18 to 37 were recruited to the experiment. One participant was excluded due to technical problems, and three, due to motion sickness during the experiment. The remaining 52 participants (21 male, 31 female) were included in the analysis ($M_{age} = 24$, $SD = 4.33$). All participants reported no previous history of any psychological, psychiatric, or neurological disorder, and had normal or corrected to normal vision. Before the experiment, participants signed a written informed consent form and completed a questionnaire about demographic information, including their age, sex, and education levels. The present study was approved by the ethics committee of the İzmir University of Economics (No: B.30.2.IEU.0.05.05-020-066) and conducted according to the Helsinki regulations.

2.2. Equipment and setup

Virtual Environment: HTC VIVE head-mounted display (HMD) was used to present a virtual environment (1080 × 1200 pixels per eye, 110° field of view, 90 Hz). The virtual environment was built using the game development platform UNITY 3D (https://unity.com/) version 2019.1. The simulated virtual reality environment was designed to be similar to the actual experimental room, by using custom assets (see Fig. 1A–B).

Virtual Bodies and Interaction with the Environment: In addition to the simulated virtual environment, two virtual characters, a male and female avatar, were constructed (see Fig. 1C–D). These two virtual bodies were created in order to match the participants' gender, using Make Human software (http://www.makehumancommunity.org/). Furthermore, Final IK asset (https://assetstore.unity.com) was used to implement inverse kinematics into virtual bodies. This helped the participants to accurately animate their body postures with natural movements. Two HTC VIVE controllers were used to reflect participants' arm movements into the virtual body during the

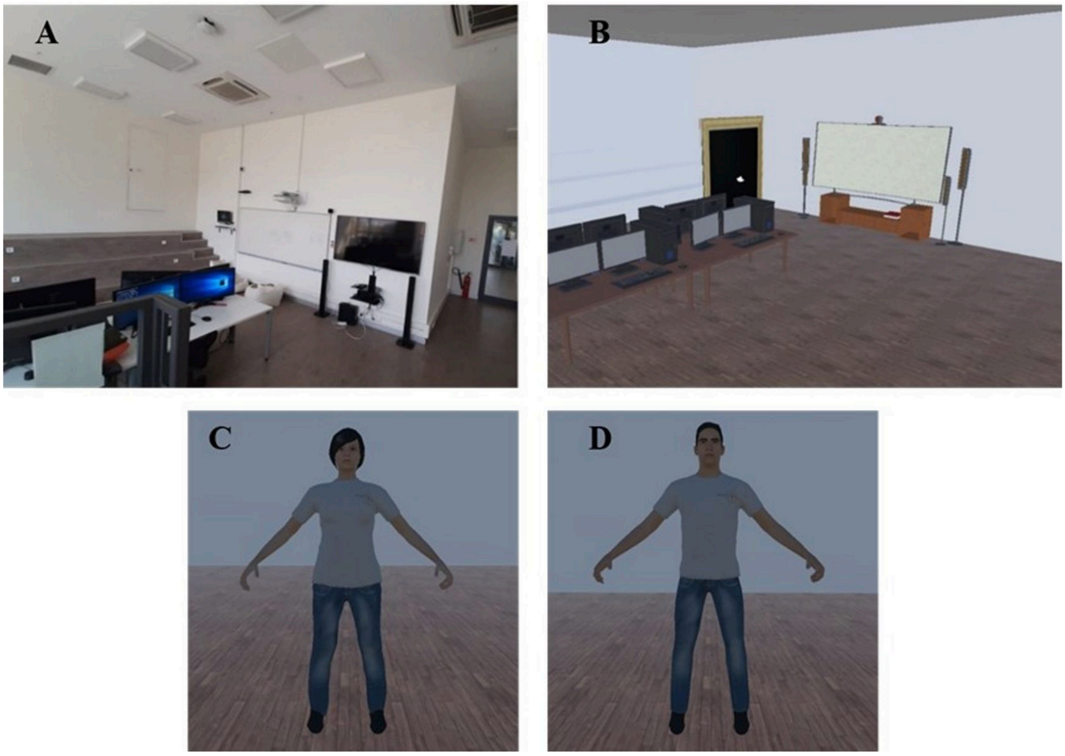

Fig. 1. Example of the experimental set-up. The real experiment room (A) was used as a model for the virtual room (B) which was presented to participants through the HMD. Each participant was assigned to a gender-matched avatar (C-D).

adaptation period of the full-body illusion. In addition, in the simulated virtual environment, a full-height virtual mirror in front of the participants allowed them to see their virtual bodies' reflection (Gonzalez-Franco, Perez-Marcos, Spanlang, & Slater, 2010; Blom, Arroyo-Palacios, & Slater, 2014).

Visuo-Tactile Stimulus Delivery: The controllers were used to present visuo-tactile stimuli either in synchrony or asynchrony during the experiment. In the synchronous condition, only one of the controllers was connected to the virtual reality (VR) system, and was used to deliver the tactile stimuli to the abdomen of the participants' physical body, and to present a spatially and temporally matched visual stimuli on the corresponding location of the virtual body. Similarly, in the asynchronous condition, one of the controllers connected to the VR system was used to present the visual stimuli on the virtual body, and the other controller, which was turned off, was used for providing tactile stimulation. The abdomen area was chosen for visuo-tactile stimulation in line with findings which showed that people are more likely to locate themselves within the face and the torso than other body regions (Alsmith & Longo, 2014). The experimenter presented the visuo-tactile stimuli randomly as either long stroking (1500 ms) or short tapping (500 ms) (Petkova & Ehrsson, 2008; Pfeiffer et al., 2013).

