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Flight of mind: Sensorimotor and multisensory embodiment with aviation robotics, flight simulator, and virtual reality

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Abstract

Normally, humans experience an ‘I’ or self as residing in one’s body and as the agent of one’s actions and thoughts. In other words, the self is experienced as being inside the body (self-location), as having a body (self-identification), and as being able to control the person’s body (agency). Over the last decade, research in cognitive neuroscience has revealed that vestibular signals contribute to such aspects of the embodied self. On the other hand, the influences of embodiment on vestibular sensations have received scant attention. In my thesis, I highlight how changes in multisensory and sensorimotor embodiment impact vestibular sensations. For this purpose, I merged technologies from photorealistic virtual reality (VR), aviation robotics such as a drone, flight simulator, haptics with knowledge of cognitive neuroscience about embodiment and bodily self-consciousness (BSC). The multidisciplinary approaches provide new paradigms to modulate embodiment and investigate related vestibular sensations based on multisensory and sensorimotor mechanisms of BSC. Also, the approaches reveal the relationship between embodiment and vestibular sensations.

In Study 1, we have objectively shown the possibility of the duplication of the self by measuring peripersonal space (PPS). To this aim, we provided participants with real-time feedback from a drone-mounted camera that autonomously followed them while they responded to multisensory stimuli on their body and in their environment and walked forward. Our results demonstrate that this setup induces two spatially distinct PPSs in healthy participants: reaction times for visuotactile stimuli were faster around both the physical body and the observed body. This resembles a heautoscopy in neurological patients, where patients experience themselves to be located both in their physical body and in the double.

In Studies 2 & 3, we have added a photorealistic avatar and a haptic vest to a robotic flight simulator to enable and investigate personalized immersive flight experiences in healthy humans. In Study 2, we showed that modulations of embodiment using sensorimotor stimulation resulted in enhanced subjective flying experience, better piloting performance, and learning. In Study 3, we showed that multisensory – visual (on the avatar) and tactile (on the participant’s physical body) – stimulation could further increase embodiment and improve piloting performance. Furthermore, in both studies, we found a positive relationship between embodiment and flight sensations.

In Studies 4 & 5, we developed a new multisensory body scanning technology platform to induce and investigate one of the most common experiences in which the center of awareness is dissociated from the physical body: out-of-body experiences (OBEs). OBEs represent an interesting link between embodiment and vestibular sensations as they are characterized by embodiment of an elevated aerial position and perspective in space that is commonly associated with prominent sensations of floating, elevation, and flight. In this study, we have investigated how several sensorimotor and audio-visual stimulation conditions affect subjective sensations of disembodiment, floating, lightness as well as behavioral measures of self-location.

In conclusion, my work developed several new paradigms to investigate embodiment, self-consciousness, and vestibular processing. My work revealed the influence of embodiment on vestibular sensations and applied these insights between embodiment and vestibular sensations to the field of field engineering by combining state-of-the-art technologies with knowledge of BSC with broad implications for robotics, neuroscience, the field of immersive virtual reality, as well as experiential technology.

Keywords

Embodiment, vestibular sensations, multisensory stimulation, sensorimotor stimulation, out-of-body experience, full-body illusion, aviation robotics, flight simulator, virtual reality

Résumé

Normalement, les humains ressentent un «je» ou un moi comme résidant dans son corps et comme agent de ses actions et de ses pensées. En d'autres termes, le soi est vécu comme étant à l'intérieur du corps (auto-localisation), comme ayant un corps (auto-identification) et comme capable de contrôler le corps de la personne (agentivité). Au cours de la dernière décennie, la recherche en neurosciences cognitives a révélé que les signaux vestibulaires contribuent à ces aspects du soi incarné (embodiment). D'un autre côté, les influences de l'incarnation sur les sensations vestibulaires n'ont guère retenu l'attention. Dans ma thèse, je souligne comment les changements dans la réalisation multisensorielle et sensorimotrice impactent les sensations vestibulaires. À cette fin, j'ai fusionné des technologies de la réalité virtuelle photoréaliste (VR), de la robotique aéronautique comme un drone, un simulateur de vol, des haptiques avec une connaissance des neurosciences cognitives sur l'incarnation et la conscience de soi corporelle (BSC). Les approches multidisciplinaires fournissent de nouveaux paradigmes pour moduler l'incarnation et étudier les sensations vestibulaires connexes basées sur les mécanismes multisensoriels et sen-sorimoteurs de la BSC. De plus, les approches révèlent la relation entre l'incarnation et les sensations vestibulaires.

Dans l'étude 1, nous avons objectivement montré la possibilité de duplication du soi en mesurant l'espace péripersonnel (PPS). Dans ce but, nous avons fourni aux participants des retours visuels en temps réel à l'aide d'une caméra montée sur un drone qui les suivait de manière autonome pendant qu'ils répondaient à des stimuli multisensoriels sur leur corps et dans leur environnement tout en marchant. Nos résultats démontrent que ce système expérimental induit deux PPS spatialement distincts chez les participants en bonne santé: les temps de réaction pour les stimuli visuo-tactiles étaient plus rapides autour du corps physique et du corps observé. Cela ressemble à une autoscopie chez les patients neurologiques, où ces derniers se sentent situés à la fois dans leur corps physique et dans leur double.

Dans les études 2 et 3, nous avons ajouté un avatar photoréaliste et un gilet haptique à un simulateur de vol robotisé pour permettre et étudier des expériences de vol immersives et personnalisées chez des personnes en bonne santé. Dans l'étude 2, nous avons démontré que les modulations de l'incarnation en utilisant la stimulation sensorimotrice ont abouti à une amélioration de l'expérience de vol subjective et à de meilleures performances de pilotage et d'apprentissage. Dans l'étude 3, nous avons montré que la stimulation multisensorielle - visuelle (sur l'avatar) et tactile (sur le corps physique du participant) pouvait encore augmenter l'incarnation et améliorer les performances de pilotage. De plus, dans les deux études, nous avons trouvé une relation positive entre l'incarnation et les sensations de vol.

Dans les études 4 et 5, nous avons développé une nouvelle plateforme technologique multisensorielle afin d'induire et d'investiguer l'une des expériences les plus courantes dans lesquelles le centre de conscience est dissocié du corps physique : les expériences extracorporelles (OBE). Les OBE représentent un lien intéressant entre l'incarnation et les sensations vestibulaires car elles sont caractérisées par l'incarnation d'une position aérienne élevée et d'une perspective dans l'espace qui est généralement associée à des sensations importantes de flottement, d'élévation et de vol. Dans cette étude, nous avons étudié comment plusieurs conditions de stimulation sensorimotrice et audiovisuelle affectent les sensations subjectives de désincarnation, de flottement, de légèreté ainsi que les mesures comportementales d'auto-localisation.

En conclusion, mon travail a développé plusieurs nouveaux paradigmes pour étudier l'incarnation, la conscience de soi et le traitement vestibulaire. Mon travail a révélé l'influence de l'incarnation sur les sensations vestibulaires et a appliqué ces connaissances entre l'incarnation et les sensations vestibulaires au domaine de l'ingénierie sur le terrain en combinant des technologies de pointe avec des connaissances en BSC avec de vastes implications pour la robotique, les neurosciences, le domaine de la réalité virtuelle immersive, ainsi que la technologie expérientielle.

Mots-clés

Incarnation, sensations vestibulaires, stimulation multisensorielle, stimulation sensorimotrice, expérience extracorporelle, illusion corporelle, robotique aéronautique, simulateur de vol, réalité virtuelle

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Chapter 1 Introduction

1.1 Common principles of embodiment and bodily self-consciousness

Embodiment is the mental state being inside, having, and/or controlling a whole body, a body part or an object as a body part (De Vignemont 2011, Kilteni, Groten et al. 2012). Embodiment is believed to be composed of three main components: self-location (the sense of being located in space), self-identification (the senses of having and identifying to a body), and agency (the sense of being the agent of one's actions) (Longo, Schüür et al. 2008, Kilteni, Groten et al. 2012, Gonzalez-Franco and Peck 2018). Embodiment has a lot of common points with bodily self-consciousness (BSC), an aspect of self-consciousness based on the processing of multisensory bodily signals (Blanke, Slater et al. 2015). Specifically, two of three main components of embodiment are also the main components of BSC (self-location, self-identification, and first-person perspective – the experience of the position from where I perceive the world (Blanke 2012)). Empirical studies have provided evidence that both embodiment and BSC are built up and constantly updated depending on the coherent integration of different multisensory signals in the brain including sensory input from visual, tactile, vestibular, auditory, olfactory, proprioceptive, motor, and interoceptive signals (Damasio 2000, Petkova, Björnsdotter et al. 2011, Blanke 2012, Park and Blanke 2019). Furthermore, the accumulation of consistent experiences will construct embodiment and BSC that 'I' 'reside in' (self-location) and 'control' (agency) 'my body' (self-identification) having 'my perspective' (first-person perspective). At the same time, embodiment and BSC can be altered by specific pathologies but also in the healthy population using experimental methods or in neurological patients due to brain damage.

1.1.1 Experimental modulations of embodiment and its measures

In normal situations, healthy people pre-reflectively experience that their bodies are their own and that they are located within their bodies. However, embodiment may also extend to include tools or prostheses if these are purposefully and continuously used (Giummarra, Gibson et al. 2008). Furthermore, embodiment can be modulated experimentally with multisensory or sensorimotor stimulation. The representative example for modulation of embodiment with multisensory stimulation is the rubber hand illusion (RHI) (Botvinick and Cohen 1998, Botvinick 2004). By seeing a fake (rubber or virtual) hand stroked synchronously with a hidden and physical hand, a person can embody the fake hand. As a result, the person feels as if the fake hand is his / her own hand and the touch sensation seemingly arises from the fake hand (**Figure 1, top left**). Embodiment mediated by a multisensory (visuotactile) stimulation can be applied to other body parts like the face and the leg and even extend to the whole body in specific conditions (Ehrsson 2007, Lenggenhager, Tadi et al. 2007, Tsakiris 2008, Pozeg, Galli et al. 2015). Several conditions are required to induce embodiment over the whole body. For instance, a participant has to see a fake body (mannequin or virtual body) from a first- or third- person viewpoint through a head-mounted display (HMD). Then, if an experimenter strokes the chest - or the back - of the physical body of the participant while synchronously stroking the chest or the back of the fake body seen through the HMD, this participant can embody the whole fake body (**Figure 1, bottom right**) (Lenggenhager, Tadi et al. 2007, Petkova and Ehrsson 2008). Illusory embodiment over the fake body has been called full-body illusion (FBI) (Lenggenhager, Tadi et al. 2007).

Not only multisensory (visuotactile) stimulation but also sensorimotor stimulation can induce embodiment of fake body parts or to the whole fake body (Stratton 1899, Slater, Perez-Marcos et al. 2009, Sanchez-Vives, Spanlang et al. 2010, Debarba, Bovet et al. 2017). In this kind of sensorimotor stimulation, a participant sees the movements of the fake body parts synchronized with the physical body parts through a mirror or an HMD. The same principles apply to the whole body. With this movement congruency, the participant can embody the fake body parts or the whole fake body (**Figure 1, bottom left**). The first study to show the possibility of changing embodiment over the whole body with a sensorimotor stimulation was G.M. Stratton (Stratton 1899). Stratton (1899) developed a special and innovative portable mirror tool enabling him to see himself from a point of view above his own head while he was walking and doing daily life stuff (**Figure 1, top right**). After using this tool for several hours, he felt as if touch sensations arose from parts such as hand, leg, or foot of the observed body and felt self-identification over the observed body as the real body. Also, he felt as if he was located above the shoulders of the observed body while looking at him below him. He felt to be outside his own body. This was the first study modulating embodiment over the whole body. Similarly, when participants saw themselves from a fixed camera viewpoint in a room through an HMD and freely walked in the room, they felt located at both the camera position and at the observed body position (Mizumoto and Ishikawa 2005). Such previous studies showed either multisensory or sensorimotor stimulation can induce embodiment and even one study showed that sensorimotor stimulation is more powerful to induce embodiment than multisensory stimulation (Kokkinara and Slater 2014). However, integrating sensorimotor stimulation and multisensory stimulation with reasonable causalities between the stimulations can result in higher embodiment and reduce the technological uncanny valley (a feeling of uncanniness) (Egeberg, Lind et al. 2016, Berger, Gonzalez-Franco et al. 2018).

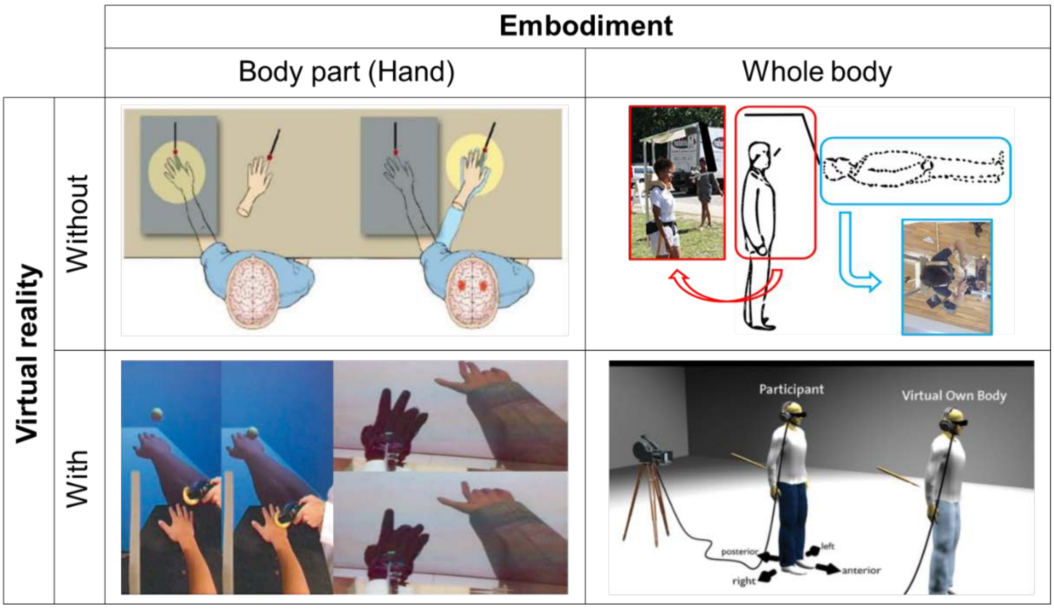

Figure 1. Experimental manipulations of embodiment | Embodiment over body parts or the whole body can be manipulated through experimental methods such as multisensory (visuotactile and visuovestibular) or sensorimotor (visuomotor) conflicts. Before the development of virtual reality, the most common modulation of embodiment was the rubber hand illusion (left top, Botvinick, 2004) and the modulation of embodiment over the whole body was rarely investigated, but one study showed that sensorimotor stimulation could evoke the full-body illusion (right top, Stratton 1899). Adapting virtual reality has made it possible to induce and investigate embodiment over body parts (left bottom, Slater et al., 2009) or the whole body (right bottom, Lenggenhager et al., 2007) in a more controlled setting and systematic ways such as inserting specific delays between multisensory or sensorimotor stimulations.

These modulations of embodiment can be measured by a questionnaire, a mental imaginary task (perspective taking), different behavioral tasks (proprioceptive or self-location drift and crossmodal congruency), physiological signals (skin conductance and temperature), and neural correlates (Ehrsson 2007, Lenggenhager, Tadi et al. 2007, Moseley, Olthof et al. 2008, Lenggenhager, Mouthon et al. 2009, Blanke, Ionta et al. 2010, Slater, Spanlang et al. 2010, Blanke 2012, Pfeiffer, Lopez et al. 2013, Guterstam, Björnsdotter et al. 2015). For example, during the RHI or the FBI, participants mislocalize their own hand or body towards the rubber hand or the virtual body (Botvinick and Cohen 1998, Lenggenhager, Tadi et al. 2007). Also, if the embodied body parts or whole body are threatened, one shows an increase of heart rhythm or skin conductance reaction (Ehrsson 2007, Slater, Spanlang et al. 2010). Furthermore, alterations of embodiment can be reflected in the modulations of peripersonal space (PPS). PPS is defined as space closely surrounding the whole body and the body part. However, it is not just space. PPS helps to protect the body from harmful stimuli and to facilitate goal-directed movements by integrating multisensory signals (Serino 2019). Studies in both humans (Serino 2019) and non-human primates (Graziano and Cooke 2006) demonstrated that PPS is encoded by multisensory, body-centered neurons with distance-responsive receptive fields, localized in a fronto-parietal network of the brain. PPS can be measured by making a participant respond to tactile stimuli at different temporal delays while dynamic but task-irrelevant auditory or visual stimuli approach from a far distance to the position of the tactile stimuli (**Figure 2A**) (Noel, Pfeiffer et al. 2015, Salomon, Noel et al. 2016). As the responses to the tactile stimuli are accelerated when auditory or visual stimuli are in the PPS, we can identify the boundary of PPS by comparing these multisensory reaction times to tactile-only stimulation. However, the boundary of PPS is not fixed but can dynamically change. By embodying a tool through purposeful and prolonged uses or by embodying a fake body through multisensory (visuotactile) stimulation - like in the FBI - the boundary of PPS can be extended from the body toward the tool or the fake body (Blanke 2012, Noel, Pfeiffer et al. 2015). Therefore, measuring PPS makes it an appropriate tool/metric to quantify embodiment.

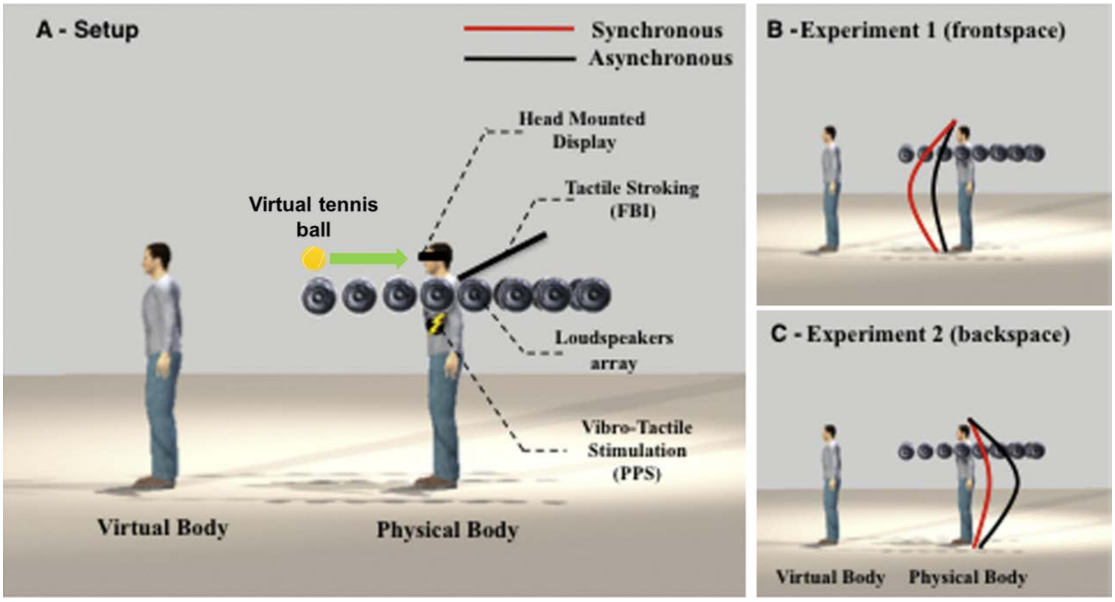

Figure 2. Peripersonal space (PPS) and influences of embodiment on the PPS | In healthy participants, boundaries of the PPS can be measured through the multisensory task (audio-tactile; Noel, Pfeiffer et al., 2015 or visuotactile; Salomon, Noel et al., 2016). For example, participants are instructed to react to tactile stimuli while task-irrelevant visual or auditory stimuli are approaching to the participants. The participants can react faster to the tactile stimuli if the visual or auditory stimuli are inside the PPS compared to the situation where only tactile stimuli are delivered without the visual or auditory stimuli. Moreover, the boundaries of the PPS can be changed depending on the alterations of embodiment. During the FBI, the front-space PPS around a physical body is extended toward a virtual body and the back-space PPS is shrunk (Noel, Pfeiffer et al., 2015).