Rod and Frame Task: Subjective visual verticality was assessed with the Rod and Frame task (RFT) in virtual reality designed by Virtualis (https://virtualisvr.com/en/). The virtual version of RFT was found to result in comparable results with classic RFT (Bringoux et al., 2009). A rod embedded into a realistic tilted room with bedroom objects was presented. This type of furnished room has been shown to induce larger errors in visual verticality judgements (Allison, Howard, & Zacher, 1999; Howard & Childerson, 1994; Passey, 1950; Witkin & Asch, 1948). The virtual RFT showed high validity and reliability (Odin et al., 2018), in line with studies validating the use of virtual reality for subjective verticality estimations (Bringoux et al., 2009; Jenkin, Dyde, Jenkin, Howard, & Harris, 2003; Ulozienė et al., 2017). During the RFT, the virtual room was tilted at an angle of 28°, either clockwise or counter-clockwise. The magnitude of the frame angle was determined based on studies reporting larger deviations for the subjective visual vertical judgements for this angle (Bringoux et al., 2009; Lichtenstein & Saucer, 1974; Oltman, 1968; Witkin & Asch, 1948). The initial tilt of the rod was set to either 28° clockwise or counter-clockwise, and presented in pseudo-random order (Pfeiffer et al., 2013; Piscicelli & Pérennou, 2017; Witkin & Asch, 1948). During the RFT, participants stand or lie on their back with their hands at their sides holding the HTC VIVE controllers, pressing the buttons on the appropriate controller to manipulate the rod either right or left.

2.3. Procedure

After signing the informed consent form and completing the demographic information sheet, all participants were asked about any previous experience of virtual reality technologies and their experience level. All participants reported no or limited (1 or 2 times) experience in virtual reality. Following that, participants attached the head-mounted display (HMD) and held the VR controllers. The experiment began with an explanation of the use of controllers. Then, the first RFT was introduced and participants were instructed to align the rod vertically with respect to their subjective judgements of verticality. Participants were pseudo-randomly assigned to the standing (pre-FBI standing) or supine (pre-FBI supine) positions for the initial RFT measurement before the FBI. During the experiment, it was ensured that the order of RFT measurements in pre-FBI standing and pre-FBI supine was counterbalanced.

After completing the RFTs in standing and supine positions (pre-FBI standing & pre-FBI supine), full-body illusion was induced by presenting the virtual body standing upright (pitch rotation) while participants were physically in supine position (see Fig. 3). As the adaptation period, which took approximately 1 min, participants were instructed to move their head and arms but not feet while observing the virtual body in the standing position, allowing familiarity with the simulated virtual environment and the virtual body. The controllers were then retrieved, and the full-body illusion was created in a two-minute period in which a visual stimulus was presented on the virtual body and a tactile stimulus on the participants' physical body. Half of the participants were assigned to synchronous and the other half to asynchronous visuo-tactile conditions. In synchronous condition, the touch seen on the virtual body with respect to the felt touch on participants' physical body was temporally and spatially matched, whereas in the asynchronous condition, the visual and tactile touch was presented as spatially incongruent with a delay (approximately 1 s). During the full-body

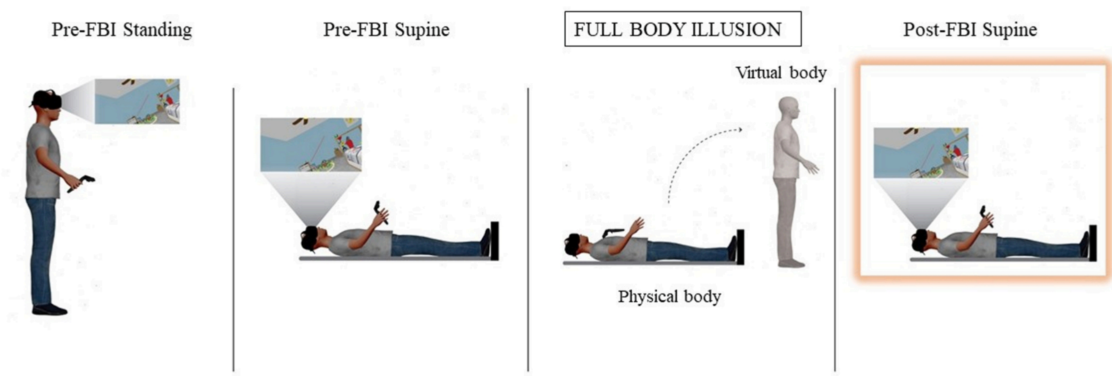

Fig. 2. Illustration of the general procedure of the experiment. After participants completed RFT in pre-FBI standing and pre-FBI supine condition, FBI was induced. Then, participants completed a final RFT which referred as post-FBI supine condition.

illusion, all participants were instructed to focus on the visual touch presented on the virtual body, and make no movements. When viewing their virtual body in the standing position, participants were able to look either directly at their virtual body, or in the virtual mirror located in the virtual environment.

After completion of full-body illusion, participants were immediately asked to close their eyes and the HMD was removed for approximately 15 s to calibrate for the RFT in the post-FBI supine condition. The experimenter then replaced the HMD and presented the RFT. Following the completion of RFTs in the post-FBI supine condition, the HMD was again removed, and participants completed the subjective report of the full-body illusion experience. Finally, participants were thanked and debriefed; any questions they had about the experiment were answered.

It is important to note that during RFT performances in pre-FBI supine condition, post-FBI supine condition and full-body illusion, a steady platform was placed under participants' feet, and a yoga block under their head to compensate the pressure from their back. This manipulation was based on previous studies that showed a significant contribution of vestibular and somatosensorial systems on the perception of body orientation (Bringoux et al., 2003; Lackner & DiZio, 2005; Mittelstaedt, 1999). The method used in this study aims to minimize tactile cues from the somatosensorial system while the contribution of the vestibular system was investigated (Trousselard, Cian, Nougier, Pla, & Raphel, 2003). The general procedure of the experiment is shown in Fig. 2.

2.3.1. Measurements

Subjective Report for the Full-Body Illusion: As an explicit measure of FBI, after the experiment, participants were asked to rate statements about their subjective experience of the illusion. The statements were reformulated based on previous experiments (Huang, Lee, Chen, & Liang, 2017; Preuss, Brynjarsdóttir, & Ehrsson, 2018; Thür et al., 2019). A 7-item, paper-based questionnaire was structured as self-report statements, shown in Table 1, and presented in a form of visual analogue scale (VAS) below each statement. VAS was presented as a continuous 10 cm horizontal line, with the left end representing "strongly disagree", and the right end, "strongly agree". Participants were instructed to make a mark on the scale representing the intensity of their agreement or disagreement. The statements of the subjective report were formulated to assess ownership (Q1), self-location (Q2), first-person perspective (Q3), orientation perception (Q4), and 3 items (Q5, Q6, Q7) were control statements to validate the full-body illusion. A further question (Q8) was included regarding participants' estimation of their perceived body orientation during the full-body illusion, in order to assess whether there was an explicit sense of body orientation (see Fig. 4). For Q8, participants were asked to draw an angled line on a graph to indicate their estimation of perceived self-tilt.

Rod and Frame Task (RFT): Rod and Frame task was used as an implicit measure of perceived body orientation. Participants completed RFTs in three conditions. Pre-FBI standing and pre-FBI supine conditions refers to RFTs completed before FBI in standing and supine position, respectively, which served as baseline conditions. We expected higher error rates in pre-FBI supine compared to pre-FBI in standing condition. Additionally, performances in pre-FBI standing condition were used to group participants as either visual-field dependent or independent. In post-FBI supine condition, which was technically the same as the pre-FBI supine condition, participants completed RFT in supine position after presentation of FBI. We compared the verticality error rates in pre- and post-FBI supine conditions to investigate the influence of FBI on self-orientation perception. In all conditions, participants were free to move their heads and trunks, and before each measurement, all devices and software were calibrated. Head orientation was controlled by fixating the view angle of HMD. For the pre-FBI standing condition, the view angle was fixated with participants wearing HMD and standing still. For pre-FBI supine and post-FBI supine conditions, HMD was removed and the view angle fixated before being replaced. Thus, participants experienced the virtual environment as if standing while in fact lying on their back. For each body orientation, RFT was performed in the tilted room with both clockwise and counter-clockwise orientations. In the literature, 6 trials for each condition were proposed as sufficient to identify verticality biases (for a review see Piscicelli & Pérennou, 2017). Thus, in the present study, each room orientation included 8 trials, resulting in 16 measurements for each body orientation, and a total of 48 measurements for each participant.

2.4. Data processing and statistical analysis

Statistical analysis was performed with SPSS 20. Firstly, Kolmogorov-Smirnov test, used to check for normality assumption, showed that the data was normally distributed. In order to understand the effectiveness of *full body illusion,* the subjective reports of participants were analysed separately for each question (Q1-Q8) by using two-way ANOVAs with the visuo-tactile stimulation (synchronous, asynchronous) and visual field dependency (FI, FD) as a between-subject factor. Additionally, we investigated the effect of full body illusion on perceived self-orientation by conducting 2×2 mixed ANOVA with visuo-tactile stimulation (synchronous, asynchronous)

Table 1
The list of statements used to measure subjective experience of the full-body illusion.

Item names	Item statements
Ownership(Q1)	I felt as if the virtual body was my own body.
Self-location(Q2)	I felt as if my body was located at where the virtual body was.
1PP(Q3)	I felt as if the position of my 1PP had changed.
Orientation perception(Q4)	I felt as if I was standing.
Control(Q5)	I felt as if I had two bodies.
Control(Q6)	I felt that the experimenter touched on my abdomen.
Control(Q7)	I felt as if the virtual room rotated around the virtual body.

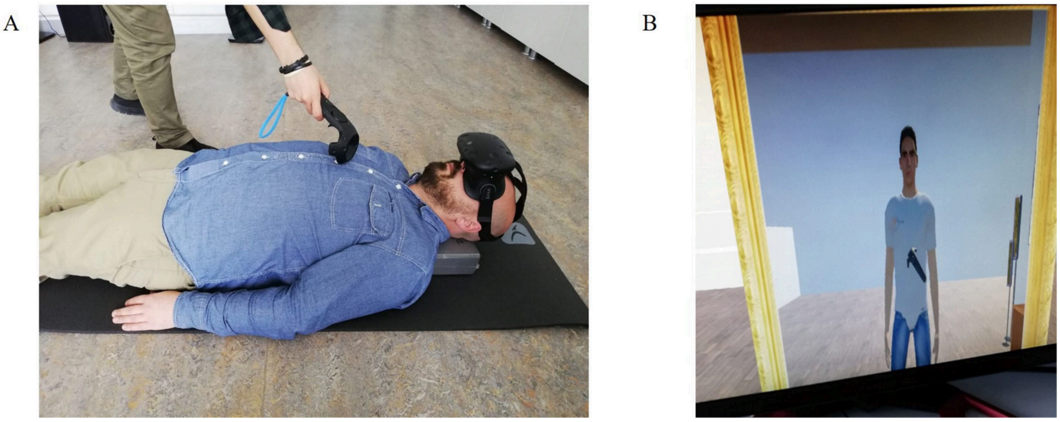

Fig. 3. Application of visuo-tactile stimulation. (A) The experimenter applies the tactile stimulus on participants' abdomen while they were in supine position. (B) Participants see the visual stimulus on abdomen of the virtual body which is in upright position.