1.1.2 Interaction between embodiment and vestibular signals

Many previous studies have demonstrated interactions between the vestibular system, bodily perception, self-consciousness, and embodiment (Mast, Preuss et al. 2014). For example, galvanic or caloric vestibular stimulation distorts the localization of a tactile stimulus on the hand's skin and leads to increases in the perceived length and width of the hand (Ferrè, Vagnoni et al. 2013, Ferrè and Haggard 2016). Also, mental imagery of visual motion affects the perception of vestibular stimuli (Mast, Berthoz et al. 2001, Mertz and Lepecq 2001). The interactions can be categorized into two directions. On the one hand, the vestibular system influences cognition and perception such as spatial perception (Mast, Preuss et al. 2014), memory (Bigelow and Agrawal 2015), bodily perception (Ferre, Bottini et al. 2013, Ferrè, Vagnoni et al. 2013), and even social interactions (Lenggenhager, Lopez et al. 2015). On the other hand, cognitive functions such as prior knowledge and embodiment also affect the vestibular system such as perceptual biases (Wertheim, Mesland et al. 2001), self-motion perception (Mast, Preuss et al. 2014, Nigmatullina, Arshad et al. 2015, Nesti, Rognini et al. 2018), and oculomotor motor mechanisms (Talkowski, Redfern et al. 2005). The present thesis will focus on the influence of embodiment on the vestibular system. Lenggenhager, Mouthon et al. (2009) and Ionta, Heydrich et al. (2011) found that it was possible to induce vestibular sensations like floating or lightness if the FBI was induced in healthy participants in a prone position with visuotactile stimulation or a supine position with visuotactile stimulation and visuovestibular conflict (while lying on the back, see the fake body in a prone position, **Figure 3**) (Lenggenhager, Mouthon et al. 2009, Ionta, Heydrich et al. 2011). Also, the participants perceived their self-location to shift upwards while they felt the vestibular sensations like flying, floating, and lightness. The FBI with this setup was similar to the characteristics of out-of-body experience in terms of elevated self-location, the direction of the first-person perspective (Pfeiffer, Lopez et al. 2013, Pfeiffer, Schmutz et al. 2014, Pfeiffer, Grivaz et al. 2016), and vestibular sensations. That is, this study was the first to induce all the known characteristics of OBEs in healthy participants experimentally. Moreover, the FBI in the supine position does not only induce OBE-like sensations including vestibular sensations but also alters vestibular perception (vection) (Nesti, Rognini et al. 2018). After inducing the FBI in healthy participants (supine position) with multisensory stimulation, they were exposed to visual rotations to evoke vection. Then, they were instructed to press a button when they felt like they were rotating. As a result, the time required to feel like oneself is rotating (complete vection) was decreased. In other words, the participants became more sensitive to vestibular-related visual stimulation. These studies indicate the possibility to investigate the role of the vestibular system and related flying sensations, by modulating embodiment in healthy participants.

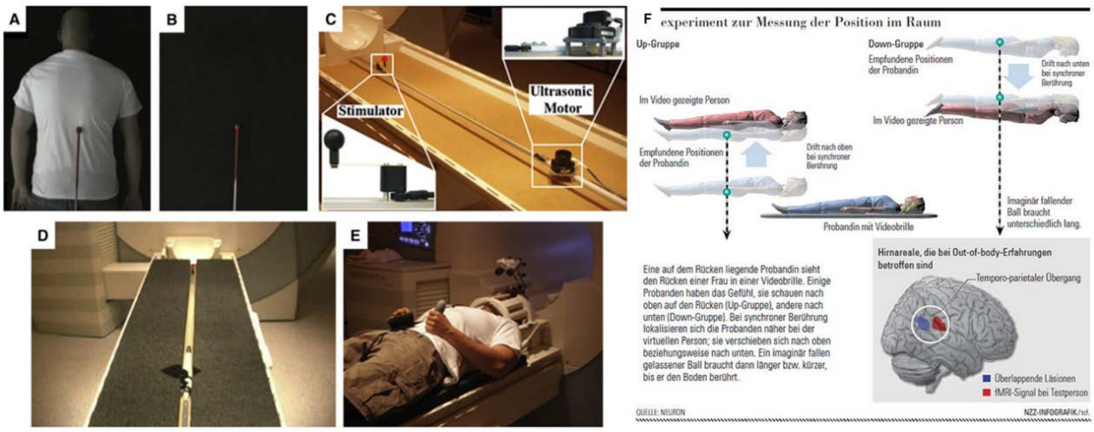

Figure 3. Modulation of embodiment for elevated self-location and vestibular sensations | Ionta and colleagues find that combining visuovestibular conflict and visuotactile stimulation can induce elevated self-location and vestibular sensations (Ionta, Heydrich et al. 2011). Lying in a supine position (**E**) and seeing a virtual body in a prone position (**A**) introduce participants visuovestibular conflict. Based on individual differences, participants are divided into two groups (Up-group and Down-group, **F**). For the up-group, the synchronous visuotactile stimulation induces elevated self-location. On the other hand, for the down-group, both the synchronous and asynchronous visuotactile stimulation lead to elevated self-location,

but the asynchronous stimulation results in higher elevated self-location. Also, while experiencing elevated self-location, participants often report vestibular sensations. Functional magnetic resonance imaging reveals that this elevated self-location is related to the temporo-parietal junction (**F**). Images A-E from Ionta, Heydrich et al. 2011 and Image F from Neue Zürcher Zeitung (2011)

1.1.3 Neurological alterations of embodiment

There are not only experimental manipulations of embodiment, but also abnormal embodiment in neurological patients. These patients may suffer from distortions of embodiment for parts of the body or the whole body. Patients who have problems with embodiment of body parts could experience the feeling that their own limbs do not belong to themselves (somatoparaphrenia) (Gallagher 2005, De Vignemont 2010), the body parts that have disappeared (asomatognosia) (Arzy, Overney et al. 2006), or they perceive an invisible limb and feel pain from the limb after amputation (phantom limbs) (Giummarra, Gibson et al. 2008). On the other hand, patients who suffer from deficits of embodiment for the whole body may experience different forms of autoscopic phenomena. The autoscopic phenomena can be classified based on different patterns of vestibular distortion, self-identification, and self-location into three main forms (Blanke and Mohr 2005, Lopez, Halje et al. 2008). In autoscopic hallucinations, patients see their body image inside their physical body without any vestibular hallucinations and usually, the body image appears as a mirror reversal (Brugger 2002). Patients who experience heautoscopy reported that they saw a doppelganger and were not sure whether they were located inside their physical body or the doppelganger's body. In addition, the patients experienced variable vestibular hallucinations, mainly rotational sensations, and the sidedness of the observed body was like a non-reversing mirror, opposite to autoscopic hallucination (Brugger 2002). In the case of OBEs, patients experience strong disembodiment such as being located outside their physical body while seeing their body and feeling vestibular sensations like floating, flying, and lightness, but still, they felt strong self-identification on the physical body. In other words, embodiment is strongly associated with vestibular sensations in OBEs. However, the link between embodiment and vestibular has been little investigated. Therefore, my PhD work will focus on OBE, because the purpose of this thesis investigates this link.

Previous studies have suggested that OBEs are caused by a failure of coherent integration of visual, tactile, proprioceptive, interoceptive, motor and vestibular signals and altered brain processes at the right temporal-parietal junction (rTPJ) (Lopez, Halje et al. 2008). The rTPJ has been well known as the important region for the integration of multisensory signals, embodiment, and egocentric perspective in the brain (Lopez, Halje et al. 2008, Tsakiris, Costantini et al. 2008, Ionta, Heydrich et al. 2011). Moreover, the rTPJ has assumed as the most important area of the vestibular cortex (Lopez, Halje et al. 2008, Lopez and Blanke 2011, Pfeiffer, Serino et al. 2014, Lenggenhager, Lopez et al. 2015). In addition, electrical stimulation on the rTPJ of an epileptic patient with intracranial electrodes induced disembodiment from the physical body (the patient was localized outside the body and could see the body from the elevated perspective) and vestibular disturbance (the feeling of floating or lightness) like OBE (Blanke, Ortigue et al. 2002), highlighting the close relationship between embodiment and vestibular perceptions.

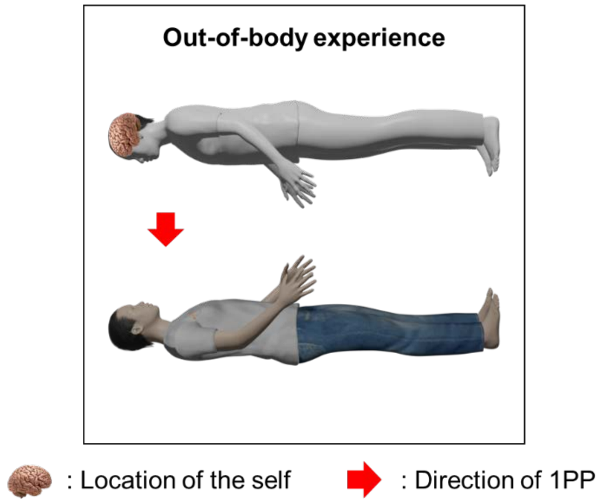

Figure 4. Characteristics of out-of-body experiences | Out-of-body experience shows the highest disembodiment where subjects feel as if they locate outside the physical body and look down their body on the ceiling and the highest vestibular dysfunction making patients feel floating, flying, or lightness. Mainly, OBE has happened in a lying position (Images are adapted from Blanke et al., 2004, and Blanke & Metzinger, 2009). The physical body is represented as wearing blue jeans and the illusory body is represented as wearing white pants. The experienced self-location and the direction of the first-person perspective are indicated with the brain image and the red arrow, respectively.

1.2 Virtual reality, aviation robotics, and flight simulator for neuroscience and the flying experience

Virtual reality (VR) can be defined as an immersive system that makes a user have the feeling of being inside a virtual environment by providing realistic interactions with a created environment simulated in real-time (Rizzo and Bouchard 2019). The introduction of VR in cognitive neuroscience expanded our understanding of it, of bodily self-consciousness and expanded possibilities for new applications. VR provided a critical role in the extension of experimental modulations of embodiment from the hand to the other body parts and the whole body. Before combining multisensory stimulation paradigms with VR, the embodiment manipulation of the body in healthy participants had been limited to a specific body part like the rubber hand illusion. However, it was possible to induce embodiment over virtual legs (virtual leg illusion) and the whole body (FBI) by using VR through an HMD (Ehrsson 2007, Lenggenhager, Tadi et al. 2007, Pozeg, Galli et al. 2015). Thanks to advancements in motion tracking, computational power, and computer graphics, it became possible to control an avatar or interact with virtual objects or environments with one's own movements in real-time. This made it easier to integrate and investigate the role of multisensory and sensorimotor components in embodiment in systematic and controlled ways (Sanchez-Vives, Spanlang et al. 2010, Kokkinara and Slater 2014, Padilla-Castañeda, Frisoli et al. 2014). Furthermore, development and improvement of depth camera like a Kinect (Microsoft XBOX) and a combination of several DSLR or depth cameras (photogrammetry) made it possible to create and control a photorealistic avatar that is almost identical in appearance in the virtual world. As the appearance of the avatar is also one of the important factors for embodiment, the photorealistic avatar helped to achieve better embodiment in VR (Waltemate, Gall et al. 2018).

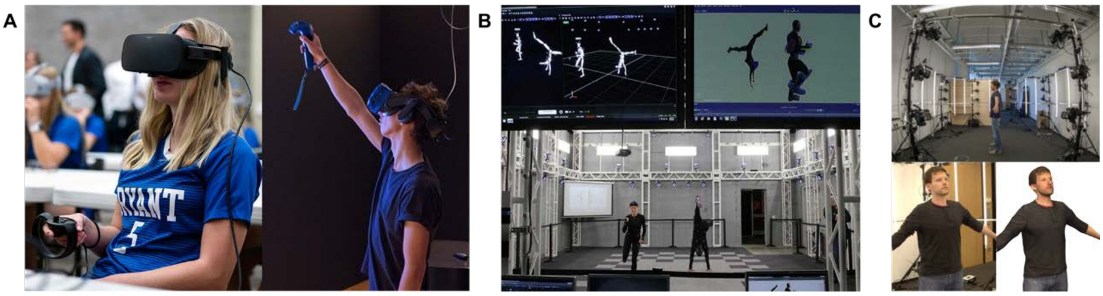

Figure 5. Improvement of VR | The development of various head-mounted displays from different companies is the biggest factor for the popularization of VR (A, left - Oculus & right - HTC Vive). Most of them are trying to provide a precise head motion tracking and higher resolution of graphics to synthesize a realistic visual environment. Moreover, motion tracking technologies contribute to the improvement of VR by providing precise and prompt controls and interactions of an avatar (B, OptiTrack). Also, the development of photogrammetry enables us to create a more realistic and personalized avatar and environment (C, Achenbach et al., 2017) inducing higher embodiment in VR (Waltemate et al. 2018).

The development of VR, aviation robotics, and flight simulators have both popularized flight experiences and provided environments to investigate flight experience systematically. For example, nowadays using a drone and HMD, people can easily have the visual experience of flying. Originally, flight simulators had focused on the development of realistic training scenarios for aircraft pilots in order to train novice pilots more efficiently and cost-effectively (Miletovic, Pool et al. 2017, Myers III, Starr et al. 2018). Therefore, in the traditional simulators, presenting in high realism and fidelity the interactions between controls in a cockpit and operations of the plane was much more important than giving the realistic experience of the flying including details of the view and multisensory feedback. Only in recent years, studies on flight simulators have started to focus on how to use modern technology to mimic the experience of flying (van Delden, Moreno et al. 2013, Eidenberger and Mossel 2015, Sikström, De Götzen et al. 2015, Cherpillod, Mintchev et al.

2017, Kryger, Wester et al. 2017, Miehlbradt, Cherpillod et al. 2018, Rognon, Mintchev et al. 2018, Yoon, Lee et al. 2018, Rognon, Koehler et al. 2019, Zhang, Riecke et al. 2019). In particular, previous studies compared the use of natural body movements, measured through wireless tracking technology, to map movements of a flying avatar or a drone with the participant's bodily movements, and used immersive technologies (robotics, immersive sound, pressure, and wind feedback) to create multisensory (visual, vestibular, tactile, auditory) scenarios and increase the realism of the simulated flight experience (Lintern and McMillan 1993, Eidenberger and Mossel 2015, Mauro, Gastaldi et al. 2016, Cherpillod, Mintchev et al. 2017). That is, the combination of VR and flight simulators is inducing the realistic bird-like flying experience (Sikström, De Götzen et al. 2015, Tong, Kitson et al. 2016, Rognon, Mintchev et al. 2018, Yoon, Lee et al. 2018).

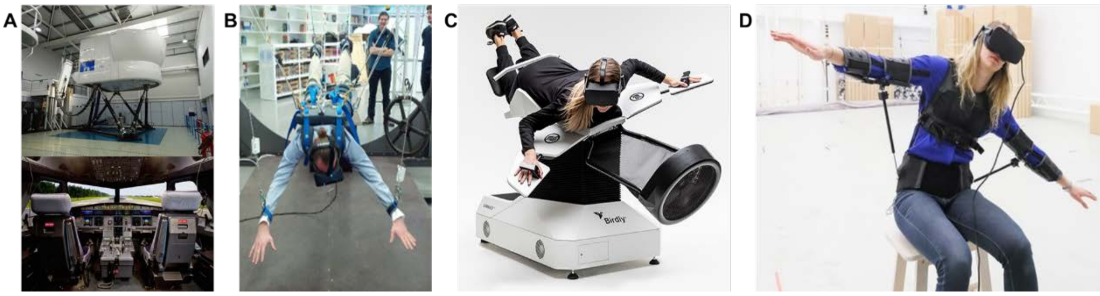

Figure 6. Different flight simulators | A traditional flight simulator was developed to train pilots of an airplane (A, SupraVue). Therefore, providing a similar interface or operating system was more emphasized. However, as virtual reality and robotics advanced and popularized, people have started to develop flight simulators for the flying experience itself. **B** Image shows device by Humphrey et al. (ARS ELECTRONICA, 2003) for virtual skydiving and **C** and **D** show Birdly (SOMNIACS, 2015) and Flyjacket (EPFL's Laboratory of Intelligent Systems, 2018) respectively.

1.3 Thesis outline

Many previous studies have investigated the influences from vestibular signals to embodiment. However, the influences of the other direction were less investigated. Therefore, in this thesis, I will focus on how embodiment affects vestibular signals, especially 'vestibular sensations'. My thesis has two main objectives: (1) investigating embodiment with sensorimotor and multisensory stimulation and (2) engineering to induce flight sensations through modulations of embodiment. For these purposes, I performed a series of studies in healthy participants investigating how embodiment can be modulated by sensorimotor and multisensory stimulation to induce the feeling of flight, using techniques like virtual reality, aviation robotics, and flight simulation.

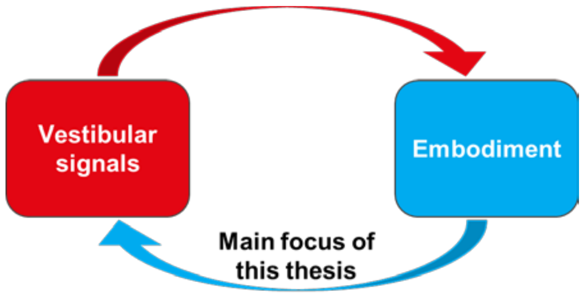

Figure 7. The schematic relationship between embodiment and vestibular signals | Embodiment and vestibular signals interact each other. Many previous studies have investigated the influences of vestibular signals on embodiment, but the effects of the other direction have received scant attention. Therefore, the influences of embodiment on vestibular signals, especially 'vestibular sensations', will be focused.

My thesis is divided into three parts:

(1) using aviation robotics (drone) and sensorimotor stimulation, I induced embodiment of an observed body and show the duplication of the self by finding distinct PPSs.

(2) using an interactive flight simulator and sensorimotor and multisensory stimulation, I manipulated the flying experience (piloting performance and flight sensations) by inducing embodiment of a flying avatar.

(3) developing a new mixed reality system to induce disembodiment from a physical body, I induced the floating experience like OBEs and investigated the effects of different factors on the OBE illusion.

In the first part (Study 1), I induced embodiment over a virtual body quantitatively and demonstrated the possibility to dissociate the position of the self and the position of the body. To this aim, participants were instructed to walk forward and respond to multisensory stimuli while seeing themselves from a drone-mounted camera that autonomously followed them. I showed that this setup induced two spatially distinct self-representations (quantified by two PPS representations) in healthy participants: reaction times for visuotactile stimuli were faster both at the location of the participants' body and the location of the virtual body. In line with seminal work by Stratton (1899), the more recent work by Mizumoto et Ishikawa (2005) and clinical observations in patients with heautoscopy (Brugger 2002, Heydrich and Blanke 2013), Study 1 showed the duplication of the self by identifying the simultaneous existence of distinct PPSs around both the viewpoint and the observed body (Stratton 1899, Mizumoto and Ishikawa 2005). Moreover, it opened new possibilities to investigate the roles of different visual viewpoints on embodiment by combining virtual reality and aviation robotics.

In the second part (Study 2, Study 3), I investigated if modulating embodiment over a virtual body could change flight sensations and piloting performance. For this purpose, I combined a photorealistic avatar and sensorimotor stimulation with a robotic flight simulator to enable and investigate personalized immersive flight experiences in healthy humans (Study 2). In Study 2, I showed that modulations of embodiment (as carefully manipulated during aviation through congruent sensorimotor stimulation) induced subjective flight sensations and importantly, also improved piloting performance; I also observed positive correlations of embodiment with flight sensations and piloting performance. Based on the positive correlations, I hypothesized that further improvement of embodiment with a synergetic combination of sensorimotor and multisensory stimulation could further boost flight sensations and piloting performance (Study 3). In Study 3, I developed and tested a haptic vest and coupled tactile stimulation on the physical body, visual stimulation on the avatar, and participants' movements. my data show further increases in embodiment and improvements in learning speed.

In the third part (Study 4, Study 5), I explored the possibility of leading the flying experience by inducing disembodiment from a physical body. To investigate the possibility, the laboratory developed a new sensorimotor body scanning platform. I investigated whether the platform can be used to induce one of the most common forms of disembodiment during which subjects experience that the center of awareness is dissociated from the physical body: the OBEs. As I mentioned above, OBEs represent an interesting link between embodiment and the subjective flight sensations as they are characterized by embodiment of an elevated aerial position and perspective in space that is commonly associated with prominent sensations of floating, elevation, and flight. In Studies 4 and 5, I showed that my virtual OBE-like scenarios could induce OBE-like sensations such as disembodiment, elevated self-location, and vestibular sensations. Also, I found that preference, spatial sound, and sensorimotor stimulation could lead to greater OBE-like sensations, depending on the awareness of spatial sound. Lastly, we newly found a positive correlation between disembodiment and vestibular sensations.

In the closing chapter, I summarize all studies and make a general discussion such as interpretation, limitations, future directions, and feasible applications of my studies while answering my main question in the current thesis: "how does modulation of embodiment influence vestibular sensations?".

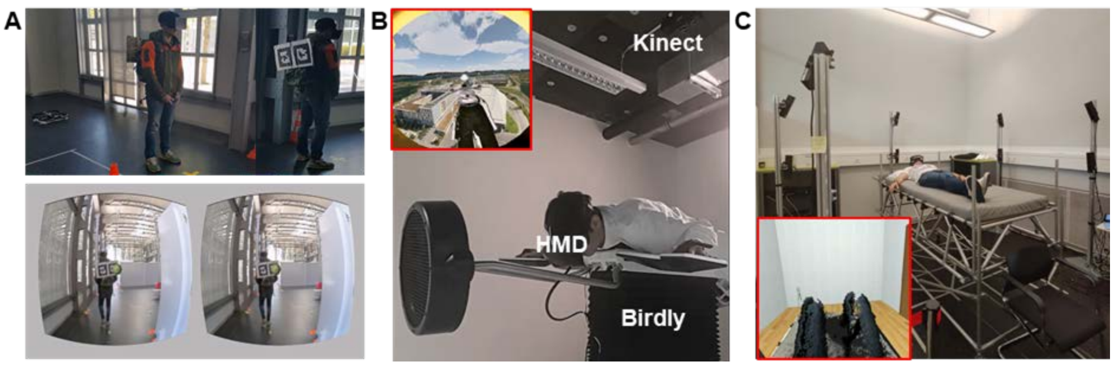

Figure 7. Experimental setups for each study | In Study 1, a drone autonomously follows a participant and he can see himself from the drone's viewpoint (**A**). While working or standing, they performed a visuo-tactile interaction task to measure PPS. In Studies 2 and 3, using an interactive flight simulator (Birdly) and a Kinect, a participant can experience a flight simulation from a third-person viewpoint seeing a photorealistic virtual body (**B**). The virtual body is the same in the appearance of the physical body and is synchronously moving with the physical body. In Studies 4 and 5, using ten Kinects, a photorealistic avatar of a participant can be created and projected into the virtual environment (**C**). In the virtual environment, the participant can synchronously move the virtual body from a first-person viewpoint like his own body. Also, he can experience a viewpoint change from first-person to a third-person viewpoint like OBEs.

1.4 Personal contribution

Study 1: M. Song, P. Grivaz, O. A. Kannape, M. Perrenoud, G. Rognini, J. B. Ruiz, D. Floreano, A. Serino & O. Blanke, Superposition of the self: Peripersonal space dynamically remaps around two distinct locations (in preparation)

Personal Contribution: Experimental design, recording, analysis, writing

Study 2 and 3: M. Song, G. Rognini, A. Cherpillod, A. Nesti, P. Grivaz, D. Floreano & O. Blanke, Flight of mind: Embodiment of the flying avatar improves flight sensations and piloting performance (in preparation)

Personal Contribution: Experimental design, recording, analysis, writing

Study 4 and 5: M. Song, S. Betka, F. Lance, O. A. Kannape, B. Herbelin, O. Blanke, Disembodied from the body: virtual Out-of-body experience (in preparation)

Personal Contribution: Experimental design, recording, analysis, writing

Chapter 2 Studies

2.1 Part A – Embodiment of an observed body and show the duplication of the self

2.1.1 Study 1 – Superposition of the self: Peripersonal space around two distinct locations. (Pilot)

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Conflict of interest
The authors declare that the research reported in this manuscript has been conducted in the absence of relationships that may be considered as a potential conflict of interest

Abstract

Multisensory processing is enhanced for stimuli that appear in close proximity to our body. The so-called peripersonal space (PPS) not only serves as an evolutionary, protective mechanism but also localizes and demarcates our body in space. Moreover, PPS is modulated by embodiment. For example, a number of previous studies have shown that usage of a tool extends PPS towards the tool that is considered to be embodied (De Vignemont 2011). However, although it is possible to embody an object or an observed body in a remote place, PPS has been investigated only near a physical body. Nobody has investigated PPS around such an embodied but remote avatar. Here we used virtual reality and drone robotics to create a full-body illusion (FBI) inducing embodiment of an observed body in a remote place: Participants were presented with real-time feedback from a drone-mounted camera that autonomously followed them as they responded to multisensory stimuli on their body and in their environment. Results demonstrate that the FBI induces two simultaneous PPSs at two distinct spatial locations: tactile processing on the body was enhanced by visual stimuli approaching both the participant's body and the location of their observed body. While previous studies have shown that PPS dynamically remaps towards the location of actions or the perceived self-location, this is the first evidence suggesting that simultaneous self-locations can be maintained in two discrete locations when an observed body is embodied in a remote place.

Introduction

Subjective experience is usually centered at the location of our physical body and within the Peripersonal space (PPS). We perceive and interact with the external environment from and within the PPS, i.e., the area around our body, distinct from far space. Studies in both humans (Serino 2019) and non-human primates (Graziano and Cooke 2006) demonstrated that PPS is encoded by multisensory, body-centered receptive fields in a fronto-parietal network. PPS can be measured using multisensory integration paradigms assessing the spatial location whereby external stimuli in the environment interact with tactile stimuli on the body and it provides an implicit measure of embodiment and perceived self-location (Noel, Pfeiffer et al. 2015). Moreover, PPS is not static but dynamically changes depending on embodiment. For example, usage of a tool induces embodiment of the tool extending PPS towards the tool. Also, during the FBI that induces embodiment to an observed body in a remote place and self-location in the observed body by using multisensory conflicts, PPS has been shown to shift towards the observed body (Noel, Pfeiffer et al. 2015). However, during the FBI, PPS has been only investigated around the physical body, but not around the observed body. Similar to the FBI, previous studies showed that seeing an observed body in a third-person viewpoint and moving the body from the viewpoint made participants feel as if they embodied and located in the viewpoint and observed body at the same time (Stratton 1899, Mizumoto and Ishikawa 2005). Furthermore, patients who had a problem with embodiment (heautoscopy) report the presence of a double, an actual duplication of the self, and experience themselves to be located both in their physical body and in that of the double. Based on these, we hypothesized that the FBI induces embodiment of and self-location in both the physical body and the observed body simultaneously. Also, the alterations will be reflected in PPS around the observed body. For the hypothesis, here we used PPS framework and assessment to investigate whether it is possible to induce in healthy participants a mild analogous of heautoscopic hallucinations, whereby that embodiment and self-location is experienced simultaneously in two positions in space. Translating seminal work by GM Stratton from the late 19th century (Stratton 1899) to current drone technology (Floreano and Wood 2015), we investigated whether presenting simultaneously participants with a first-person perspective point of view and a visual double of their physical body (observed body), seen at another location, would create a heautoscopic experience where one's perceived self-location appears to be temporarily superposed in more than one place at once, momentarily collapsing onto one's own or one's double's position. We measured PPS as a proxy for embodiment and self-location and expected that, under such circumstances, two distinct PPSs - assessed as the location of enhanced multisensory interaction between bodily and external stimuli occur – would emerge.

Materials and methods

Participants

Seven participants (25.9 ± 1.68 SD years, 2 females) took part in this experiment. The study was conducted in accordance with the Declaration of Helsinki and the participants gave their informed consent.

Materials (See Movie S1 for Details of Materials)

Materials used during the experiment can be decomposed into wearable materials (**Figure 1A**) and drone materials (**Figure 1B**). Throughout the experiment, wearable materials were carried by a participant to provide visual stimuli and tactile stimuli. Each subject carried a backpack that hosted a laptop computer with an in=house running python-based software (ExpyVR, lnco.epfl.ch/expyvr) which managed both the reception and the projection of the online video from the drone to the head-mounted display (HMD, Oculus Rift DK 1), the rendering of the 3-dimensional visual stimulus (virtual ball) and instructions into the HMD, the timing and the delivery of tactile stimuli and the recording of button presses. The incoming video was received using an analogous receiver functioning at radio frequency (Uno5800 5.8GHz A/V Rx, ImmersioRC, https://www.immersionrc.com/) and was digitalized using analog-to-digital USB transformer (DVD EZMaker 7, AVerMedia, https://www.avermedia.com/). Tactile stimuli were delivered simultaneously on the right cheek and the back of the neck of the participant at specific time intervals by means of a custom-made set of parallel-port triggered buzzers (taped using medical tape to the skin) controlled using a pre-programmed printed circuit board. Responses by the participants were provided using the thumb of their dominant hand using a USB gamepad (Gamepad F310, Logitech, https://www.logitech.com/). All these electro equipment were battery-powered so as to make it wearable. Besides, mounted on the backpack was a pair of Quick Response (QR) tags that were tracked by the drone and used for the autonomous following of the subject as he moved forward (see below).

To provide the participant with an online video of himself/herself seen from the back and to follow him/her autonomously, we adapted a commercially available flying quadrotor (AR Drone 2, Parrot ©, **Figure 1B**). A low-latency analog video was recorded using a front-facing wide-angle analog video camera (FAT SHARK) mounted on top of the drone chassis and transmitted using a wireless radiofrequency analog video transmitter (25mW 5.8GHz A/V Tx, ImmersionRC). Both of these devices were powered using the same battery as the drone and the transmitted video was received by the analog receiver carried by the participant and the subsequent video was projected into the HMD (**Figure 1A**), which consisted of the only visual information the participant possessed for actively navigating in space. A second digital built-in frontal camera on the drone was used to transmit online but with perceivable latency a high-quality video via the Wifi network directly to the drone control laptop (carried by the experimenter, **Figure 1B**). The video channel, as well as other flight-related information from the embedded drone sensors, was imported into a custom-made C#-based drone control program running on the drone control laptop. This software tracked positional information about the QR tags (http://chili.epfl.ch/sftware) on the back of the participant and, using a PID controller, instructed the quadrotor in real-time to adapt its flight trajectory in order to maintain the same relative position with respect to the tags (i.e. 4 meters behind the tags and in-line with the facing direction of the participant, **Figure 2A**). In addition, this autonomous behavior could, at any time, be overridden by the experimenter using a drone control pad. This was done during the drone take-off and landing phases, for the repositioning of the drone when the end of the pathway was reached (see later) and to correct manually for the trajectory path of the drone if necessary.

Participants either stood still or walked alone along a straight path, always using an online video from the viewpoint of the drone autonomously following them from behind as their only visual feedback. The walking was done indoors in a large room where a 3m wide corridor has been delineated with small cones and scotch tape of bright yellow color on the ground to facilitate navigation within its boundaries (**Figure 2A**). Either end of the 75m-long corridor was marked with larger orange-colored cones to signal participants to stop, turn around and continue walking in the opposite direction when instructed so by the experimenter.

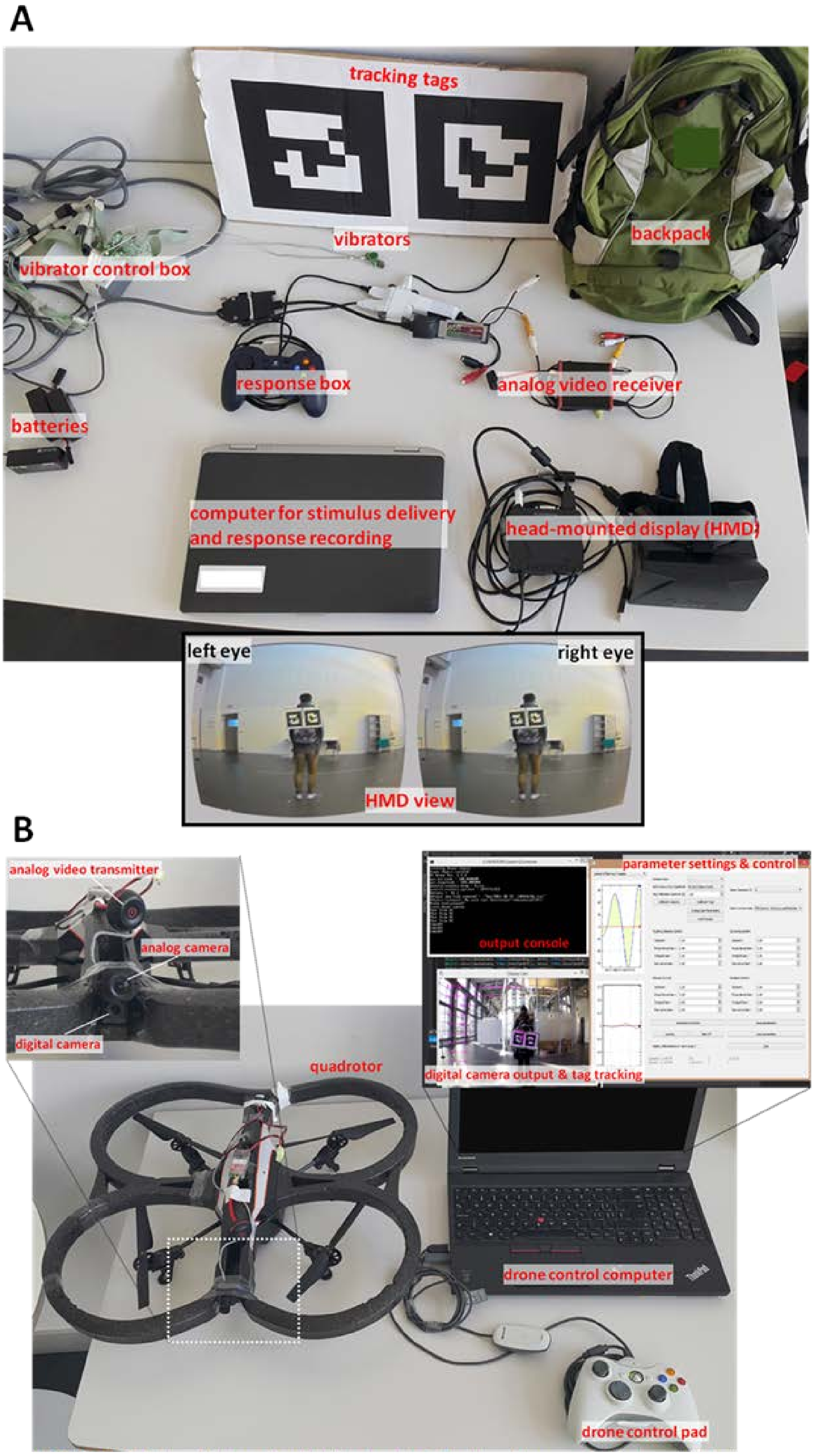

Figure 1 | Experimental equipment. (**A**) Wearable materials carried by a participant (**B**) Airborne equipment and material carried by an experimenter

Experimental procedure (See Movie S1 for Details of procedure)

In this experiment, we aimed at measuring alterations of peripersonal space (PPS) following an active walking condition, during which participants constantly viewed themselves from a disembodied third-person perspective (i.e. from the viewpoint of the drone, **Figure 2A**), or a passive standing condition with otherwise matching perspective. Thus, in two separate blocks, lasting approximately 15 minutes each, participants were instructed to either stand or walk in a straight line and at their preferred pace and press a button as fast as possible when and only when they perceived a touch stimulus on their cheek/neck (experimental PPS trials). At regular intervals and for 5 seconds, a "stop" instruction appeared on the screen during which participants were asked to progressively come to a halt in case they were walking or remain standing in case they were standing (**Figure 2B**). No experimental trials were conducted at those times. When the "stop" instruction disappeared, participants were asked to resume the current block (i.e. either walk or continue standing). Participants were further instructed to not respond to the delivery of a tactile stimulus in cases when they were not walking when they should have been (in the walking block) or when they did not see their virtual own body in the HMD. Indeed, especially in the walking block, due to the difficulty of walking from a disembodied viewpoint and despite some practice trials, some participants had to stop from time-to-time to reposition themselves in the correct direction. Likewise, on some rare occasions, the drone could drift off sideways, leaving the participant without proper visual feedback of themselves. In such cases, participants were asked to stop walking until the normal situation was restored.

To assess the shape and boundaries of PPS, we used a visuo-tactile interaction (Canzoneri, Magosso et al. 2012) that relied on measuring RTs in response to the delivery of a tactile stimulus concurrently to the right cheek and the back of the neck of the participants. The touch was delivered either on its own (i.e. tactile only baseline trials) or in the presence of a dynamically moving 3-dimensional tennis ball (i.e. visuo-tactile trials). The tennis ball could either appear close to and recede away from the viewpoint (thus looming towards the observed body) or appear far from and loom towards the viewpoint (thus recede from the observed body). The trajectory, as well as the speed and moving duration (3.5 seconds) of the virtual tennis ball, always remained identical, only its direction changed. Critically, touch was delivered once within each visuo-tactile trial with one of 6 different temporal offsets (T1, …, T6) with respect to the appearance of the virtual tennis ball. In other words, touch was delivered at instances when the virtual ball was perceived at one of 6 different depths from the viewpoint (D1, …, D6). Participants were instructed to respond as quickly as possible following the delivery of touch. The current experiment thus consisted of a 2-by-2-by-6 full-factorial design with factors **Context** (Passive (Standing), Active (Walking)), **Direction** (Looming, Receding) and **Distance** (D1, D2, D3, D4, D5, D6), where the distances and virtual ball movement directions were always with respect to the viewpoint reference (i.e. quadrotor frontal camera). In addition, we included measures of RTs to unimodal conditions where either only a tactile stimulus was delivered at the temporal offsets T1, T3, or T6, or only the looming or receding visual stimulus was shown without the delivery of touch. The prior was used to assess the baseline RTs (see below), whereas the latter served as a control for attention and compliance and to verify that participants do not automatically associate the dynamic visual stimuli with button response. Half of the participants started with the walking block whereas the other half with the Standing block. On average, participants completed each experimental condition 9.28 ± 2.26 SD times.