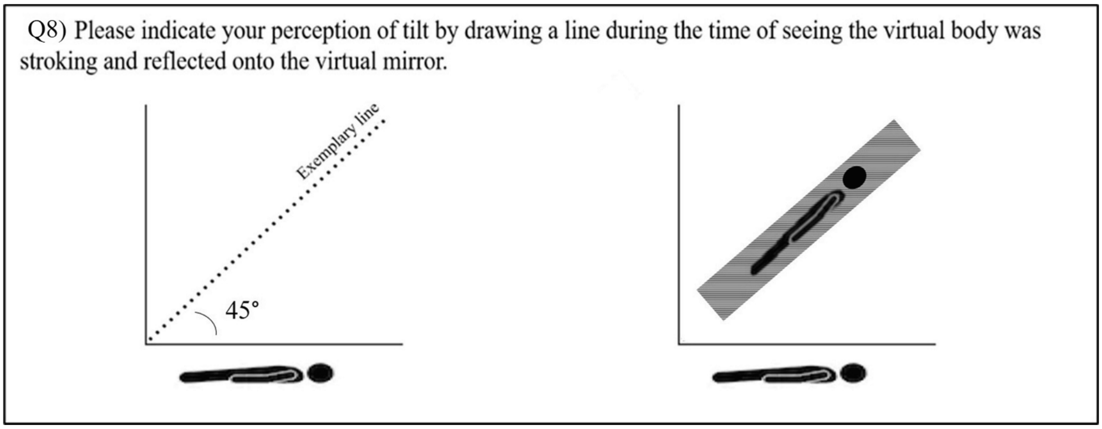

Fig. 4. Drawing used in Q8 that measure self-tilt for body orientation. Participants draw a line to indicate their perceived orientation. As an example, a participant can plot a line with an angle of 45° (the left image). This means that the participant perceived himself/herself as tilted 45° towards to upright position.

as a between-subject factor and RFT condition (pre-FBI supine, post-FBI supine) as a within-subject factor. For further analysis, to explore the influence of visual field dependency, we conducted a 2 × 2 × 2 mixed ANOVA where visual field dependency (FI, FD), and visuo-tactile stimulation (synchronous, asynchronous) was included as between subject factors, and RFT condition (pre-FBI supine, post-FBI supine) was included as a within-subject factor.

Visual Field Dependency/Independency: For each participant, subjective visual verticality was calculated by adding or subtracting the head angle from/to each trial, depending on the direction of the head angle and perceived visual verticality judgement. The means were then calculated for each body orientation condition and a hierarchical cluster analysis was conducted on the data for the standing

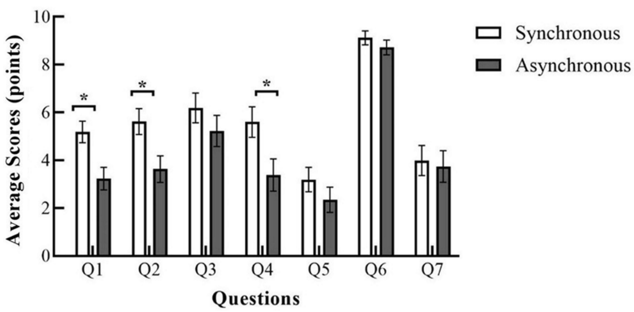

Fig. 5. Average scores of the subjective report of full-body illusion. Error bars represent standard errors of the mean.

condition to categorise participants as visual field-dependent (FD) or visual field-independent (FI). As a standard procedure for the hierarchical clustering analysis, squared Euclidean distance and Ward's aggregation method was used (Lopez et al., 2006; Pfeiffer et al., 2013; Thür et al., 2019). The dendrogram obtained with hierarchical cluster analysis revealed a group of 24 visual FD participants (mean value of subjective visual vertical = 14.48, *SE* = 1.08) and a group of 28 visual FI participants (mean value of subjective visual vertical = 4.55, *SE* = 0.36). Inspection of the data revealed that 13 FD and 14 FI participants were in the synchronous visuo-tactile stimulation, and11 FD and 14 FI participants in the asynchronous visuo-tactile stimulation.

3. Results

3.1. The effect of visuo-tactile synchrony and visual field dependency on subjective reports for full-body illusion

In order to investigate the effects of visuo-tactile stimulation and visual field dependency, separate two-way ANOVAs were conducted for each item in the subjective report. The summary of the subjective report results is presented in Fig. 5. Statistical analysis for the ownership (Q1) showed a significant main effect of visuo-tactile stimuli, $F(1,48) = 9.10$, $p = .004$, *partial* $\eta^2 = 0.159$. That is, the sense of ownership was rated statistically significantly higher after synchronous visuo-tactile stroking ($M = 5.19$, $SE = 0.45$) compared to asynchronous stroking ($M = 3.23$, $SE = 0.47$). However, the effect of visual field dependency on ownership was not statistically significant, $F(1,48) = 0.43$, $p > .05$ and there was no significant interaction between visuo-tactile stimulation and visual field dependency for the ownership statement, $F(1,48) = 0.09$, $p > .05$. Moreover, statistical analysis for the self-location statement (Q2) revealed a significant main effect of visuo-tactile stimulation, $F(1,48) = 6.64$, $p = .013$, *partial* $\eta^2 = 0.112$. This reveals that participants had stronger perceptions of themselves at the location of the virtual body after synchronous visuo-tactile stimuli ($M = 5.62$, $SE = 0.54$) compared to asynchronous visuo-tactile stimuli ($M = 3.63$, $SE = 0.56$). Additionally, a significant interaction effect of visuo-tactile stimuli and visual field dependency was found for the self-location (Q2), $F(1,48) = 8.36$, $p = .006$, *partial* $\eta^2 = 0.148$. Simple main effect analysis showed that FD participants had significantly stronger feeling of themselves at the location of the virtual body than FI participants after synchronous visuo-tactile stimuli ($p = .007$, uncorrected, $p = .049$ after multiple comparisons), but not during the asynchronous visuo-tactile stimuli condition ($p = .192$, uncorrected) (see Fig. 6). For the 1PP item (Q3), there was no significant main effects of visuo-tactile stimulation, $F(1,48) = 1.158$, $p > .05$, or visual field dependency, $F(1,48) = 0.746$, $p > .05$. The interaction effect was also not statistically significant, $F(1,48) = 0.282$, $p > .05$.