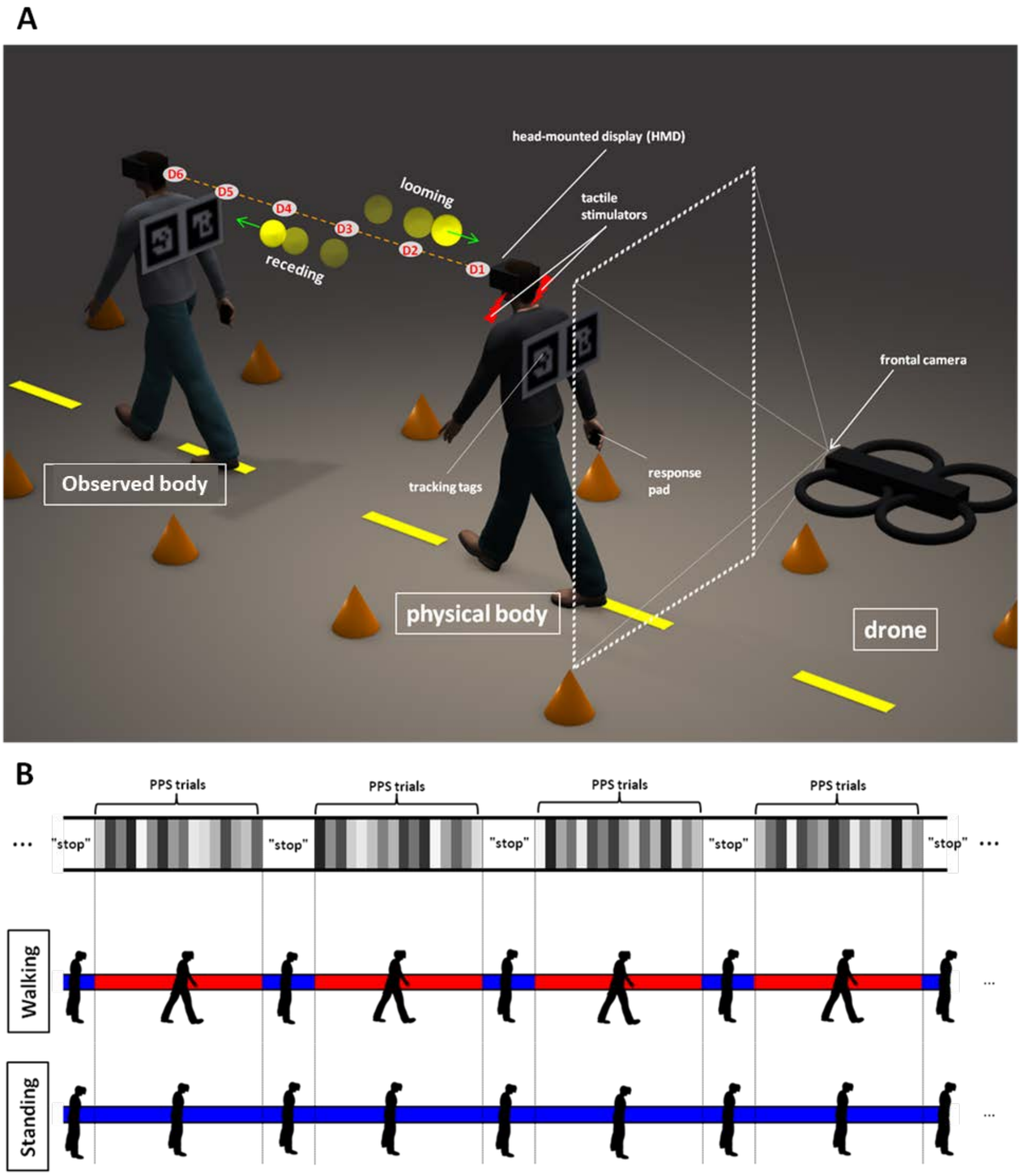

Figure 2 | Experimental setup and paradigm. (**A**) Participants (physical body) viewed an online video of themselves from the back (observed body) through a head-mounted display, i.e. from the viewpoint of a frontal camera of a drone that followed them autonomously. To measure PPS, participants were required to press a button as fast as possible whenever touch was delivered to their cheek and neck (always simultaneous). Touch was delivered once at one of 6 different temporal offsets with respect to the appearance of a virtual tennis ball that either loomed towards the viewpoint from far depth or receded away from the viewpoint from near depth. (**B**) Furthermore, PPS trials were conducted at the same time that participants were either Standing or Walking (in separate blocks) while viewing themselves from a disembodied viewpoint. Small pauses, when participants were asked to halt and when no PPS trials were delivered, were included for participants' comfort.

Dependent variable

Reaction Times: RTs to Multimodal (visuo-tactile) and unimodal (tactile) were used to describe the facilitation effect and boundaries of the PPS. RTs that were either negative (suggesting a button press prior to the delivery of a tactile stimulus) or larger than 2 seconds (suggesting a low level of attention) were discarded. From the residual trials, we further excluded outliers that were outside of the interval corresponding to the individual condition-wise mean ± 2.5 standard deviations (less than 1.6% of the remaining data). We then recalculated, for very individual and every experimental condition, the new means. The baseline was defined as the arithmetic mean between the mean RTs to the three different unimodal conditions where only a tactile stimulus was delivered (i.e. in the absence of the virtual ball). On average, participants responded wrongfully in the vision-only conditions 3.41% of the time, suggesting overall good task compliance.

Statistical Analysis

Two types of statistical analyses investigating two different aspects of PPS were conducted. The first analysis aimed at assessing whether PPS existed and was differentially affected in the two conditions (active vs passive) or when the virtual ball was looming or receding. To identify the existence of PPS and quantify a multisensory facilitation effect of PPS, we calculated an RT slope for each participant as a function of Distance for each Context and each Direction (Passive + Looming - PL, Passive + Receding - PR, Active + Looming - AL, Active + Receding - AR). The slopes were computed through linear mixed models on the baseline-corrected RTs with a factor Distance (D1, D2, D3, D4, D5, D6) as a fixed effect and intercepts for participants and random slopes for Distance as random effects. As the baseline measures differed significantly depending on whether they were conducted in the Passive (Standing) or Active (Walking) block ($t(363.70) = 6.54$, $p < 0.001$), we used the block-specific baseline measures for baseline correction. From these models, we could identify the existence of PPS if the RT slope is bigger than zero because multisensory processing is boosted for stimuli that appear within PPS. In turn, to access the different influence of Context and Direction on PPS, we built a 2-by-2 linear mixed model for the slopes with factors Context, Direction, and interaction as fixed effects and intercepts for participants as random effects. Additionally, the mixed model included random slopes for Context and Direction based on a likelihood ratio test. Post-hoc comparisons, where applicable, were conducted using pairwise comparisons of R package “emmeans”.

The second analysis aimed at assessing for which visuo-tactile experimental conditions RTs significantly sped up with respect to the unimodal tactile baseline. Thus, we assessed the location of the boundaries of the PPS. To do so, we built linear mixed models on the baseline-uncorrected RTs for Contexts and Directions showing the existence of PPS in the first analysis (PL, AL, and AR) with the factor Distance (D1, D2, D3, D4, D5, D6, Baseline) as a fixed effect and intercepts for participants as random effects. As in the first analysis, random slopes for Distance were selected, depending on a likelihood ratio test. In cases of a main effect of Distance, posthoc comparisons were conducted using Tukey’s HSD.

Results

First of all, linear mixed models on the RTs showed main effects of Distance in the PL ($F(1,6.20) = 17.11$, $p < 0.01$), AL ($F(1,67.78) = 10.38$, $p < 0.01$), and AR ($F(1,6.52) = 5.84$, $p < 0.05$) and slopes of these conditions were significantly larger than zero. In other words, PPS existed only around the viewpoint in a passive context, but around both the viewpoint and the observed body in an active context.

The 2-by-2 linear mixed model on the slopes of the RTs yielded main effects for Context ($F(1,8.99) = 9.95$, $p < 0.05$) and Direction ($F(1,21.00) = 14.94$, $p < 0.001$) and a two-way interaction for these ($F(1,21.00) = 19.06$, $p < 0.001$). Following the Context-by-Direction interaction, post-hoc comparisons revealed that the slopes in PL, AL, and AR were significantly greater than the slopes in PR (PL vs. PR: $t(16.33) = -5.39$, $p < 0.001$; PR vs. AL: $t(17.28) = -4.49$, $p < 0.01$; PR vs. AR: $t(17.28) = -4.77$, $p < 0.001$). There was no difference between PL, AL, and AR (all p-values > 0.05).

The analysis investigating the boundaries of PPS using linear mixed models revealed a main effect of Distance for the three conditions having PPS: PL ($F(6,552.03) = 6.88$, $p < 0.001$), AL ($F(6,569.29) = 5.10$, $p < 0.001$), and AR ($F(6,584.18) = 4.40$, $p < 0.001$). Post-hoc pairwise comparisons revealed a significant speeding up of RTs for some the following distances: PL and the AL: D1 ($p < 0.001$) and D2 ($p < 0.01$, all other $p > 0.05$); AR: D1 ($p < 0.001$), D2 ($p < 0.05$), and D3 ($p < 0.05$, all other $p > 0.05$). To summarize, irrespective of whether the participants were walking or standing, we observed the same PPS boundaries around the visual viewpoint for the looming stimuli. However, for receding stimuli, PPS was only observed in the Active context, i.e. walking, with the expanded boundary. That is, the presence of a looming or receding stimulus and the touch delivered when the stimulus was within PPS boundaries led to a facilitation effect on RTs to touch with respect to when the visual stimulus was absent (i.e. baseline). However, in Active context, we could observe larger PPS in Receding direction.

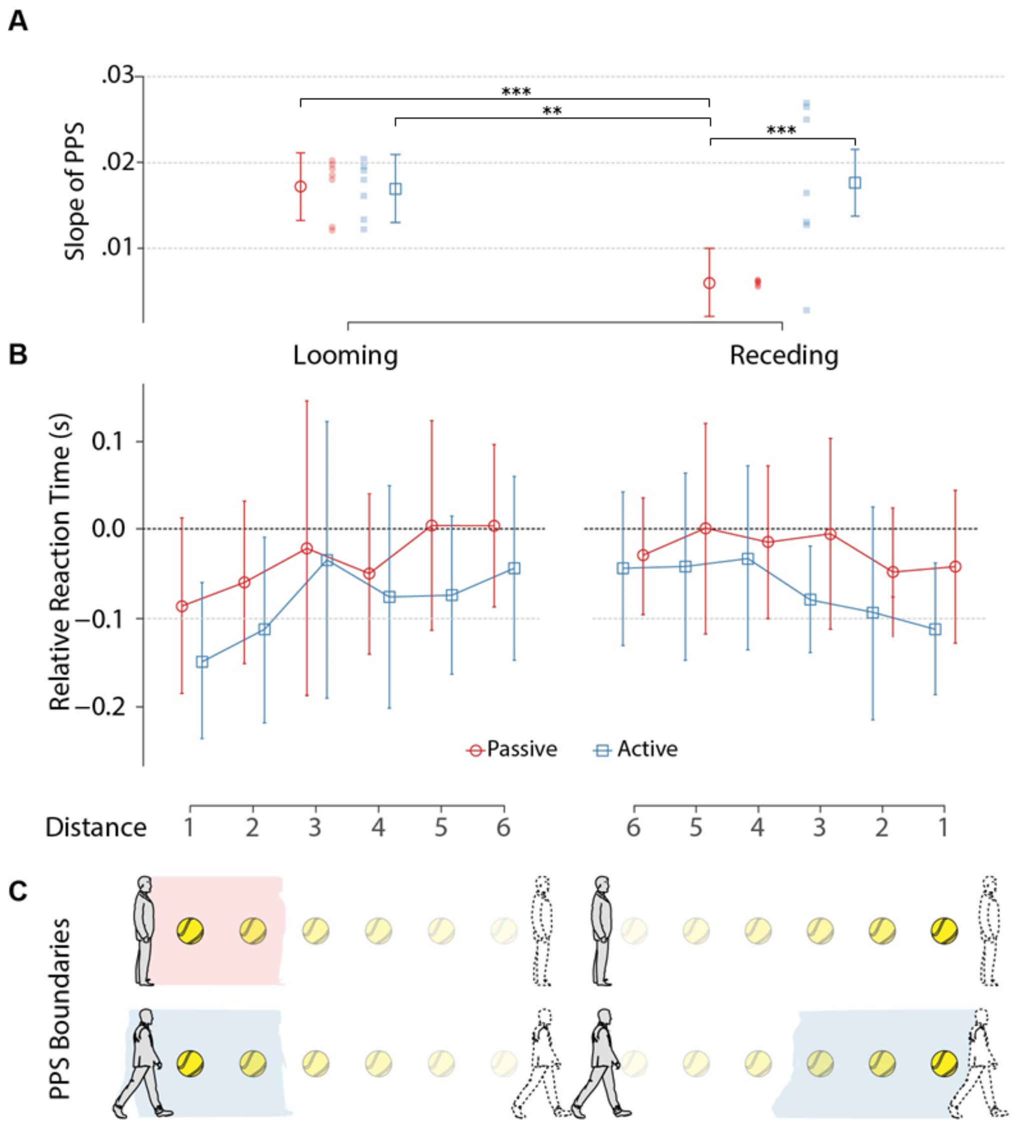

Figure 3 | Results. (A) Slopes of PPS for each direction and each context. (**B**) Baseline-corrected RTs to touch for looming and receding balls perceived at different depths for the passive (standing) and the active (walking) contexts. (**C**) Boundaries of PPS for each direction and each context

Discussion

In this experiment, through the PPS framework and aviation robotic, we show that reaction times to multisensory stimuli are enhanced around the viewpoint and the observed body during walking. In other words, the simultaneous existence of distinct PPSs around both the viewpoint and the observed body quantitatively demonstrates that the FBI using active sensorimotor stimulation induces embodiment to and self-location in both the viewpoint and the observed body. This is a novel finding that is important for both our understanding of the self and its experienced unity. The fact that PPS can be observed in two discrete locations is counterintuitive. Yet by using an autonomous drone to create an augmented heautoscopic context in which the coexistence of two self-locations becomes plausible, we demonstrate that our brain spontaneously adapts to facilitate multisensory integration, maintain distinct PPSs, and therefore also to locate oneself at two distinct spatial locations.

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Supplementary material

Supplementary Video

Movie S1: **https://drive.google.com/open?id=1igCTEf24Ekq2lwUohIXnAm4ruVI6J1-N**

2.2 Part B – Embodiment of the flying avatar improves flight sensations and piloting performance

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Abstract

Have you ever imagined or dreamed of flying in the sky like a bird? Since ancient times humans have entertained the idea of flying, been keen on developing aviation technology, and also wondered what it may feel like to fly. Yet, most efforts focused on the development of aviation technology for transportation rather than the subjective experience of flying with one's own physical body. In more recent times, the continued improvement of immersive virtual reality, aviation robotics, and flight simulator has made it possible to induce and investigate the flying experience in controlled settings and has helped to democratize the experience of flying. Yet, so far researchers have tried to develop various interfaces to induce embodiment for the flying experience by providing intuitive controls and realistic environment, but they have not investigated the underlying multisensory and sensorimotor mechanisms supporting the flying experience; crucially, the link between embodiment, flying experience and piloting performance is still unknown. In Studies 2 & 3, our purposes were modulating the flying experience and piloting performance by inducing embodiment to a flying avatar using sensorimotor and multisensory stimulation. To achieve these purposes, we have combined a photorealistic avatar and a haptic vest to a robotic flight simulator to enable and investigate personalized immersive flight experiences in healthy humans. In Study 2, participants experienced a flight simulation on the robotic simulator while seeing a flying avatar that synchronously moved with movements of the physical body. As a result, we showed that modulations of embodiment using synchronous sensorimotor stimulation) resulted in enhanced subjective flying experience, better piloting performance, faster learning. In Study 3, we added multisensory stimulation synchronized with physical movements on the setup of Study 2. We showed that the multisensory – visual (on the avatar) and tactile (on the participant's physical body) – stimulation with our haptic vest could further increase embodiment and improve learning speed.

Introduction

Since ancient times humans have entertained the idea of flying (Graves 1984), we're keen to develop aviation technology, and also wondered what it may feel like to fly. Combining their admiration for the aviation abilities of birds, bees, or flies with research and engineering, earliest aviation engineers such as Clement Ader and Leonardo da Vinci envisioned flying machines and Wright brothers finally accomplished practical powered airplane flight (Grant 2003). The development of aviation technology, airplanes, helicopters, and drones, has revolutionized transportation and created entire engineering fields, research, and powerful business sectors (Grant 2003, Michel, Gettinger et al. 2018), but did not focus on a person's subjective flight sensations and even attempts to avoid or minimize them. Thus, humans have pursued the experience of flight sensations by other means such as parachuting, sky diving, base jumps, or paragliding. Yet, none of these approaches are widely accessible and most are dangerous and sometimes life-threatening (Laver, Pengas et al. 2017), requiring specific training, preparation, and equipment. In more recent times, the continued improvement of immersive virtual reality (VR) and drone technologies has made it possible to induce and investigate these experiences in controlled settings and has helped to democratize the experience of flying (Ikeuchi, Otsuka et al. 2014, Cherpillod, Mintchev et al. 2017). These advances are contributing to the creation of the psychology of flight sensations.

Of course, there are some safe ways to experience flying and flight simulators are the representative example. However, flight simulators have been designed for the development of realistic training scenarios for aircraft pilots to train novice pilots more efficiently and cost-effectively (Miletovic, Pool et al. 2017, Myers III, Starr et al. 2018). As robotics has developed, flight simulators are able to provide motion feedback and a more realistic airplane experience. However, traditional flight simulators had still focused on teaching how to control the operating system of airplanes rather than the flying experience per se. Recent research on flight simulators has also investigated optimal ways to mimic the experience of flying (van Delden, Moreno et al. 2013, Cherpillod, Mintchev et al. 2017, Kryger, Wester et al. 2017, Miehlbradt, Cherpillod et al. 2018, Rognon, Mintchev et al. 2018, Rognon, Koehler et al. 2019, Zhang, Riecke et al. 2019) and compared the use of natural body movements, as measured through wireless tracking technology, to map movements of a simulated flight with the participant's bodily movements, and used immersive technologies (e.g. robotics, immersive sound, and tactile wind feedback) to create multisensory scenarios (e.g. not only visual and vestibular but also tactile and auditory feedback) to increase the realism of the simulated flight experience (Lintern and McMillan 1993, Mauro, Gastaldi et al. 2016, Cherpillod, Mintchev et al. 2017). Globally, these studies aimed at improving piloting performance by developing more realistic, intuitive and performing human-machine interfaces (Tong, Kitson et al. 2016, Rognon, Mintchev et al. 2018).

Some studies initiated to consider embodiment in flight simulators to make pilots immersive to the simulated flight experience by extending the human-machine interfaces to a flying virtual avatar (Eidenberger and Mossel 2015, Sikström, De Götzen et al. 2015, Yoon, Lee et al. 2018). Embodiment is a state that some properties of an object or a system are processed as if the properties of one's body are dealt with (De Vignemont 2011). Embodiment includes three main components: self-location (the sense of being located in space), self-identification (the senses of owning a body), and agency (the sense of being the agent of one's actions) (Longo, Schüür et al. 2008, Kilteni, Groten et al. 2012, Gonzalez-Franco and Peck 2018). In other words, if pilots embody the flying avatar, they felt as if they are in the simulated flight environment, the avatar is their own body, and they directly control the avatar. Yet, so far researchers have tested how different interfaces induce embodiment to the flying avatar and flight sensations, but they did not investigate the underlying multisensory and sensorimotor mechanisms supporting these experiences and, crucially, the link between avatar's embodiment, flying experience and piloting performance is still unknown.

Out-of-body experiences are an interesting link between embodiment and the subjective flight sensations and characterized by embodiment of an elevated aerial position and perspective in space that is commonly associated with prominent sensations of floating, elevation, and flight (Blanke and Mohr 2005). Inspired by out-of-body experiences, recent research in cognitive neuroscience has developed experimental procedures in which participants are exposed to controlled multisensory and sensorimotor stimulation about the location and orientation of their own body concerning an avatar's body (12-19). Notably, it has been shown that the sense of owning the body of the avatar (illusory body ownership), the sense of being located within the avatar's body (illusory self-location), and the sense of being in control of the avatar's actions (illusory sense of agency) can be altered in predictable ways by interfering with specific multisensory and sensorimotor brain mechanisms (Jeannerod 2006, Serino and Haggard 2010, Blanke 2012, Blanke, Slater et al. 2015). For example. one prominent line of research has shown that it is possible to experimentally manipulate agency and ownership by exposing subjects to a variety of sensorimotor conflicts (Daprati, Franck et al. 1997, Farrer, Franck et al. 2003, Knoblich and Kircher 2004, Jeannerod 2006), typically spatial or spatio-temporal mismatches between the participant's goal-directed action and the related visual feedback (Tsakiris, Prabhu et al. 2006, Sanchez-Vives, Spanlang et al. 2010, Kalckert and Ehrsson 2014). The sense of ownership and agency have also been investigated in VR - where seeing a virtual hand that synchronously moved with a physical hand could result in ownership and agency over the virtual hand (Virtual hand illusion, VHI) (Sanchez-Vives, Spanlang et al. 2010, Rognini, Sengül et al. 2013) - and for the body as a whole (Kannape, Schwabe et al. 2010, Kannape and Blanke 2012). In this article, we generally refer to these aspects with the term embodiment.

Here, to create personalized and immersive flight experiences, and to investigate the role of embodiment and sensorimotor processing on flight sensations and piloting performance, we created an immersive flying experience scenario by combining a flight stimulator composed of a robotic platform (Birdly) with immersive VR, body scanning, and online embodiment manipulations. Birdly recorded body movements and provide inertial stimulation to the participant during simulated flights and VR provided immersive visual feedback. To enhance the immersion in the custom-made VR flight scenario, we created a photorealistic avatar for each participant with body scanning technology and integrated this photorealistic avatar into the VR scenario in real-time, creating a mixed-reality scene in which participants saw their own "real" flying avatar into the virtual scene.

In Study 2, we tested in 25 participants whether changes in embodiment (as carefully manipulated during aviation through sensorimotor stimulation) would enhance subjective flight sensations and result in better piloting performance and faster learning. Also, we hypothesized positive relationships of embodiment with flight sensations and piloting performance

2.2.1 Study 2 – Sensorimotor embodiment improves flight sensations and piloting performance

To investigate the role of embodiment, manipulated by sensorimotor stimulation, on flight sensations and piloting performance, we used a flight stimulator composed of a robotic platform, the "Birdly" (Somniacs, Switzerland) - able to record full-body movements and provide inertial and wind feedback to the participant -, immersive 3D VR with a head-mounted display (HMD, HTC Vive, Taiwan), and head tracking, to render a strongly immersive experience. In addition, Kinect V2 (Microsoft, USA) was used to track each participant's movements and to synchronize them with the shown avatar. We also created a photorealistic avatar for each participant so that the avatar seen in the virtual world showed the same appearance of the person's body (Fig. 1). Following familiarization with the platform, participants saw the avatar from a third-person viewpoint (Fig. 1A) and were instructed to pilot the flying avatar through a 3D path in the virtual world as indicated by a sequence of virtual clouds (or as close as possible, target) by controlling the Birdly interface. We decided to show the avatar from a third-person viewpoint based on three main reasons: (1) this is the viewpoint used during our previous embodiment research using full-body illusions paradigms (Lenggenhager, Tadi et al. 2007), (2) the viewpoint classically taken in gaming (Salamin, Thalmann et al. 2008, Salamin, Tadi et al. 2010), and (3) the viewpoint typically reported during out-of-body experiences (Blanke, Landis et al. 2004, Blanke and Mohr 2005, Lopez and Elziere 2018). 25 healthy participants took part in Study 2 (Supplementary Text S1) and we measured avatar embodiment, flight sensations, as well as the piloting performance in an experimental condition and compared with two control conditions. In the experimental condition, participants piloted their flying avatar while they received synchronous movement feedback (e.g. online undelayed feedback between the participant's movements on the Birdly platform and the avatar's movements in the visual flight simulation world (Fig. 1B; Movie S1) (avatar-synchronous condition). In one control condition, we artificially inserted a 5-second delay between the participant's movements on the Birdly and the avatar's movements (avatar-asynchronous condition). The second control condition was added to control for attentional (versus embodiment) effects and was identical with the avatar-synchronous condition, with the only exception that the avatar was replaced by a rectangular box of similar size (Lenggenhager, Tadi et al. 2007) (object-synchronous condition, Fig. 1C; Movie S1; participants could see movements of the box synchronized with their physical body movements). This condition was designed to test whether the bodily-like appearance of the avatar is crucial for inducing sensations of embodiment. Crucially, the experiment was designed so that the delay in the avatar-asynchronous condition only affected the avatar's movements, but not the actual flight trajectory (see Materials and Methods for detailed explanation) (see Fig. 1B; Movie S1). Thus, we were able to selectively manipulate sensorimotor bodily signals (between participant and avatar or object), but not the actual flight trajectories, making our sensorimotor manipulation task independent.

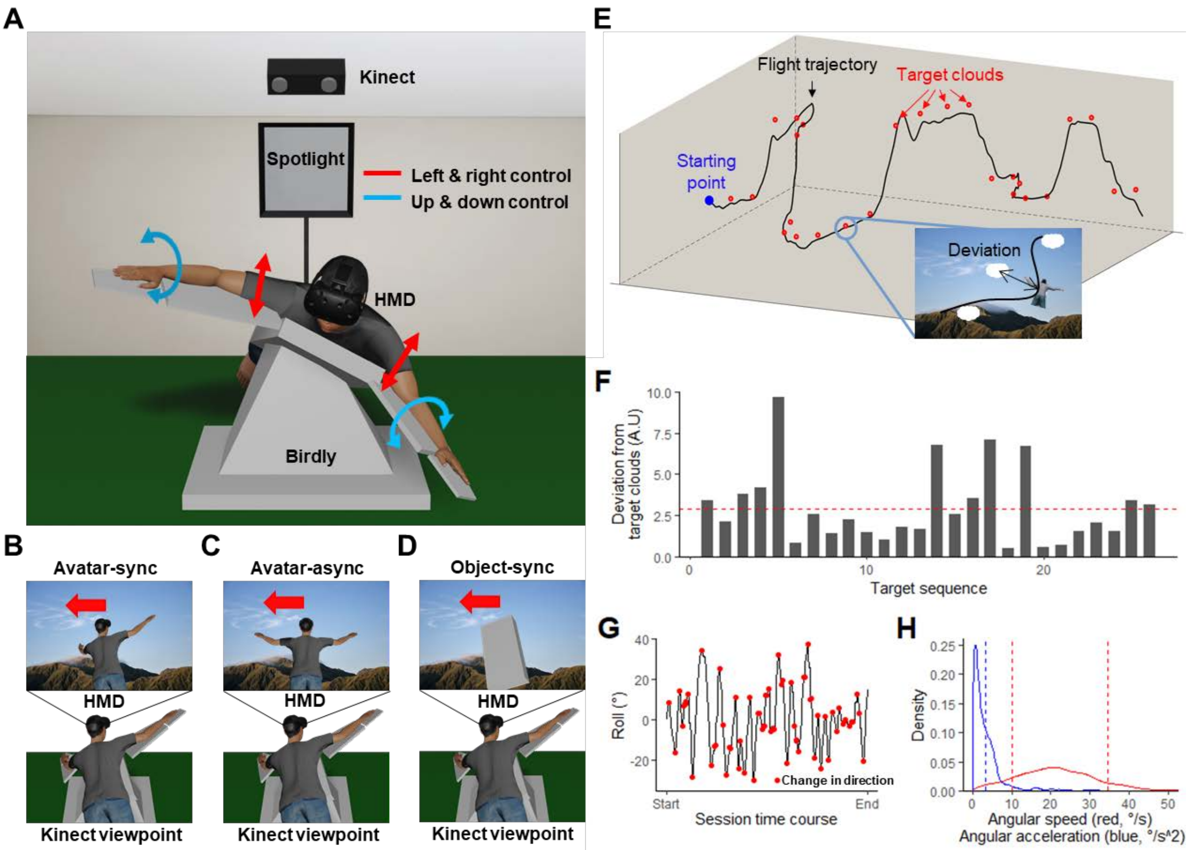

Fig. 1. Study 2: Experimental setup and procedure (A-B-C-D). A) Schematic representation of a participant using the Birdly system, while wearing an HMD. The HMD provided head movement tracking, allowing participants to freely explore the VR environment with head movements. Participants were trained to use their upper limbs and whole body to control the Birdly interface and fly the avatar in the virtual world, as seen on the HMD. Participants were asked to pilot the avatar as closely as possible to the center of each cloud target. Kinect V2 (Microsoft, USA) was used to create a photorealistic avatar for each participant and provide synchronized avatar motions with motions of each participant. A dedicated light ("Spotlight" in the figure) was utilized for providing the illumination needed for the proper functioning of the Kinect. Participants carried out three different conditions (1 experimental, 2 control). **B**) In the experimental condition, participants controlled their virtual avatar and received synchronous sensorimotor feedback (avatar-synchronous condition; Avatar-sync). **C**) In the asynchronous control condition, a 5-second delay was inserted between the movements of the participant on the Birdly and the avatar's movements (avatar-asynchronous condition; Avatar-async). **D**) In the object-synchronous condition (Object-sync), participants piloted a virtual box (instead of their avatar) with everything else being equal to the experimental condition. **Flight trajectory and piloting performance metrics (E-F-G-H).** The 3D flying trajectory from one participant as well as the piloting performance metrics are shown. **E**) 3D flight trajectory for one participant is shown. Red circles represent target clouds; deviation represents the Euclidian distance between the avatar's and the cloud's center (inset). **F**) Inverse deviations and inverse variance of the deviations were used to calculated accuracy and precision. When the deviations are smaller than the radius of the cloud targets, it is assumed that the target is hit (hit rate); all values in the figure below the dashed red line represent hit targets. The accuracy, precision, and hit rate are normalized and integrated with equal weight into a global measure of targeting of piloting performance. **G**) Roll change over time course is shown. We calculated the number of direction changes based on the roll, pitch, and yaw (control effort). Each red dot visualizes a change in direction. **H**) Distribution of angular speed variability and mean of angular acceleration throughout the experiment. Density values (y-axes) indicate the occurrence of angular speed or angular acceleration values (x-axes). Control effort, the variability of angular speed, and mean of angular acceleration were normalized and combined for path stability.

After each flight session (lasting 90 seconds), we quantified subjective experiences during the experiment via a standardized questionnaire and asked participants to answer seven questions, four about embodiment and two about flight sensations (there also was one control question) (for all questions see Supplementary Table S1). To simplify the analysis, we created three main categories (also called indexes; embodiment, flight sensations, control), by averaging the ratings reported on the items belonging to each category. Statistical analysis was performed for three indexes separately (for detailed results on each question see Supplementary text S1; Fig. S1). Piloting performance was quantified by recording the following movement parameters. These were related to the (1) distance of the avatar to the cloud targets and (2) stability of piloting. *Targeting* was defined as accuracy and precision while approaching the target (hit rate). *Path stability* was defined as the variability (position, angular speed, angular acceleration) of a participant on the chosen path. Global indexes were created for targeting and path stability of piloting performance by equally weighting different parameters belonging to each category and statistical analysis was performed for each index separately (for detailed results on each variable see Supplementary text S1; Fig. S2). Also, the experiment was divided into 6 sessions, each of which contained all the conditions presented in a randomized order, allowing us to test for possible effects on learning on the piloting performance. As a result, statistical analysis was performed for targeting, path stability, and learning rates of these separately.

Sensorimotor congruency boosts embodiment of a flying avatar. Analysis using the linear mixed model on questionnaire data concerning embodiment showed a main effect of sensorimotor congruency ($F(2,24.00) = 22.06$, $p < 0.001$). As predicted, planned comparisons between the experimental condition and the control conditions revealed that embodiment of the avatar was higher in the avatar-synchronous condition (5.41 ± 0.08, mean ± standard error) vs. the avatar-asynchronous condition (4.60 ± 0.10, $t(24.00) = -4.72$, $p < 0.001$) and the object-synchronous condition (4.14 ± 0.09, $t(23.99) = -6.20$, $p < 0.001$) (Fig. 2A). Concerning the strength of the effects, embodiment of the flying avatar in the main experimental (avatar-asynchronous) condition was on average 17.8% (and 30.9%) higher than in the avatar-asynchronous (object-synchronous) condition. 19 (and 21) out of a total of 24 participants reported stronger embodiment in the experimental condition vs the avatar-asynchronous (object-synchronous) condition.

Sensorimotor congruency affects flight sensations but does not affect the control question. The same analysis about flight sensations revealed a similar pattern ($F(2,24.25) = 9.03$, $p < 0.01$): in the avatar-synchronous condition, the condition inducing the strongest sensation of embodiment, flight sensations were rated (5.14 ± 0.10) as stronger than in the avatar-asynchronous (4.77 ± 0.10, $t(24.26) = -3.73$, $p < 0.01$) and the object-synchronous conditions (4.48 ± 0.11, $t(24.08) = -3.84$, $p < 0.001$) (Fig. 2B). Concerning the strength of the effects, the main experimental (avatar-synchronous) condition was on average 7.6% (14.4%) higher than in the avatar-asynchronous (object-synchronous) condition. Similarly, 16 out of 24 participants reported stronger embodiment in the main condition vs the avatar-asynchronous (object-synchronous) condition. However, there was no difference between conditions in the control question ($F(2,408) = 1.43$, $p = 0.24$)

Embodiment mediates flight sensations. Moreover, there was a significant correlation between embodiment and flight sensations, as assessed through a linear mixed model (estimated regression coefficient (β) = 0.47, significantly different than zero; $F(1,426.61) = 125.26$, $p < 0.001$) (Fig. 2D). This correlation was specific, as there was no correlation between embodiment and control question ($F(1,425.50) = 0.05$, $p = 0.83$). Moreover, the association of embodiment and flight sensations did not depend on conditions and was found in all three conditions ($F(2,411.48) = 0.43$, $p = 0.65$). Performing mediation analysis, we found that flight sensations were fully mediated by embodiment (Average Causal Mediation Effects, ACME = 0.50, $p < 0.001$) and not by the sensorimotor stimulation per se (Average Direct Effects, ADE = 0.01, $p = 0.93$) (Fig. 2F). These data show that sensorimotor congruency between the participant's movements on the Birdly interface and the avatar's movements in the 3D mixed world lead to stronger sensations of embodiment of the virtual avatar, which induce stronger flight sensations. These sensations do not depend on potential attentional differences related to the different sensorimotor stimulation conditions but are specific to processes related to the visuomotor congruence between the participant on the Birdly and the virtual avatar and the presence of a bodily-shaped avatar.

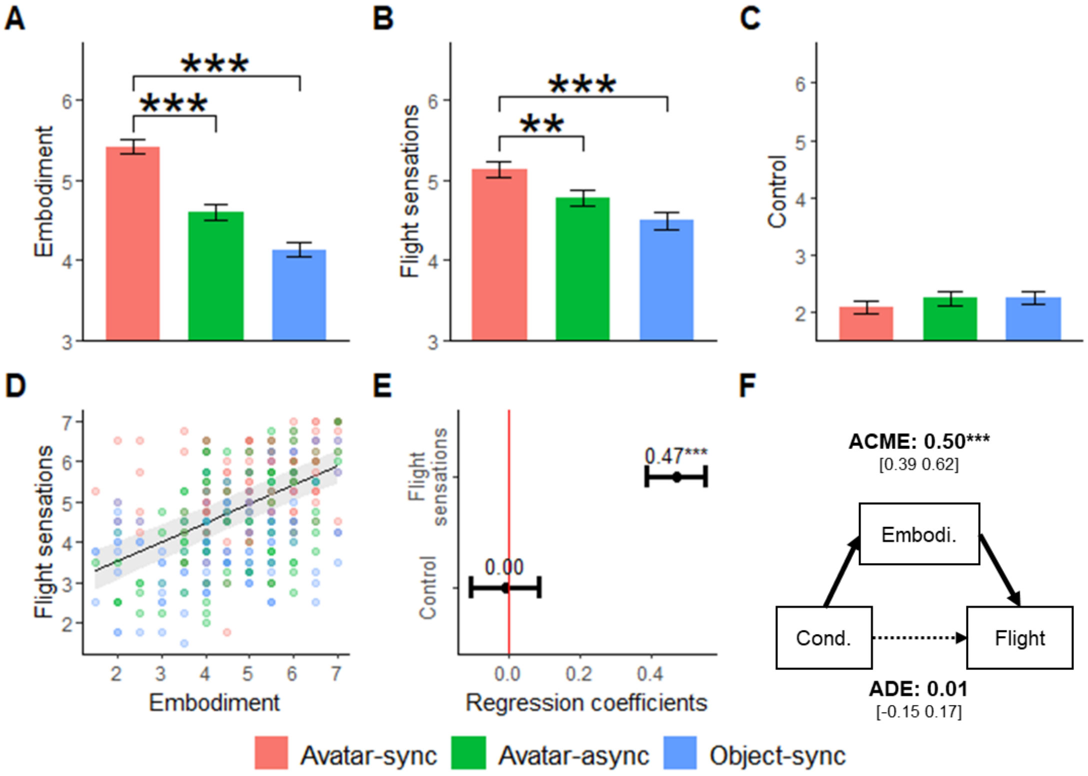

Fig. 2. Study 2: Embodiment and flight sensations. (Upper panel) Ratings about embodiment and flight sensations for each condition are shown. Data show that online sensorimotor stimulation boosts embodiment (**A**) and flight sensations (**B**) when applied synchronously (pink). **C**) Control items were not manipulated by the experimental conditions. Data in the two control conditions (green & light-blue) reveal that conflicting sensorimotor stimulation is not sufficient (Avatar-asynchronous condition; Avatar-async) to induce these effects and that attentional mechanism cannot account for these findings either (Object-synchronous condition; Object-sync). Error bars represent standard error of the mean. **D**) Correlations of embodiment with flight sensations. Correlation data from all subjects are shown; each data point indicates results from each session, from each participant and each condition. The X-axis and Y-axis represent embodiment ratings and flight sensations, respectively. Grey shadow represents 95% confidence intervals. **E**) The graph shows regression coefficients for flight sensations (top) and control question (bottom) with embodiment. Error bars show 95% confidence intervals. The regression coefficients indicate that embodiment has a significant and positive correlation with flight sensations, but not with the control question. **F**) The graph describes a causal relationship among sensorimotor stimulation, embodiment, and flight sensations as resulting from mediation analysis. A solid line represents a significant causal relationship and a dashed line corresponds to a non-significant causal relationship. ACME and ADE are shown. Mediation analysis shows that flight sensations were fully mediated by embodiment. 95% confidential intervals are shown in squared brackets. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

Sensorimotor congruency improves targeting of piloting performance. In Study 2, we next tested our main hypothesis about piloting performance, namely whether differences in online sensorimotor stimulation (associated with systematic changes in avatar embodiment and flight sensations; Fig.2) would impact piloting performance. Linear mixed model on targeting performance showed significant differences among the three conditions ($F(2,25.71) = 7.79$, $p < 0.01$). Planned comparisons showed that targeting performance in the avatar-synchronous condition was better than in both control conditions (avatar-synchronous (0.29 ± 0.01) vs. avatar-asynchronous (0.26 ± 0.01): $t(25.42) = -3.75$, $p < 0.001$; avatar-synchronous vs. object-synchronous (0.27 ± 0.01) – $t(25.74) = -2.07$, $p = 0.049$) (Fig. 3). Concerning the strength of the effects, targeting performance in the main experimental (avatar-synchronous) condition was on average 11.68% (6.70%) higher than in the avatar-asynchronous condition (object-synchronous condition). 18 (17) out of 24 participants showed better targeting performance as compared to both the avatar-asynchronous (object-synchronous) condition. Path stability of piloting performance did not differ between the three conditions ($F(2,27.93)=1.21$, $p = 0.31$).

The highest embodiment condition results in the fastest learning. Next, we also tested for learning effects throughout the experiment on *targeting* of piloting performance. Through linear mixed models with session as a fixed effect and random slopes, the learning effect of each condition was identified and learning rates of each participant for each condition were calculated. Significant learning effects were present for *targeting* in all conditions (Fig. 3B, avatar-synchronous: $F(1,24) = 60.26$, avatar-asynchronous: $F(1,30.05) = 44.54$, object-synchronous: $F(1,24) = 32.74$, all p-values < 0.001). Crucially, the avatar-synchronous condition had a higher learning rate as compared to both control conditions (Fig. 3C, avatar-synchronous vs. avatar-asynchronous: $t(50.09) = 3.25$, $p < 0.01$; avatar-synchronous vs. object-synchronous: $t(50.09) = 4.76$, $p < 0.001$). However, for path stability we did not observe any learning effect. (all p values > 0.05) (Fig. 3C, 3D, and 3E).

These data show that sensorimotor congruency between the participant's own bodily movements and the avatar's movements, as well as the presence of a bodily-shaped avatar, leads to better targeting performance, but did not improve path stability. The condition with the best piloting performance and the highest learning rate was the same condition where embodiment and flight sensations were rated the highest: the avatar-synchronous condition.