Statistical analysis for the orientation perception (Q4) revealed a significant main effect of visuo-tactile stimuli, $F(1,48) = 5.79$, $p = .020$, $\eta^2 = 0.108$. This suggests that participants experienced illusory change of their perceived orientation after synchronous visuo-tactile stimuli. There was no significant main effect of visual field dependency, $F(1,48) = 0.64$, $p > .05$ or interaction effect, $F(1,48) = 0.23$, $p > .05$. In addition, as expected, none of the control questions (Q5, Q6, Q7) showed a statistically significant difference between the groups, (all $F < 1.373$, $p > .247$). Finally, for the perceived self-tilt item (Q8), a significant main effect of visuo-tactile stimuli was also found, $F(1,48) = 6.21$, $p = .016$, *partial* $\eta^2 = 0.114$. Participants had a greater illusory sense of self-tilt towards the position of virtual body after synchronous visuo-tactile stimuli ($M = 43.41$, $SE = 6.24$) compared to the asynchronous visuo-tactile stimuli ($M = 20.93$, $SE = 6.52$) (see Fig. 7). There was no main effect of visual field dependency, $F(1,48) = 0.27$, $p > .05$ and the interaction effect was found statistically insignificant, $F(1,48) = 1.05$, $p > .05$.

3.2. The effect of visuo-tactile synchrony, visual field dependency, and RFT condition on subjective visual verticality

According to previous studies, supine position compared to the upright position leads to greater errors in RFT (Goodenough et al., 1981; Templeton, 1973; Sigman et al., 1978). Therefore, as a first step, regardless of the type visuo-tactile stimulation (synchronous, asynchronous) and visual field dependency (FI, FD), we firstly investigated the overall RFT data from pre-FBI standing and pre-FBI supine conditions to verify the differences in subjective visual verticality judgements across body orientations (for a review see

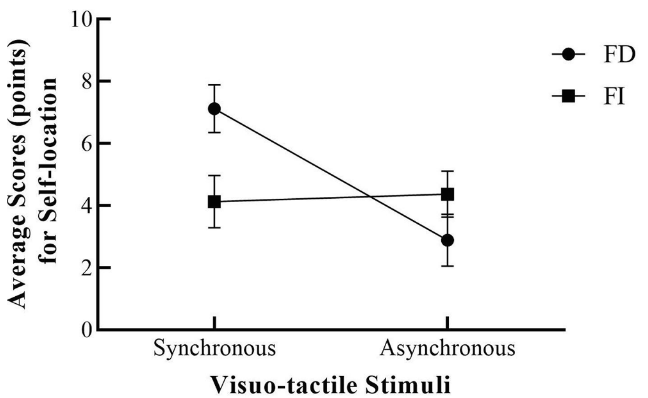

Fig. 6. Average scores for the self-location item (Q2) on the subjective report for FD and FI participants based on visuo-tactile stimuli. Error bars represent standard errors of the mean.

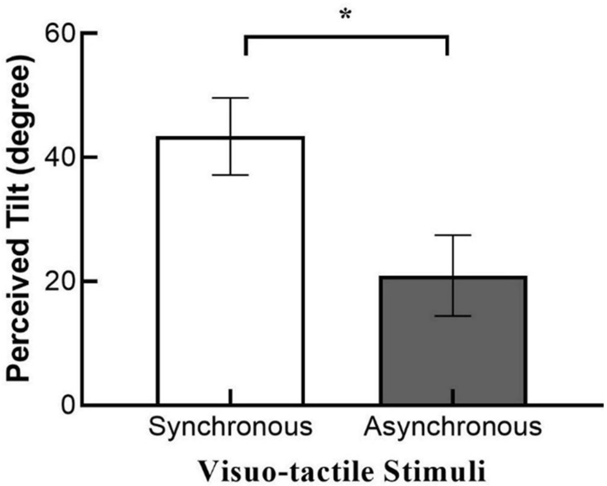

Fig. 7. The means of estimations of perceived self-tilt (Q8). Error bars represent standard error of the mean.