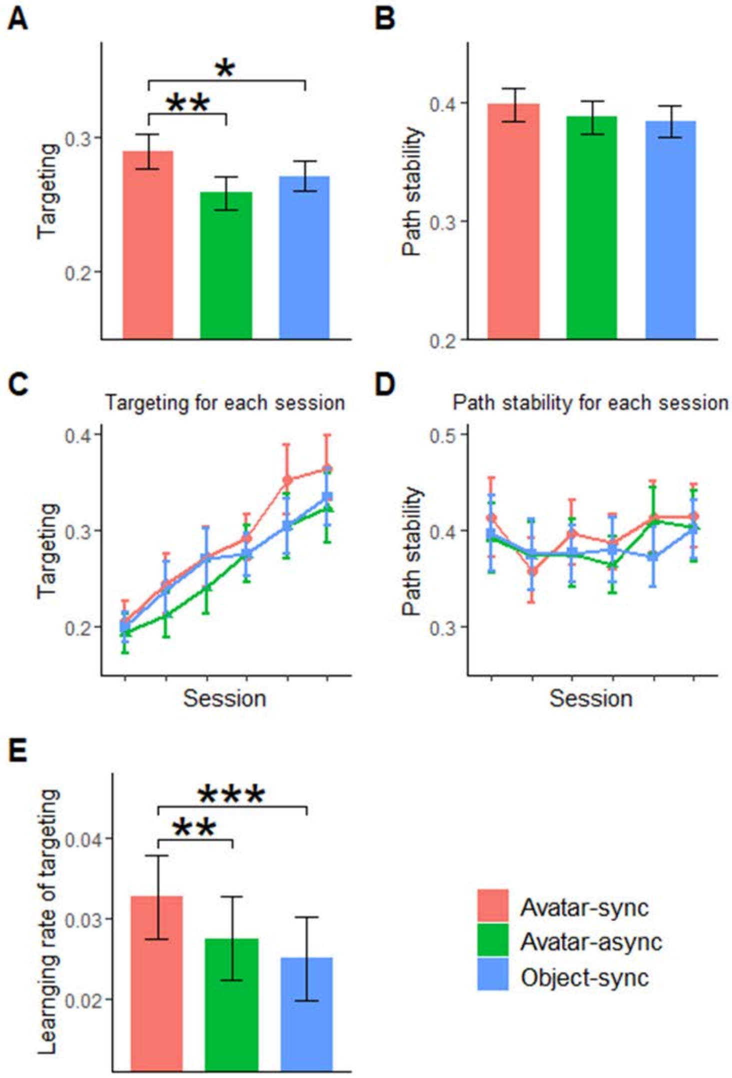

Fig. 3. Study 2: Piloting performance. Piloting performance for the different experimental conditions is shown. **A**) The avatar-synchronous condition (Avatar-sync) resulted in significantly better targeting performance than the two control conditions (avatar-asynchronous and object-synchronous; Avatar-sync and Object-sync). **B**) No difference was found for path stability. **C-D**) Linear mixed models with the session as a fixed effect revealed learning effect for all conditions throughout the experiment for the targeting performance (**C**), but not for path stability (**D**). **E**) Learning rates during the Avatar-synchronous condition were higher than those observed in the two control conditions. Error bar represents standard error of the mean, and *, **, and *** represent the significant difference between conditions with $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively.

Embodiment enhances the targeting of piloting performance. As the condition with the best piloting performance and the highest learning rate was the same condition where also embodiment and flight sensations were rated the highest: the avatar-synchronous condition, we next investigated possible connections between subjective (embodiment and flight sensations) and an objective measure (targeting). Linear mixed model analyses between each subjective measure and the objective measure revealed significant correlations of embodiment ($\beta = 0.01$, significantly different than zero; $F(1,423.21) = 6.39$, $p = 0.01$) and flight sensations ($\beta = 0.01$, significantly different than zero; $F(1,429.81) = 4.14$, $p = 0.04$) with targeting performance (Fig. 4). These relationships did not differ between the different conditions.

Through mediation analysis, we found that embodiment fully mediated the improvement of targeting performance (positive correlation; ACME = 0.009, $p = 0.03$ and ADE = 0.015, $p = 0.07$). That is, the observed increase in targeting performance can be fully caused by embodiment and not by the sensorimotor stimulation. Moreover, this analysis revealed that flight sensations did not mediate the targeting performance (positive correlation, but ACME = 0.003, $p = 0.06$ and ADE = 0.02, $p < 0.01$).

These correlations between embodiment and targeting performance were positive, showing that the stronger feelings of embodiment our participants had, the better they navigated through the virtual world hitting the target clouds, regardless of the experimental condition.

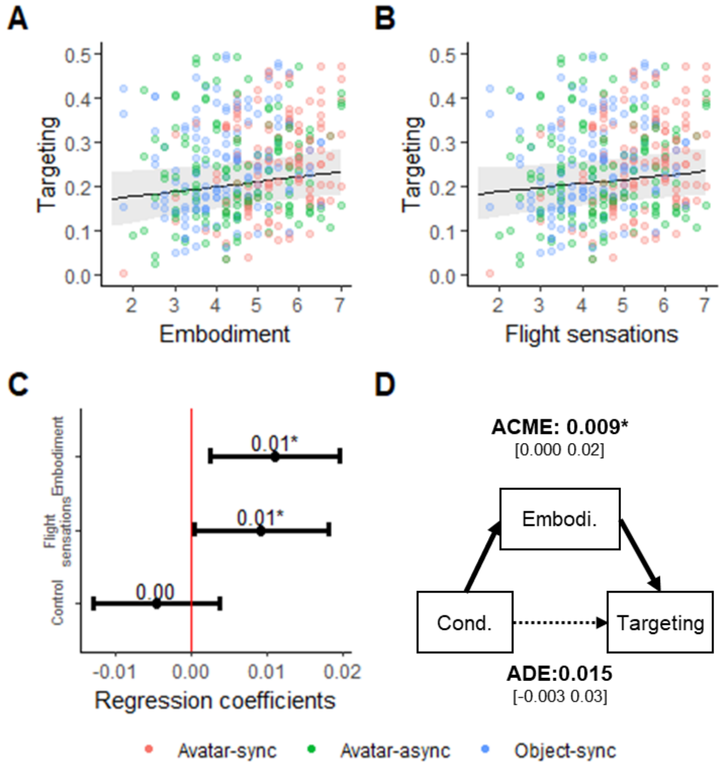

Fig. 4. Study 2: Embodiment and flight sensations correlate with targeting performance. **A & B**) Correlations of embodiment and flight sensations with targeting performance are shown; each data point indicates results from each session, from each participant. X-axis and Y-axis represent embodiment and normalized targeting performance, respectively. Grey shadow represents 95% confidence intervals. **C**) A graph shows regression coefficients for targeting performance with subjective experience. Regression coefficients were significantly different than zero for embodiment and flight sensations with targeting performance. the stronger sensation of embodiment and flight sensations is achieved, the better the targeting performance is induced. Error bars show 95% confidence intervals. **D & E**) The graph describes a causal relationship among sensorimotor stimulation, embodiment, and targeting performance as resulting from mediation analysis. A solid line represents a significant causal relationship. Meditation analysis showed that the targeting performance was fully mediated by embodiment (significant ACME) and not by the experimental condition (non-significant ADE). 95% confidential intervals are shown in squared brackets. *p < 0.01.

2.2.2 Study 3 – Multisensory embodiment improves flight sensations and piloting performance

As expected from Study 2, we observed positive relationships of embodiment with flight sensations and piloting performance. That is, the stronger sensations of embodiment (based on the sensorimotor stimulations that we provided online during simulated aviation), the better was flight sensations and piloting performance of our participants. Based on this finding, we hypothesized that by further increasing embodiment sensations we could further increase piloting performance. Previous studies have shown that stronger sensations of embodiments rely not only on sensorimotor congruencies but also on multisensory bodily stimulations (Serino and Haggard 2010, Blanke 2012). One line of work has developed powerful approaches to experimentally study BSC through the administration of visuo-tactile stimulation regarding the appearance and location of a body part, for example, a hand in the rubber hand illusion (RHI) (Botvinick and Cohen 1998), legs in the virtual leg illusion (VLI) (Pozeg, Galli et al. 2015) or the whole body in the full-body illusion paradigm (FBI) (Ehrsson 2007, Lenggenhager, Tadi et al. 2007). These paradigms are efficient at transiently inducing illusory tactile perception and sense of ownership for artificial body parts or the whole body, and have shown efficacy to restore bodily experience in amputation, and tetraplegia (Ehrsson, Rosén et al. 2008, Marasco, Kim et al. 2011, Lenggenhager, Scivoletto et al. 2013, Bolognini, Russo et al. 2015, Rognini, Petrini et al. 2018).

Based on these findings and the results from Study 2, in Study 3, we, therefore, sought to further increase flight sensations, piloting performance, and learning speed by modulating embodiment through multisensory stimulation (administered as visuo-tactile stimulation by adding a wearable haptic device, based on vibration technology) and tested 30 new participants (using the same task and 3D flight simulation environment as in Study 2 (Supplementary Text S1) but in three different conditions, including the again avatar-synchronous condition as used in Study 2 (now referred to as Baseline; this condition had strongest sensations of embodiment, flight sensations, piloting performance). In the two new conditions of Study 3, we manipulated the synchrony of additional multisensory feedback between a tactile cue applied to the body of our participants and a visual cue applied to the avatar that the participants saw as part of the flight simulation environment (visuo-tactile stimulation; Fig 5C & 5D). Thus, in the multisensory-synchronous condition visuo-tactile stimulation was provided in synchrony with the participants' bodily movements and thereby with the seen movements of the avatar. Thus, a leftward flying movement of the participant on the Birdly interface (Fig. 5C) was associated with tactile stimulation on the left side of the back that was also seen on the avatar in the flight simulation environment, as illumination on the left side of the avatar's back. Movements. All changes in the position of the Birdly were translated in this visuo-tactile stimulation in a congruent fashion. Conversely, in the multisensory-asynchronous condition, we artificially introduced a 5-second delay between the participant's movements and the visuo-tactile stimulation provided on the participant's and avatar's body. Importantly, in line with findings from Study 2, in all conditions, the participant's and avatar's movements within the 3R VR environment were always congruent (Fig. 5) (Movie S2). Visual cues (for visuo-tactile stimulation) were provided through virtual LEDs located on the avatar's back, whereas tactile cues (for visuo-tactile stimulation) were provided on the participant's back, through a custom-made wearable haptic device (Movie S2). Note that no delay was ever-present between LED and haptic stimuli of visuo-tactile stimulation (i.e. the 5-second delay was inserted between the movements of the participant and onset of visuo-tactile stimulation).

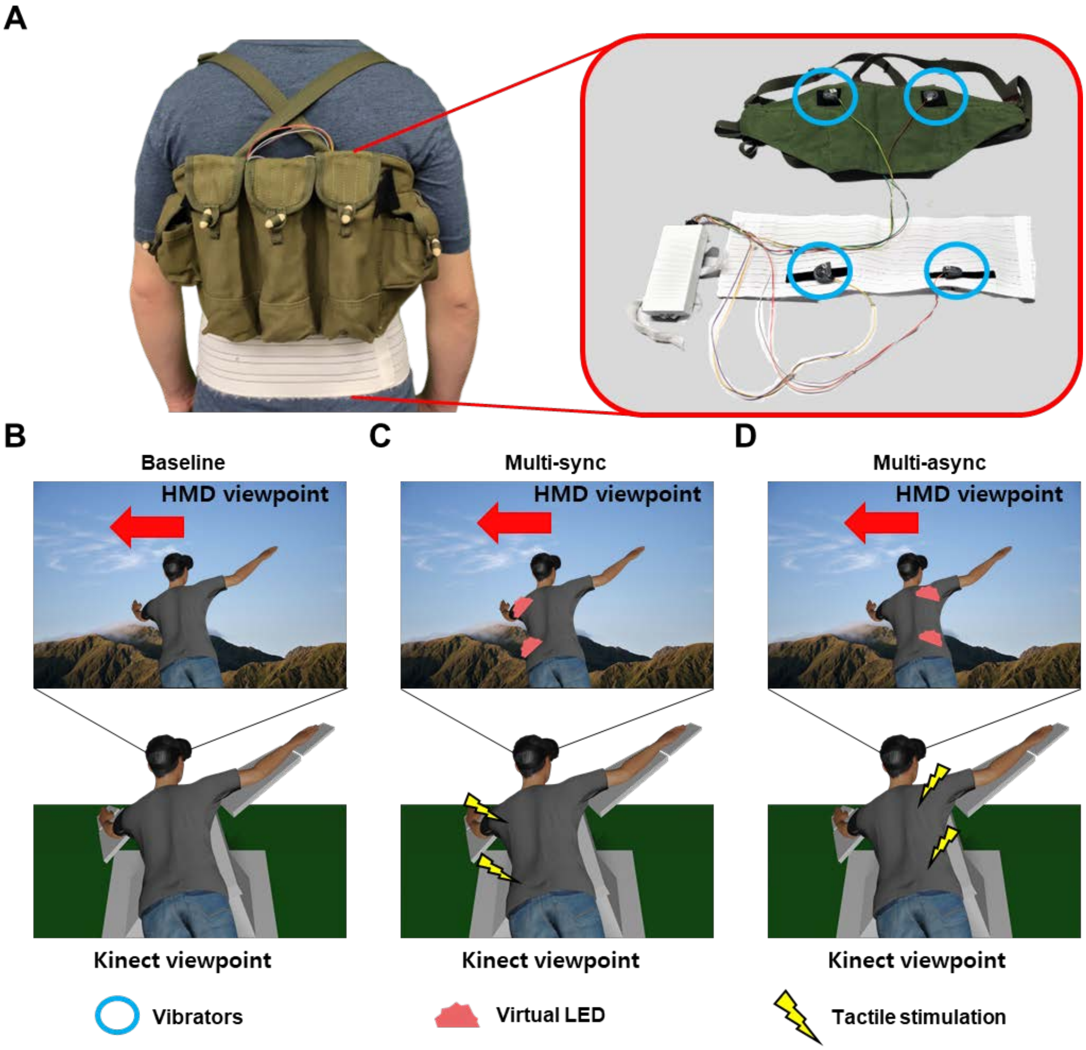

Fig. 5. Study 3: Experimental setup and procedure. A) In Study 3, we used the same robotic and VR platform described in Study 2, with the addition of a wearable haptic device to deliver multisensory stimulation to the participants. The haptic device was composed of 4 vibrators located on the participant's back (at the location indicated by the blue circles) and a micro-controller. Participants wore the haptic device with a small backpack and an elastic belt. To provide visuo-tactile stimulation during the task, visual cues (i.e. LED: Virtual LED, pink in the figure) were shown on the avatar's back in a position corresponding to the location of the vibrators on the participant's back (right and left upper back, right and left lower back). **B**) A baseline condition was the same avatar-synchronous condition used in Study 2 (no visuo-tactile stimulation. **C**) In the multisensory-synchronous condition (Multi-sync), vibration and LED cues were provided in synchrony with the participants' and avatar's bodily movements, whereas in the multisensory-asynchronous condition (Multi-async) (**D**) a 5-second delay was inserted between the participants' movements and the visuo-tactile stimulation.

Multisensory bodily stimulation induces a stronger sensation of embodiment of the flying avatar. Linear mixed models on subjective responses revealed a main effect of condition for embodiment sensations ($F(2,26.06) = 3.55$, $p = 0.04$) and, as predicted, showed that avatar embodiment was rated stronger in the multisensory-synchronous condition compared to both other control conditions (multisensory-synchronous (5.31 ± 0.07) vs. baseline (4.98 ± 0.08), $t(26.00) = -2.32$, $p = 0.03$); multisensory-synchronous vs. multisensory-asynchronous (5.06 ± 0.08) – $t(26.08) = -2.44$, $p = 0.02$) (Fig. 6A). Concerning the strength of the effects, the subjective sensation of embodiment of the virtual avatar in the main experimental condition (Multi-sync) was on average 6.6% (4.9%) higher than in the body synchronous (the multisensory-asynchronous) condition. 19 (18) out of 26 participants reported stronger embodiment in the main condition vs. the body synchronous (the multisensory-asynchronous) condition.

Embodiment mediates flight sensations. Like Study 2, embodiment positively correlated with flight sensations ($F(1,459.43) = 177.33$, $p < 0.001$; estimated regression coefficient (β) = 0.63, significantly different than zero; Fig. 6D), regardless of the conditions ($F(2, 443.08) = 0.60$, $p = 0.55$; no interaction between embodiment and conditions), whereas flight sensations were not modulated significantly ($F(2,25.97) = 1.11$, $p = 0.35$, Fig. 6B), as was control question ($F(2,47.07) = 0.62$, $p = 0.54$).

Replicating results of Study 2, meditation analysis showed that flight sensations were fully mediated by embodiment and not by the experimental manipulation (ACME = 0.18, $p < 0.001$ and ADE = 0.01, $p = 0.87$ (Fig. 6F).

These data show, as predicted, that additional visuo-tactile stimulation synchronized with movements of the participant further enhances embodiment (but not flight sensations) as compared to a condition where such stimulation was absent or a condition where such stimulation was not delivered synchronously with the participant's bodily movements.

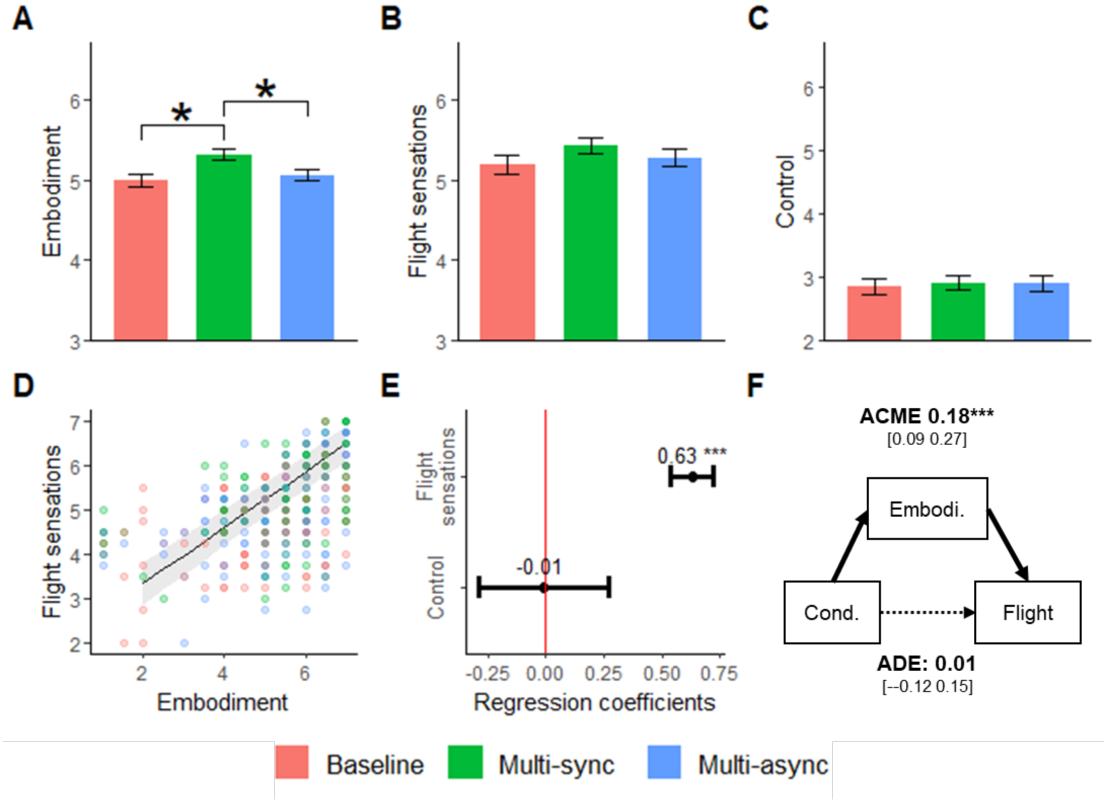

Fig. 6. Study 3: Embodiment, flight sensations, and the correlation between these. (Upper panel) Ratings about embodiment and flight sensations for each condition are shown (Baseline, pink in the figure, refers to the avatar-synchronous, no multisensory stimulation, as in Study 2). Results reveal that the subjective feeling of embodiment is significantly higher in the multisensory-synchronous condition (Multi-sync) as compared to the other two control conditions (Baseline & multisensory-asynchronous; Multi-async) (**A**). Flight sensations and a control question were not modulated by our experimental manipulation (**B-C**). Error bars represent standard error of the mean. **D**) Correlations between embodiment with flight sensations. Correlation data from all subjects are shown; each data point means a result from each session, from each participant (Right). X-axis and Y-axis correspond to flight sensations and embodiment ratings, respectively. Grey shadow represents 95% confidence intervals. **E**) The graph shows regression coefficients for flight sensations (top) and control question (bottom) with embodiment. Error bars indicate 95% confidence intervals. **F**) Meditation analysis showed that flight sensations were fully mediated by embodiment (significant ACME) and not by the experimental condition (non-significant ADE). 95% confidential intervals are shown in squared brackets. *: $p < 0.05$; ***: $p < 0.001$.