Carriot et al., 2008). To achieve this, we conducted separate paired sample *t*-test between pre-FBI standing/pre-FBI supine, pre-FBI supine/post-FBI supine and pre-FBI standing/post-FBI supine measurements. Although the mean deviations for the RFT measurement were higher in the pre-FBI supine ($M = 10.17°$, $SE = 0.99$) compared to pre-FBI standing ($M = 9.14°$, $SE = 0.87$) condition, the results showed that this difference was not statistically significant, $t(51) = -1.66$, $p = .103$. Furthermore, as predicted, there was a significant difference in verticality judgements between the pre-FBI supine ($M = 10.17$, $SE = 0.99$) and the post-FBI supine condition ($M = 8.77$, $SE = 0.75$), $t(51) = 2.06$, $p = .044$. Finally, no significant difference was observed between pre-FBI standing and post-FBI supine RFT, $t(51) = 0.69$, $p = .494$. A figure representing the results is available in supplementary material (Fig. S1). Moreover, in order to further examine the form of insignificant difference between pre-FBI standing/pre-FBI supine we conducted further analysis based visual field dependency (FI, FD) (Lichtenstein & Saucer, 1974). The results showed a strong tendency towards statistical significance for FI participants in the comparison of pre-FBI standing ($M = 4.55$, $SE = 0.365$) and pre-FBI supine ($M = 5.58$, $SE = 0.499$), $t(27) = -1.99$, $p = .057$. As we expected, no significant difference was observed for FD participants during pre-FBI standing ($M = 14.49$, $SE = 1.078$) and pre-FBI supine conditions ($M = 15.53$, $SE = 0.1.452$). These results suggest that there is profound difference in RFT errors between supine and standing position when the participants were further divided based on visual field dependency. This might suggest that FI participants, who are more reliant on somatosensory and proprioceptive modality, made more errors in supine position compared to FD participants, who are more reliant on visual modality. For further comparison of verticality errors between pre-FBI standing and post-FBI supine standing conditions, please refer to Supplementary Text1. Descriptive graph for verticality judgements during different RFT conditions based on visual field dependency before FBI and additionally for type of visuo-tactile stimulation after FBI also can be found in supplementary materials (Fig. S2).

As a second step, in order to test our main hypotheses, we explored the changes in subjective verticality judgements by conducting a 2×2 mixed ANOVA including visuo-tactile stimulation (synchronous, asynchronous) as a between-subject factor and RFT condition (pre-FBI supine, post-FBI supine) as a within-subject factor. The results revealed a significant main effect of RFT condition on subjective visual verticality judgements, $F(1,50) = 4.15$, $p = .047$, *partial* $\eta^2 = 0.077$ but no significant main effect of visuo-tactile stimulation, $F(1,50) = 1.137$, $p > .05$. It is worth noting that we manipulated the visuo-tactile stimulus only during full-body illusion, thus the expectation was to find an effect of visuo-tactile stimulation on post-FBI supine condition. Although this effect was not

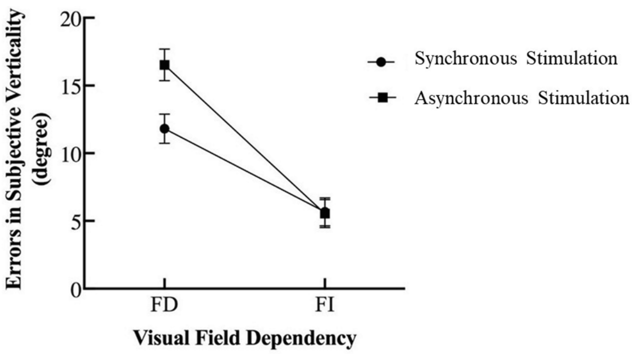

Fig. 8. Average estimation errors in subjective verticality in synchronous and asynchronous visuo-tactile stimuli for FD and FI participants. Error bars represent standard error of the mean.

found, the result showed that participants in the supine condition made similar verticality judgements independently of visuo-tactile stimulus, providing evidence against the influence of visuo-tactile manipulation before full-body illusion. There was no statistically significant interaction effect between RFT condition and visuo-tactile stimulation, $F(1,50) = 3.054$, $p > .05$.

In order to investigate the full data, we conducted a 2 × 2 × 2 ANOVA with between-subject factors visual field dependency (FD, FI), visuo-tactile stimulation (synchronous, asynchronous) and within-subject factor RFT condition (pre-FBI supine, post-FBI supine). The results revealed a significant main effect of visuo-tactile stimulation, visual field dependency and RFT condition respectively $F(1,48) = 4.24$, $p = .041$, *partial* $\eta^2 = 0.084$, $F(1,48) = 62.09$, $p < .01$, *partial* $\eta^2 = 0.564$, $F(1,48) = 5.20$, $p = .027$, *partial* $\eta^2 = 0.098$.

Furthermore, significant two-way interaction effect was found between visuo-tactile stimulation X visual field dependency, $F(1,48) = 4.98$, $p = .030$, partial $\eta^2 = 0.094$. Simple effect analysis showed that FD participants made significantly higher errors in estimating verticality after asynchronous visuo-tactile stimuli compared to synchronous visuo-tactile stimuli condition ($p = .005$). This suggests that FI participants were not affected by the type of visuo-tactile stimuli, and thus performed similarly, with greater accuracy in verticality estimations both in synchronous and asynchronous conditions ($p = .924$) (see Fig. 8). This interaction shows that the effect of the type of visuo-tactile stimuli on subjective verticality estimations depends on the type of visual field dependency.

Additionally, significant interaction effect was found for the visual field dependency X RFT condition, $F(1,48) = 5.69$, $p = .021$, partial $\eta^2 = 0.106$. Simple main effect analysis revealed more accurate FD participants' verticality judgements in the post-FBI supine condition compared to pre-FBI supine condition ($p = .002$). Accuracy of verticality judgements for FI participants was similar, regardless of the condition ($p = .939$) (see Fig. 9). This interaction reflects the effect of FBI on subjective verticality estimations. There was no three-way interaction among visuo-tactile stimulation X visual field dependency X RFT condition, $F(1,48) = 0.07$, $p = .789$, *partial* $\eta^2 = 0.002$.