Multisensory stimulation improves piloting performance. Linear mixed models on piloting performance showed that both targeting of piloting performance ($F(2, 363.70) = 3.88$, $p = 0.02$) and path stability ($F(2, 359.94) = 3.17$, $p = 0.04$) were modulated by the experimental conditions. During the multisensory-synchronous condition participants were better in reaching the cloud targets (targeting, 0.32 ± 0.01) vs. the multisensory-asynchronous condition (0.30 ± 0.01; $t(363.80) = -2.56$ $p = 0.01$). No such difference was found between the multisensory-synchronous and the baseline condition (0.32 ± 0.01; $t(363.49) = -0.318$, $p = 0.75$) (Fig. 7A). Targeting performance was also better in the baseline condition vs. multisensory-asynchronous condition ($t(364.48) = -2.238$, $p = 0.03$), but no difference was found between the multisensory-synchronous and the baseline condition (0.32 ± 0.01; $t(363.49) = -0.318$, $p = 0.75$) (Fig. 7A). Targeting performance in the multisensory-synchronous condition was 6.67% higher than those observed in the multisensory-asynchronous condition, with 18 out of 26 participants achieving better performance in the former condition. Planned comparisons showed that path stability in the multisensory-synchronous condition (0.39 ± 0.01) was significantly better than that in the baseline condition (0.40 ± 0.01, $t(359.73) = 1.97$, $p = 0.049$; i.e. smaller values indicate better performance). No difference between the multisensory-synchronous and multisensory-asynchronous (0.38 ± 0.01) conditions was found ($t(360.04) = -0.37$, $p = 0.71$)). Path stability in the multisensory-synchronous condition was 2.48% higher than those observed in the baseline condition, with 15 out of 26 participants achieving better performance in the former condition. Next, we investigated a possible general effect of multisensory stimulation. To that aim, we averaged the two multisensory conditions into one condition and tested it against the body synchronous condition. We found better path stability in the combined multisensory condition than the body synchronous condition ($t(314.21)=-2.48$, $p = 0.01$; Fig. 7B).

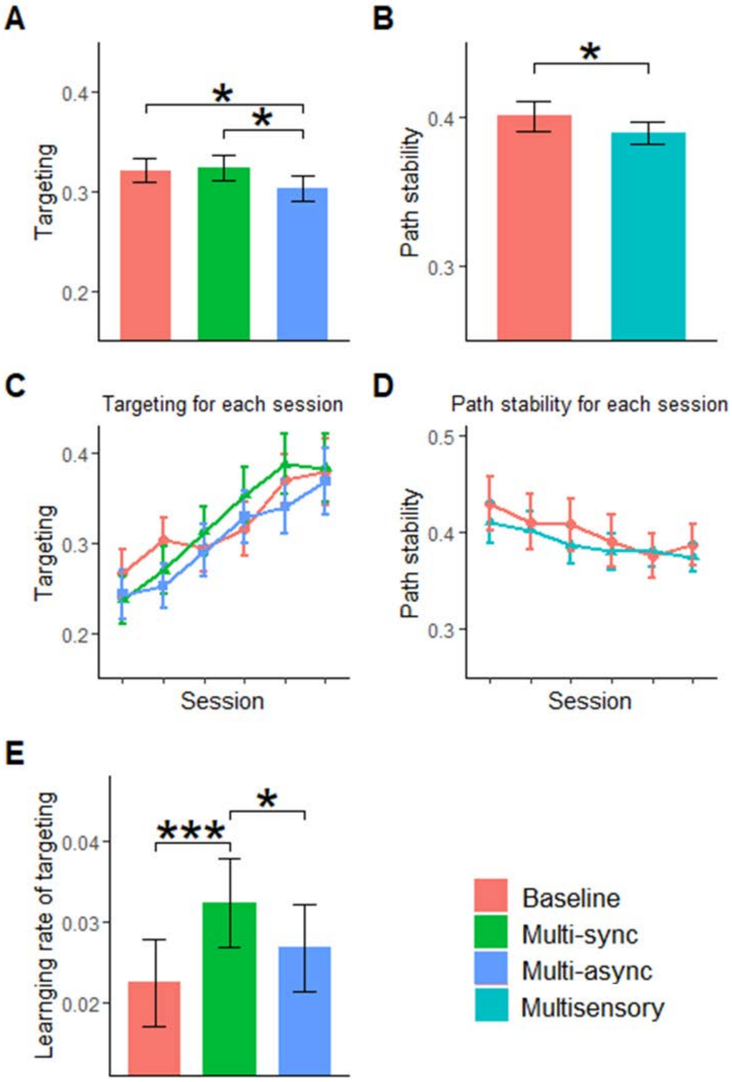

Fig. 7. Study 3: Piloting performance. Piloting performance for the different experimental conditions is shown. **A**) The multisensory-synchronous condition (Multi-sync) resulted in significantly better targeting performance than the multisensory-asynchronous condition (Multi-async), but not the baseline (avatar-synchronous condition of Study 2). **B**) The multisensory conditions resulted in significantly better path stability than the avatar-synchronous condition. Smaller values indicate better performance. **C**) Similar to Study 2, results revealed positive learning rates in all conditions for the targeting performance. **D**) Learning rates significantly different than zero were also observed for path stability for both the baseline and the multisensory (average of Multi-sync and Multi-Async) condition. **E**) The multisensory-synchronous condition resulted in the largest learning rate in comparison with other control conditions. That is, the main experimental condition induced the fastest learning for targeting performance. Error bar represents standard error of the mean. *p < 0.05.

Multisensory-synchronous condition leads to the fastest learning rate. Concerning targeting performance, we found positive learning effects for all conditions (baseline: $F(1,26) = 25.94$; multisensory-synchronous: $F(1,26) = 35.90$; multi-sensory-asynchronous: $F(1,54.85) = 48.82$; all p-values < 0.001; Fig. 7C). Moreover, the condition that showed the strongest sensation of embodiment (multisensory-synchronous condition) had a higher learning rate compared to both control conditions ($F(2,52) = 8.51$, $p < 0.001$; Multi-sync vs. Baseline: $t(54.08) = 4.03$, $p < 0.001$; Multi-sync vs. Multi-async: $t(54.08) = 2.28$, $p = 0.03$; Fig. 7E).

However, in terms of path stability performance, both the avatar-synchronous condition (baseline) and the combined-multisensory condition (averaged multisensory-synchronous and asynchronous conditions) showed learning effects significantly higher than zero (baseline: $F(1,26) = 6.57$, $p = 0.02$; combined-multisensory: $F(1,26.04) = 6.71$, $p = 0.02$; Fig. 7D). The learning rate between the combined-multisensory condition and the baseline condition did not differ ($F(1,26) = 3.27$, $p = 0.08$).

Globally, results from Study 3 show that although there was no difference in targeting between the multisensory-synchronous condition and baseline, the multisensory-synchronous condition showed the fastest learning as compared to the other control conditions. In conclusion, considering piloting performance results from both Study 2 and Study 3, the multisensory-synchronous condition resulted in the best flight performance as compared to all other conditions.

Flight sensations correlate with targeting performance. Unlike Study 2, we find no correlation between embodiment and targeting performance ($\beta = 0.00$; $F(1,454.32) = 1.72$, $p = 0.19$), but a significant correlation between flight sensations and targeting performance ($\beta = 0.02$; $F(1,462.08) = 13.02$, $p < 0.001$,Fig. 8), regardless of the experimental manipulation (no interaction between flight sensations and conditions; $F(2,441.96) = 1.20$, $p = 0.30$). There was no correlation between targeting performance and control items ($F(1,458.75) = 1.77$, $p = 0.18$).

Next, we performed meditation analysis to further investigate the relationship between embodiment and targeting performance. We found that flight sensation fully mediated the improvement of targeting performance (ACME = 0.003, $p < 0.01$ and ADE = 0.00, $p = 0.24$). That is, the observed increase in targeting performance can be fully attributed to flight sensations and not to the different experimental conditions.

These results show that the stronger flight sensations the better targeting performance, regardless of the experimental condition.

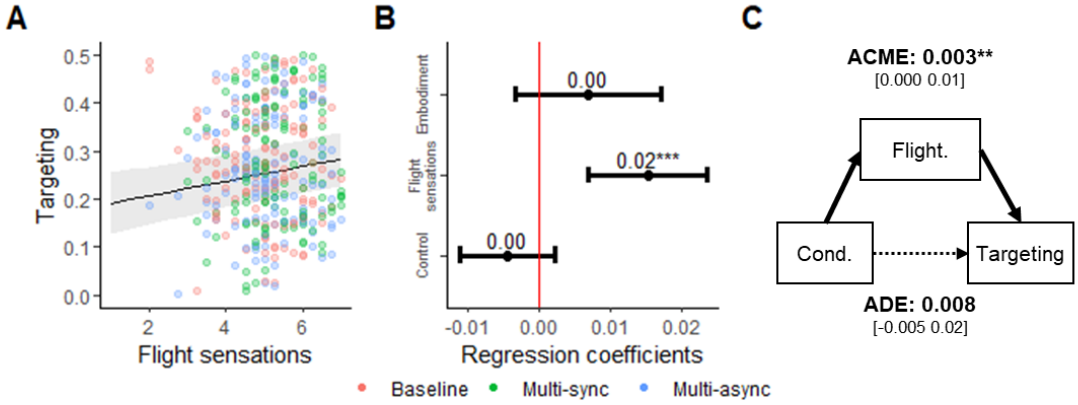

Fig. 8. Study 3: Flight sensations correlate with targeting performance. A) Correlation between flight sensations and targeting performance is shown. Each data point indicates results from each session, from each participant. X-axis and Y-axis represent flight sensations ratings and normalized targeting performance, respectively. Grey shadow represents 95% confidence intervals. **B**) A regression coefficient was significantly different than zero only for flight sensations and targeting performance. That is, the stronger the flight sensations are felt, the better the targeting performance is achieved. Error bars show 95% confidence intervals. **C**) Meditation analysis showed that the effect on targeting performance was fully mediated by flight sensations (significant ACME) and not by the experimental condition (non-significant ADE). 95% confidential intervals are shown in squared brackets. **: $p < 0.01$; ***: $p < 0.001$.

Discussion

We have added a photorealistic avatar and a haptic vest to a robotic flight simulator to enable and investigate personalized immersive flight experiences in healthy humans. Previous studies in the field of human-machine interactions have focused on the development of interfaces to facilitate control over a flying avatar in VR or a drone (van Delden, Moreno et al. 2013, Eidenberger and Mossel 2015, Sikström, De Götzen et al. 2015, Cherpillod, Mintchev et al. 2017, Miehlbradt, Cherpillod et al. 2018, Rognon, Mintchev et al. 2018, Yoon, Lee et al. 2018, Rognon, Koehler et al. 2019). These studies have compared the use of natural body movements to map movements of a flying avatar or a drone with the participant's bodily movements and used immersive technologies (robotics, immersive sound, and wind feedback) to create multisensory (visual, vestibular, tactile, auditory) scenarios and increase the realism of the simulated flight experience (5-11). Here, we have built and used a new immersive platform to investigate the underlying multisensory and sensorimotor mechanisms supporting simulated flying experiences, and the link between avatar's embodiment, flying sensations and piloting performance.

Embodiment. In Study 2, we have shown that the sensation of embodiment of the virtual avatar depends on mechanisms of sensorimotor integration. Thus, sensorimotor congruency between the participant's own bodily movements and the avatar's movements leads to stronger sensations of embodiment, as assessed through dedicated questionnaires. These sensations were found sensitive to temporal visuomotor mismatch and the shape of the avatar. The two control conditions were used to rule out that sensorimotor stimulation, and related attentional processes, per se, could be the cause of improvement in embodiment. Thus, the avatar-asynchronous condition controlled for the importance of the matching of sensorimotor information, whereas the object synchronous condition controlled for a possible role of attention. These results confirm previous findings in healthy participants showing that sensorimotor congruency induces sensations of embodiment, including ownership and agency, over virtual bodies in different postures, and extend them to the case of simulated flight experiences (Daprati, Franck et al. 1997, Farrer, Franck et al. 2003, Knoblich and Kircher 2004, Jeannerod 2006, Serino and Haggard 2010, Blanke 2012, Blanke, Slater et al. 2015). The strength of the feelings of embodiment, as assessed through the explicit questionnaire, were similar to other well-known bodily illusions (Botvinick and Cohen 1998, Ehrsson, Spence et al. 2004, Ehrsson, Holmes et al. 2005, Tsakiris and Haggard 2005, Ehrsson 2007, Lenggenhager, Tadi et al. 2007, Barnsley, McAuley et al. 2011, Ionta, Heydrich et al. 2011, Petkova, Björnsdotter et al. 2011, Banakou and Slater 2014).

In Study 3, we devised a method to provide multisensory stimulation during the use of our flight simulator, by integrating a wearable haptic device into the flight simulator. Questionnaire data from Study 3 show that multisensory bodily stimulation induces the stronger sensation of embodiment as compared to a condition where such stimulation was absent, such as the sensorimotor congruent condition of Study 2, or a condition where such stimulation was not delivered synchronously with the participant's bodily movements. These results are in line with previous research using multisensory stimulation to manipulate BSC for different body parts (Botvinick and Cohen 1998, Pozeg, Galli et al. 2015) or the whole body (Ehrsson 2007, Lenggenhager, Tadi et al. 2007). Evolutions of these paradigms are efficient at transiently inducing illusory tactile perception and sense of ownership for artificial body parts or the whole body, and have shown efficacy to restore bodily experience in amputation, and tetraplegia (Ehrsson, Rosén et al. 2008, Marasco, Kim et al. 2011, Lenggenhager, Scivoletto et al. 2013, Bolognini, Russo et al. 2015, Rognini, Petrini et al. 2018). Our study extends these findings to the case of embodying a flying avatar. In line with recent studies in the field, our findings also show that the multisensory stimulation necessary to induce changes in embodiment does not need to be linked to realistic or functionally relevant interactions (e.g. the passive touch on the avatar's body by a virtual object) as long as it respects the fundamental constraints of embodiment and multisensory integration (Blanke, Slater et al. 2015, Collins, Guterstam et al. 2017, Rognini, Petrini et al. 2018).

Flight sensations. Flight sensations in Study 2 were characterized by a similar pattern that we observed for embodiment. Thus, sensorimotor congruency between the participant's own bodily movements and the avatar's movements leads to stronger flight sensations, as assessed through dedicated questionnaires. As for embodiment, these sensations were found sensitive to temporal visuomotor mismatch and the shape of the avatar (object-like control shape).

Our sensorimotor flight task involved continuous full-body movements in a lying position and, our experimental conditions manipulated the congruency between visual and motor-vestibular information. Thus, the observed difference in flight sensations in the synchronous vs asynchronous sensorimotor condition highlights the importance of visuo-motor-vestibular integration for flight sensations. This is in line with previous findings where alterations of BSC caused by neurological disease were found to be associated with illusory vestibular sensations, including illusory self-motion and illusory changes in self-location (i.e. out-of-body experiences and heautoscopy (Blanke and Mohr 2005, Heydrich and Blanke 2013)). Similarly, patients with impaired or absent vestibular sensitivity are more inclined than healthy individuals to spontaneous (Lopez and Elziere 2018) and experimentally induced out-of-body experiences (Kaliuzhna, Vibert et al. 2015). Additional evidence for the contribution of vestibular information in BSC comes from recent experiments showing that low-intensity electrical stimulation of the vestibular system can alter perceived ownership of body parts in neurological patients (André, Martinet et al. 2001), and induce illusory body ownership or abnormal embodiment in healthy participants (Lopez and Blanke 2007, Lopez, Lenggenhager et al. 2010). Finally, a recent study in healthy subjects showed that full bodily illusions such as the FBI (Lenggenhager, Tadi et al. 2007) are associated with higher vestibular sensitivity (Zacharias and Young 1981). Globally, these studies indicate an important contribution of vestibular cues in "anchoring" the self to the body, and that such link can be "weakened" (i.e. the relative contribution of vestibular cues can be reduced) using controlled manipulations of visuo-vestibular cues. We propose that the flight sensations observed in our study might stem from similar mechanisms of visuo-vestibular integration. More specifically, results observed during the congruent sensorimotor condition are compatible with a higher weighting of visual over vestibular cues in such condition, leading to a weakening of the link between the self and body that resulted in stronger flight sensations (and embodiment of the avatar). This account is also in line with the absence of any experimental modulation of flight sensations observed in Study 3, where visuo-vestibular congruency in was not manipulated.

Stronger embodiment leads to stronger flight sensations. Although previous studies investigated embodiment and flight sensations during flight simulated tasks (Amato, Perény et al. 2019, Zhang, Riecke et al. 2019), they were not able to show between the two subjective experiences. Meditation analysis performed in both Studies 2 and 3 shows that stronger sensations of embodiment induced stronger flight sensations. This positive correlation was valid across all conditions and put the link between embodiment and flight sensations, anecdotally reported during OBEs, on the solid experimental ground (Blanke and Mohr 2005).

Artificial flight experiences and out-of-body experiences. OBEs are defined as a pathological mental state in which self-location and the origin of the first-person perspective are never at the position of the physical body and are associated with a sense of disembodiment (the experience that the subject of conscious experience is localized outside the person's bodily borders) (Blanke, Landis et al. 2004). Recent neuroanatomical analysis in neurological patients indicated that OBE is caused by damage to the temporo-parietal cortex of the left and right hemisphere, respectively (Blanke and Mohr 2005, Heydrich and Blanke 2013). Based on OBE research, global aspects of bodily self-consciousness, notably global ownership (or self-identification with a whole-body) and self-location, have been experimentally manipulated through the combined use of VR and multisensory conflict situations (Ehrsson 2007, Lenggenhager, Tadi et al. 2007). These studies show that self-identification (body-ownership) and self-location (i.e. where I am in space) for one's own entire body rely on visual-somatosensory integrative mechanisms, in line with previous neurological studies in patients reporting out-of-body experiences (Devinsky, Feldmann et al. 1989, Brugger, Regard et al. 1997, Blanke, Ortigue et al. 2002, Blanke, Landis et al. 2004, Blanke, Arzy et al. 2008, Heydrich and Blanke 2013). Recently, researches have also started to study the neural mechanisms underpinning these global aspects of bodily self-consciousness in fMRI environments. For instance, recent investigations have reported self-identification with a virtual body to be associated with activity in the bilateral ventral premotor cortex, left intra parietal sulcus and left putamen (Petkova, Björnsdotter et al. 2011), whereas in another study, self-identification with a virtual body was associated with activation in the right middle-inferior temporal cortex (Ionta, Heydrich et al. 2011), and self-localization was associated with bilateral activation of the temporal-parietal junction (Ionta, Heydrich et al. 2011). We argue that the present sensorimotor and multisensory manipulations inducing sensations sharing similarities with those reported during out-of-body experiences are most likely based on interference with bodily representations in temporo-parietal cortex that have been described in neurological patients and healthy subjects during full body illusions and that could meditate the present embodiment and flight sensations effects.

Targeting of piloting performance. Previous studies on flight simulators or drone piloting used targeting of piloting performance (such as accuracy and precision while approaching the target) as a metric to evaluate new piloting interfaces (Meyer, Wong et al. 2012, Miehlbradt, Cherpillod et al. 2018, Rognon, Mintchev et al. 2018, Yoon, Lee et al. 2018, Rognon, Koehler et al. 2019). They showed that full-body human-machine interfaces can achieve better pilot targeting performance and shorter learning time as compared to traditional interfaces such a joystick (Miehlbradt, Cherpillod et al. 2018, Rognon, Mintchev et al. 2018, Yoon, Lee et al. 2018). Other studies focused on the realism of the simulated flight experience, by adding haptic or auditory feedback in addition to visual feedback (Meyer, Wong et al. 2012, Rognon, Koehler et al. 2019). These approaches were not able to improve targeting performance, but they significantly increased the realism of the flight experience(Rognon, Koehler et al. 2019) or could induce transferrable performance improvement from training (Meyer, Wong et al. 2012).

In Study 2, we found that targeting of piloting performance was modulated by the type of sensorimotor stimulation conditions. Thus, sensorimotor congruency between the participant's own bodily movements and the avatar's movements leads to better targeting of piloting performance. Similar to embodiment and flight sensations, the improvement in the targeting of piloting performance was found sensitive to temporal visuomotor mismatch and the shape of the avatar. Interestingly, we observed the same experimental modulation for the targeting performance learning rate. Thus, participants improved their targeting performance at a faster rate during the avatar-synchronous rather than the other two control conditions. These results show that targeting piloting performance, as well as learning, depends on the body-specific mechanism of sensorimotor integration that is similar to those underlying both embodiment and flight sensations.