4. Discussion

In the current study, given the importance of vestibular inputs on BSC, a visuo-vestibular conflict was included during the FBI by presenting participants with standing virtual body while they were physically in the supine position. We considered that this newly introduced conflict between the virtual and the real body as compared to gravity would provide a more direct indication of the effect of vestibular system, when the reliability of the visual modality is controlled (i.e., visual field dependency). Based on that assumption, the results of the current study replicated previous findings and confirmed our initial hypothesis, which suggested that there should be an increase in sense of ownership (Q1) and sense of self-location (Q2) for the virtual body after synchronous visuo-tactile stimulation. Both expectations were confirmed by participants' subjective reports after the full-body illusion, which showed a significant increase in the sense of ownership over the virtual body and in the self-location experienced at the location of the virtual body after synchronous visuo-tactile stimulation. This finding suggests that ownership of a virtual body can be achieved even in a strong visuo-vestibular conflict condition. Additional support for the previous findings was also provided by the ratings to the self-orientation (Q4) and perceived self-tilt (Q8) statements, which showed that participants with synchronous visuo-tactile stimulation reported greater feeling of change in self-orientation and higher degrees of perceived self-tilt indicating greater impression of being upright.

More specifically, regarding the findings related to the sense of ownership, in their study, Pfeiffer et al. (2013) found that strong visuo-vestibular conflict can in fact reduce the feeling of ownership. Although this finding seems to conflict with our findings, when experimental differences are considered, there is in fact no disagreement, because during the experiment, Pfeiffer et al. (2013) created the visuo-vestibular conflict by manipulating gravitational cues on the virtual body, rather than rotating participant. Furthermore, in line with the findings for the ownership in the current study, the study by Thür and colleagues (2019) showed no significant effect for the visuo-tactile synchrony on ownership during visuo-vestibular conflict. These differences in the feeling of ownership might be interpreted in two ways. Firstly, as mentioned earlier, in the current study, participants experienced an illusory sense of ownership from the 1PP. This could be advantageous compared to previous studies that used 3PP (Debarba et al., 2017; Lenggenhager, Tadi,

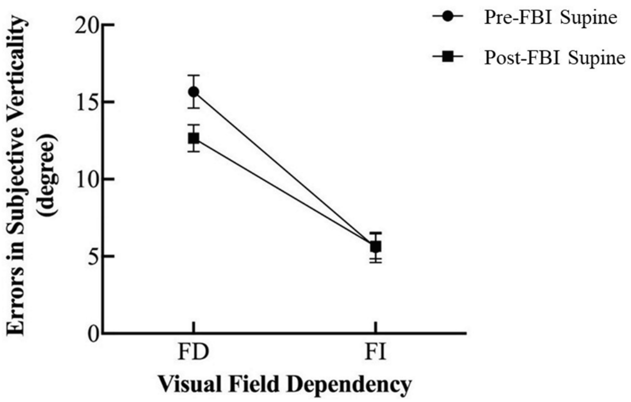

Fig. 9. Average estimation errors in subjective verticality in pre-FBI supine and post-FBI supine conditions for FD and FI participants. Error bars represent standard error of the mean.

Metzinger, & Blanke, 2007). An alternative, and more plausible, explanation for the observed findings relates to the decreased contribution of vestibular signals on bodily self-consciousness in the supine body position and greater reliance on the visual information. The support for this argument comes from the studies showing that OBEs mostly occur in the supine position (Blanke & Mohr, 2005). Since the participants were in the supine position in our study, these findings point out that decreasing vestibular sensitivity may enhance the visual signals, resulting in stronger feeling of ownership over the virtual body (Lopez & Blanke, 2010). This feeling could also be related to the influence of somatosensory information during the weighting process of the sensory signals. For instance, a previous study showed that tilted participants supported by a rigid surface are more reliant on visual information, and those supported by a soft surface, on vestibular information (Nyborg, 1971). Thus, the successful induction of the feeling of ownership during relatively strong visuo-vestibular conflict might be explained by the use of the rigid foot support, which might have made participants more reliant on visual information. However, it is important to note that previous studies suggest that vestibular signals are related more with self-location and 1PP, whereas sense of ownership depends more on visual, somatosensory and proprioceptive signals (Lopez, Halje, & Blanke, 2008; for a review see Blanke, 2012). Additional future experiments that compare 1PP and 3PP visuo-vestibular conflict will provide a more detailed explanation for this finding.

4.1. The influence of visual field dependency on full-body illusion

Previous studies revealed that the influence of visual field dependency on proprioceptive drift during a rubber hand illusion (David et al., 2014) and 1PP in full-body illusion (Pfeiffer et al., 2013). We found that FD participants made less error in verticality judgements after synchronous visuo-tactile stimulation compared to the asynchronous visuo-tactile stimulation. This effect of synchronous stimulation might suggest that FD participants experienced themselves in the orientation of the virtual body as standing upright, and thus made less error. This is in line with the findings of Thür et al. (2019) showing that FD participants adjust their body orientation with respect to the virtually seen body. This adaptation of the real body into the virtual body orientation is further supported by the perceived self-tilt item in the subjective report of full-body illusion. Participants depict themselves as closer to the orientation of the virtual body after synchronous visuo-tactile stimuli, regardless of visual field dependency. The influence of visual field dependency for RFT performance, but not for the perceived self-tilt item (Q8), agrees with studies showing that implicit measures for the influence of visual field dependency are not precisely mirrored by the explicit measures (Berger, Schulte-Pelkum, & Bülthoff, 2010; Prsa, Gale, & Blanke, 2012; Thür et al., 2019).

Secondly, we also found a significant effect for the influence of FBI (pre-FBI supine vs post-FBI supine) on self-orientation, depending on the visual field dependency. FD participants made fewer verticality errors in the post-FBI supine condition compared to the pre-FBI supine condition. That is, FD participants experienced themselves as if standing upright after FBI, independent of the visuo-tactile stimulation. FD individuals were known to have a greater dependence on visual information, irrespective of the reliability of other sensory information (Borger, Whitney, Redfern, & Furman, 1999). This result suggests that the FD participants' stronger reliance on visual cues might predominate the multisensory conflicts -visual information from the virtual body and perhaps by the influence of pressure under their feet give the impression of standing upright, whereas tactile cues from their backs and vestibular signals confirm being in supine position – and thus eliminated the need for visuo-tactile stimulation. This supports the key role of visual field dependency for the spatial aspect of bodily self-consciousness. This finding is also in line with findings from a rubber hand illusion, which shows correlation between proprioceptive drift and type of visual field dependency (David et al., 2014). Taken together, the current findings indicate the importance of sensory weighting strategies for full-body illusion, particularly during decreased vestibular condition (supine position). An alternative explanation for the changes in perceived verticality without visuo-tactile stimulation is the awareness of body orientation. It was shown that body awareness provided by congruent vestibular and somatosensory information modulates the visual verticality judgements (Barra, Pérennou, Thilo, Gresty, & Bronstein, 2012). In the present study, congruence between visual information, and somatosensory information detected by participants' feet indicates that standing upright might have increased FD participants' awareness about their body orientation. It is important to not that although the information from vestibular system and pressure from the back imply being in supine position, the tendency of FD participants to overweight visual cues might account for this illusory awareness of body orientation independently of the visuo-tactile stimulation.

In addition to the proposed hypothesis, the current study revealed further findings on self-location and visual field dependency. Firstly, we found a significant influence of visual field dependency with respect to the visuo-tactile synchrony for the sense of self-location; FD participants reported a stronger experience of being at the location of the virtual body compared to FI participants after synchronous visuo-tactile stimuli, suggesting that the individual sensory weighting style is important for self-location. Pfeiffer et al. (2013) found a direct influence of visual field dependency on the experienced direction of 1PP during visuo-vestibular conflict. In addition, they showed an influence of 1PP on self-location but did not link the visual field dependency with self-location. Serino et al. (2013) proposal that self-location and 1PP are closely related is supported in the present study by extending the findings regarding visual field dependency on 1PP into self-location. A possible explanation for the selective role of visual field dependency, in addition to the synchronous visuo-tactile stimulation, on self-location in the present study might be related with sensory weighting. It is well known that sensory signals are reweighted based on their reliability during multisensory integration (Carver, Kiemel, & Jeka, 2006). FBI was induced in supine position, therefore reweighting of visual-somatosensory-vestibular signals during decreased vestibular signals could account for this illusory change in self-location (see de Winkel, Katliar, & Diers, 2018 for a discussion).

An alternative possible explanation for the significant effect of visual field dependency on self-location relates to multisensory integration from an egocentric reference frame. The spatial position of the body might be encoded either in egocentric or in allocentric reference frame (Howard & Templeton, 1966). The former corresponds to the body-centred coordinate system, the latter reflects the coordinate system relative to the world (Burgess, 2006). We normally observe our body from an egocentric reference frame, which is known to be fundamental for the sense of self (Petkova et al., 2011). Also, we have constant access to egocentric cues from the body, and allocentric cues from the environment relative to the world. In the current study, we presented participants with the egocentric reference frame of the virtual body, and the allocentric reference frame relative to the virtual environment. As it has been proposed that visual reorientation illusions are evoked by a change in allocentric reference frame relative to the body (Oman, 2007), we believe that the current study provided natural reference frames, as in the real world, thus resulting in a significant change in self-location.

5. Limitations

We believe that a small number of limitations may have influenced the results of the current study. Firstly, based on our experimental setup there is a mismatch between the tactile/pressure cues (lying on the back versus standing). Similar to the effect of physical support under participants' feet, discussed earlier, it is possible that observed effect might also be due to the tactile/pressure cues, and not derived only from the vestibular conflict (standing/supine). Therefore, one should be cautious in interpreting the contribution of the vestibular system, and should also recognise the possibility of the involvement of other sensory modality systems i.e., somatosensory. Secondly, in order to provide clear evidence for the influence of vestibular signals, future studies might induce FBI by presenting the virtual body in supine position while participants physically standing upright (the opposite of he current setup) in order to compare the effect of the two different types of visuo-vestibular conflict on FBI.

6. Conclusion

In the current study, it was shown that full-body illusion can be induced when the positions of the virtual and the physical body are in conflict, in regard to gravity. To reveal this, it was necessary to devise a new experimental paradigm for investigating the influence of this visuo-vestibular conflict on bodily self, by including RFT into FBI as an implicit measure of perceived self-orientation.

The present data showed that subjective experience of the sense of ownership was greater after synchronous visuo-tactile stimuli condition compared to asynchronous visuo-tactile stimulation, as expected. The data from the subjective reports also provided evidence that, after synchronous visuo-tactile stimulation, the participants had greater changes in their perceived self-orientation, i.e., a greater sense of being in standing position. Furthermore, we found that, after synchronous visuo-tactile stimulation, FD participants experienced a stronger feeling of being in location of the virtual body compared to FI participants, demonstrating the link between sensory weighting strategies and the sense of self-location. Supporting this finding, inspection of RFT before and after FBI showed that, after synchronous visuo-tactile stimulation, FD participants made less verticality errors, which might suggest feeling as if standing upright.

In conclusion, the results of the present study suggest that FD participants are more prone to synchronous/asynchronous stimulation manipulations, and that they might utilize different sensory weighting strategies on body ownership, self-location, and orientation perception. Thus, we believed that the results provide important insight into future studies for understanding full-body illusion.

CRediT authorship contribution statement

Ege Tekgün: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Formal analysis, Visualization. **Burak Erdeniz:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Formal analysis, Visualization, Validation, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.concog.2021.103108.

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