The multisensory-synchronous stimulation administered in Study 3, and associated with stronger sensations of embodiment, was not able to improve targeting performance. Yet, it did improve learning rates as compared with the other control conditions. Importantly, this improvement was for the main condition of Study 2, the avatar synchronous condition where sensorimotor information was administered in a congruent way. This is in line with (Meyer, Wong et al. 2012), where multisensory stimulation did not improve targeting performance but did improve learning rates.

Stronger embodiment or flight sensations lead to better targeting performance. To the best of our knowledge, no previous study has investigated the link between embodiment, flight sensations and piloting performance. Correlation analysis in Study 2 showed that both embodiment and flight sensations were positively correlated with targeting performance. Meditation analysis in Study 2 showed that the improvement in targeting performance was fully mediated by stronger sensations of embodiment; while mediation analysis in Study 3 showed that the improvement in targeting performance was fully mediated by stronger flight sensations. These results show that pilot targeting performance depends on the body-specific mechanism of sensorimotor integration that is similar to those underlying both embodiment and flight sensations. Although we did not find a direct correlation between embodiment and targeting performance in Study 3, we found a positive correlation between targeting performance and flight sensations, which in turn were positively correlated with and fully mediated by feelings of embodiment.

In Study 3, we also observed that the multisensory-asynchronous stimulation was associated with worse targeting performance as compared to multisensory-synchronous stimulation or no multisensory stimulation (i.e. avatar-synchronous condition used in Study 2). These data suggest the presence of a threshold at which a stronger feeling of embodiment does not translate into better targeting performance. Yet, in the weaker feeling of embodiment were associated with reduced targeting performance as shown by the difference in performance in the multisensory-synchronous and the multisensory-asynchronous stimulation condition, confirming an association between embodiment and targeting performance.

Globally, our data show that targeting of piloting performance not only depends on the similar mechanism of sensorimotor and multisensory integration such as embodiment and flight sensations but crucially, they directly depend on the degree of subjective immersion into the flight simulation scenario, with stronger immersion (embodiment and flight sensations) inducing better targeting of piloting performance.

Multisensory stimulation enhances path stability of piloting performance. In Study 2, we observed no modulation of path stability (i.e. how smooth the trajectory followed during the task was), suggesting that this is not depending on the body-specific mechanism of sensorimotor integration, differently than embodiment, flight sensations, and targeting of piloting performance.

In Study 3, we also observed the experimental modulation of path stability performance as well as learning rates of path stability performance. More specifically, multisensory stimulation per se increases stability performance. In other words, an average of the multisensory stimulation conditions leads to better stability as compared to the body synchronous condition, where no multisensory stimulation was provided. The same pattern was found for learning rates of stability of piloting performance.

Postural control is complex and involves the integration of visual, vestibular and somatosensory signals that provide information about spatial positioning, acceleration and mechanical forces acting on the body during standing balance (Simoneau, Ulbrecht et al. 1995, Blackburn, Guskiewicz et al. 2000, Sarabon, Rosker et al. 2013). When these sensory channels are altered, due to aging or a variety of medical conditions, the result is an abnormal postural control (Du Pasquier, Blanc et al. 2003, Hijmans, Geertzen et al. 2007). Studies administering either cutaneous stimulation or compression on participants' lower limbs including foot, ankle, and legs, have reported a positive effect on postural control (Simoneau, Ulbrecht et al. 1995, Simoneau, Degner et al. 1997, You, Granata et al. 2004, Menz, Lord et al. 2006, Hijmans, Geertzen et al. 2007, Sarabon, Rosker et al. 2013). It has been argued that these effects are due to enhance somatosensory awareness caused by the stimulation of the mechanoreceptors in the skin, facilitating feedback for correction of directional change (Simoneau, Ulbrecht et al. 1995, Simoneau, Degner et al. 1997, You, Granata et al. 2004, Menz, Lord et al. 2006, Hijmans, Geertzen et al. 2007, Sarabon, Rosker et al. 2013). Yet, the precise physiological mechanisms underlying these effects are still unknown. Our data extend these studies on tactile stimulation and postural balance while standing, to the case of simulated flight experiences, where participants were lying on the

Birdly interface. Our results are compatible with the hypothesis that tactile stimulation may have increased participants' sensitivity to the somatosensory inputs used in postural control, facilitating path stability.

Overall, considering both questionnaire and piloting performance results from both Study 2 and Study 3, the multisensory-synchronous condition resulted in the best flight experience and piloting performance as compared to all other conditions. Indeed, in such condition we observed A) stronger sensation of embodiment as compared to all other conditions (including the avatar-synchronous condition of Study 2, which was called baseline in Study 3); B) the same level of flight sensations of the avatar-synchronous (baseline) condition of Study 2 (2); C) the same targeting performance, but better path stability performance, as compared to the avatar-synchronous condition – where participants achieved the best targeting performance in Study 2; D) higher learning rate of targeting performance as compared to all other conditions.

Embodiment, motor performance and implications for VR research. In both Study 2 and Study 3, we observed a positive correlation between embodiment and flight sensations, and between the two sensations and targeting performance. Despite ownership and agency for one's own body and actions always occur under dynamic conditions, only a few studies have investigated them using interactive paradigms (Sengül, Rognini et al. 2013, Pozeg, Galli et al. 2015). Moreover, only a few studies showed that an enhanced feeling of embodiment is linked to better motor performances (Wen, Yamashita et al. 2015, Shibuya, Unenaka et al. 2018). However, these previous works provide only indirect, correlational, evidence as the performed experimental conditions do not selectively manipulate movement trajectories and bodily experience (task-dependent body manipulation). Besides, these studies focus on body parts instead of full-body embodiment (Wen, Yamashita et al. 2015, Shibuya, Unenaka et al. 2018). Our results, observed in two independent groups of participants across different experimental conditions, extend previous work in the field and provide a first direct link between subjective experiences (i.e. embodiment and flight sensations) with motor performance. This link is crucial for the translation of embodiment research into VR applications, as VR is an interactive dynamic environment with the potential to tailor experiences and tasks to each user to boost engagement, or speed up learning and recovery (Bohil, Alicea et al. 2011). Yet, most VR technological efforts to date focus on realism, whereas knowledge and methods to personalize experience and training in VR are still in their infancy. Our results suggest that the reported manipulation of embodiment can be used as a method to induce an improvement in motor performance.

Current development in VR already focuses on minimizing sensorimotor latencies, implicitly respecting the sensorimotor constraints on embodiment and flight sensations highlighted in Study 2 (Elbamby, Perfecto et al. 2018). Yet, task-independent multisensory bodily stimulation is not currently used to increase embodiment during VR interactions. We suggest that, in addition to the minimization of sensorimotor latencies, the immersive VR system should integrate the form of continuous multisensory stimulation to optimize embodiment as well as motor performance in VR scenarios.

Conclusion

To conclude, previous work on the engineering of the experience of flying has focused on different human-machine interfaces to facilitate control over a flying avatar in VR or a drone (Miehlbradt, Cherpillod et al. 2018, Rognon, Mintchev et al. 2018, Yoon, Lee et al. 2018). These studies tried to improve flight sensations and piloting performance by developing intuitive and performing human-machine interfaces. The present approach focuses on complementary aspects of embodiment for a flying avatar as manipulated via automatized sensorimotor and multisensory stimulations and reveals how protocols combining robotic flight simulators, photorealistic immersive VR, and wearable haptics could induce and boost embodiment, flight sensations and improve piloting performance. Finally, we argue that our results will have broad implications for the study of embodiment and motor performance in VR, especially in the important fields of motor skill training, and motor rehabilitation (Gallagher, Ritter et al. 2005, Holden 2005, Reznick and MacRae 2006, Laver, Lange et al. 2017). Increasing embodiment (immersion) and motor performance in VR environments by manipulating bodily experience would represent a promising solution to personalize and improve VR experiences in a task-independent, and potentially highly generalizable, fashion, as the experience of our body pertains to any activity we perform.

Materials and Methods

Study 2.

Participants. Twenty-five healthy participants (age = 27.25 ± 2.92 years, twelve females) with no record of neurological or psychiatric illness took part in the experiment. The study was approved by EPFL HUMAN RESEARCH ETHICS COMMITTEE. Participants gave their written informed consent and received 30 CHF for compensation after having participated.

Apparatus. The experimental setup, depicted in Fig. 1A included Birdly®, an immersive and interactive flight simulator (Somniacs^{SA}, Zurich, Switzerland http://www.somniacs.co/), and an HMD (HTC Vive, dual AMOLED display 3.5" diagonal, 1080 × 1200 pixels per eye, 90 Hz refresh rate, 110-degree field of view, https://www.vive.com). Participants lied on the Birdly system and controlled the flight simulation using hand gestures (to move up and down in the virtual environment) and arm movements (to move left and right). The setup provided participants with visual and motion (pitch, roll, and heave) feedback, and was further equipped with a fan in front of the participants to provide air cues proportional to the simulated flight velocity. A Kinect V2 (Microsft, USA) was installed behind the participants' back at approximately 2 m. The camera stream was combined with the visual scene in order to provide participants with a third-person point of view of a photorealistic avatar of themselves (Fig.1B & 1C, https://developer.microsoft.com/ko-kr/windows/kinect/develop). The inherent latency of Kinect V2 is < 60 milliseconds (ms) (Amon, Fuhrmann et al. 2014). The virtual environment was implemented in Unity 5.4 (https://unity3d.com/) and presented to the participants through HMD, which further allowed the head motion and position tracking (SteamVR tracking, G-sensor, gyroscope, and proximity sensor).

Stimulus. Participants were instructed to fly a virtual object (either their avatar or a box), from the third-person viewpoint. Their task consisted in passing through the center of round-shaped clouds (Fig. 1B & 1C). These clouds had a diameter of 5.73 arbitrary units (au; 0.79 au corresponded approximately to the participants' shoulders width) with a variation of 0.1 au and the trajectory of the clouds was randomly created for every session. The creation of the trajectory included 5 types of direction change (up, down, left, right, or no change). Each type of direction change was repeated 5 times and the order was randomized. The distance between clouds depended on the direction change: 1) baseline – 9.5 au (forward distance 9.5 au, vertical distance: 0 au, lateral distance: 0 au); 2) up & down – 24.7 au (forward distance: 10 au, vertical distance: 3.75 au, lateral distance: 0 au); and 3) left & right – 9.9 au (forward distance: 7.5 au, vertical distance: 0 au, lateral distance: 6.4 au). The virtual world was constructed based on the top view of the École Polytechnique Fédérale de Lausanne campus (Route Cantonale, 1015 Lausanne, Vaud, Switzerland). Participants were presented with a back view of the virtual avatar that consisted of the upper part of the body, including the buttocks. The width, height, and length of the avatar and the virtual box were 0.79 au., 0.12 au, and 2.15 au respectively. Participants' viewpoint was located at 2.32 au behind their virtual avatar and elevated by an angle of 21.4°. Participants were requested to fixate the virtual body or box center during the experiment but could make free head movements, and thereby could have different views of the virtual scene. Flight speed was fixed at 12 au/s for the entire flight simulation, and participants could only control the direction of the virtual body or box.

Procedure. Participants were required to complete the task (i.e. flying through the center of the spherical clouds) in three different conditions. In the first condition, participants controlled their virtual avatar and received synchronous visuomotor feedback (i.e. the delay between participants' movements and the movements of the avatar was approximately 60 ms (Amon, Fuhrmann et al. 2014); avatar-synchronous condition); in the second condition, a 5-second delay was introduced between the motion of the physical body and that of the virtual avatar (avatar-asynchronous condition); in the third condition, participants controlled, with approximately no delay (i.e. 60 ms), a virtual box instead of their avatar (object-synchronous condition, Fig. 1C). Importantly, in the avatar-asynchronous condition the delay only influenced the virtual avatar's motion and posture, but not its trajectory, which was updated in real-time (i.e. if a participant turns right, the avatar turns right without delay, but the arm motion of the participant is performed by the avatar only after 5 seconds (see Supplementary Video 1). The purpose of this condition was to selectively manipulate the bodily experience related to the seen avatar, without experimentally manipulating the performance of the steering task. Before starting the experiment, the participants practiced the avatar-synchronous condition for approximately 5 min. In one session, each condition lasted 90 seconds and was repeated two times. There were three sessions and resulted in a total of eighteen sessions per participant. The order of the conditions was randomized. The total experiment lasted on average one and a half hours per participant.

Subjective experiences concerning embodiment and flight sensations were measured using a questionnaire comprising eight items (Table S1, adapted from (Kalckert and Ehrsson 2012, Aspell, Heydrich et al. 2013, Noel, Pfeiffer et al. 2015)). Both Q1 and Q2 were used to gauge the sense of agency. Specifically, Q1 was designed to assess the sense of agency over the control of the trajectory of the virtual object, whereas Q2 was designed to quantify the sense of agency for the motion of the virtual object. The remaining questions measured self-identification over the virtual object (Q3), self-location in the virtual avatar position (Q4), floating sensations (Q5), and flying sensations (Q6). Finally, we included Q7 to control for suggestibility.

Participants were asked to rate each question items by using a Likert scale ranging from 1 to 7 (1: strongly disagree, 7: strongly agree). The order of the questions was randomized and sequentially appeared on the HMD after each session. Answers were provided by the participants using two buttons, installed on the wings of the Birdly. After answering the questionnaire, participants were allowed to rest for about 15 seconds on the Birdly. After completion of each session, they could take a longer break of 10 minutes and exit the Birdly.

Study 3.

Participants. Thirty-one participants (age = 25.5 ± 4.4 years, nine females) took part in the experiment. They didn't participate in the first experiment and reported no record of neurological or psychiatric illness. EPFL HUMAN RESEARCH ETHICS COMMITTEE approved this experiment. Participants submitted their written informed consent and we gave them 30 CHF for compensation after having participated.

Apparatus. We used the same experimental setup of the first experiment, with the addition of a haptic device. This haptic device consisted of an elastic belt and a backpack with 4 vibrators, placed at each corner of the participant's back (upper right and left, lower right and left, Fig. 5A & 5B).

Stimulus. The stimuli were adapted from Study 2 based on participants' spontaneous reports. First, we changed a distance and an angle between a viewpoint and a virtual avatar (2.5 au behind their virtual avatar and 21.8^{o}, instead of 2.32 au and 21.4^{o}). In the previous experiment, some participants reported that it was a little bit difficult to focus on an avatar and a target stimulus (i.e. the virtual cloud) at the same time. Therefore, to make participants give attention to the avatar more easily, we provided a better field of view by increasing the distance between the avatar and the viewpoint and decreasing the angle. Second, we added visual stimuli on the virtual avatar's back, corresponding to the vibrators' location (upper right and left, lower right and left, Fig. 5C). The shapes of the stimuli were pentagons, flashing and rotating. Also, the sizes of the visual stimuli were synchronized with the intensity of the vibrations. As the intensity of a vibration increases, the size of a visual stimulus on the same location with the vibrator increases (min size: 0 au, max size: 0.3 au).

Procedure. Participants were asked to perform the same task as in Study 2 (i.e. flying through the center of the spherical clouds) with different three conditions. The procedure was the same as in the first experiment with also a randomized condition order (Practice – ((flight task with one condition; body synchronous, multisensory-synchronous, or multisensory-asynchronous condition – questionnaire – 10 seconds rest) × 6 – break) × 6).

The questionnaire was the same used in the first experiment except for the change of the control question. The item "I felt dizzy" was substituted with ("I felt as if I had more than one body") (Table S2, adapted from (Kalckert and Ehrsson 2012, Aspell, Heydrich et al. 2013, Pfeiffer, Lopez et al. 2013, Noel, Pfeiffer et al. 2015)).

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Supplementary material

Supplementary Text

Data analysis. Only data from participants who finished the whole experiment were used for analysis. One participant dropped out of the experiment because of dizziness. That is, 25 participants' data were analyzed. At first, questionnaire ratings were categorized into embodiment or flight sensations and were averaged for each participant and each session based on this category. Embodiment ratings include the sense of agency over the trajectory control (Q1) and the avatar (Q2), self- identification (Q3) / location (Q4) to/in the avatar. Flight sensations ratings contain floating (Q5) and flying (Q6) sensations. The dizziness question (Q7) was a control question. We noted that the ratings of the control question were comparatively low across participants than others (average: 2.27, other questions' average: 3.96 – 5.86) and were not affected by our experimental manipulation.

We analyzed participants' piloting performance as objective measurements. Specifically, for each experimental condition, we quantified six performance: accuracy, precision, hit rate, control effort, the standard deviation of angular speed, and mean of angular acceleration (the last three variables were related to the driving performance of a vehicle, especially about path stability) (van Driel, Hoedemaeker et al. 2007). Accuracy was quantified by computing the inverse of deviations between the avatar/object and the cloud. To calculate the inverse deviation, we first defined an infinite plane that had a direction vector from the previous cloud to the next cloud as a norm vector for each cloud. Given these planes, deviations were quantified by calculating the distances between the cloud center and the avatar or object center when participants passed through the planes during the session. We inversed these deviations to obtain an indicator of how well participants could perform the task for any given session. Precision was calculated as the inverse variance ($1/\sigma^2$) of the deviations. The hit rate was calculated by the ratio of clouds touched by the avatar. To compute the hit rate for each session, we divided the number of hit clouds participants flew through by the total number of clouds. A hit cloud was determined based on the radius of a cloud target (2.865 + 0.05 (variation of radius) au). That is, if the deviation from a cloud was less than the average radius of the cloud, the cloud was considered as being hit. As the time for each session was fixed (90 seconds), the total number of cloud targets varies across conditions and participants depending on individual performance. To check whether the total amount of clouds presented did not differ across conditions, we performed a linear mixed model over the total number of clouds with the condition as a fixed effect and intercepts for participants as random effects. Control effort was quantified, on a session-by-session basis, as the number of direction changes (reversals in roll, pitch, and yaw control signal) during the task. For the standard deviation (σ) of angular speed, we combined the speed of roll, pitch, and yaw (angular speed = $\sqrt{Roll^2 + Pitch^2 + Yaw^2}$) to get a single angular speed and calculated σ of angular speed. Moreover, by differentiating angular speed, we computed the mean (μ) of angular acceleration. For control effort, σ of angular speed, and μ of angular acceleration, lower values indicate better performance.

Similar to the questionnaire results, piloting performance was categorized into targeting or path stability of piloting performance and was averaged for each participant and each session depending on this category. To give equal weight in this procedure, before averaging piloting performance based on each category, each performance was standardized through range scaling that changed the values of each performance between 0 and 1 (van den Berg, Hoefsloot et al. 2006). Accuracy, precision, and hit rate were integrated for targeting performance and control effort, σ of angular speed, and of angular acceleration were integrated for path stability.

To investigate a potential modulation of subjective experience and piloting performance depending on the different experimental conditions and in agreement with our hypothesis that the avatar-synchronous condition would lead to higher performance, we only compared the results between the motion-synchronous and the avatar-asynchronous condition, and between the avatar-synchronous and the object-synchronous condition.

Moreover, correlations between each subjective experience (embodiment, flight sensations, and control question) and each piloting performance (targeting and path stability) were investigated.

Finally, influences of our experimental manipulation on subjective experience and piloting performance and correlations were analyzed with linear mixed models (R package "lme4") having intercepts for participants as random effects to consider repeated measures. Also, when we built the models, sessions as a fixed effect and random slopes were considered and by using the likelihood ratio test, we selected the best model for our data. For each condition, learning effects and learning rates were also calculated through linear mixed models on piloting performance with the session as a fixed effect, random intercepts for each participant, and random slopes over session. Moreover, in the mixed models of correlations, we excluded interactions with conditions, because there was no significant interaction. In all models, p-values were calculated by likelihood ratio tests and degrees of freedom were approximated using the Satterthwaite's method. Besides, to identify the causal relationship between embodiment, flight sensations, and piloting performance, we performed mediation analyses between the experimental manipulation and flight sensations or piloting performance with embodiment or flight sensations as a mediator. The analyses were done with the R package "mediation" (Tingley, Yamamoto et al. 2014), and we showed an average causal mediation effect and average direct effect estimated by quasi-Bayesian Monte Carlo simulation (1000 simulations, $p < 0.05$). All statistical analyses were performed using the software R (version 3.4.0) and MATLAB (Mathworks Inc., Natick, MA). In Studies 2 and 3, the same data analyses were applied.

Supplementary Movies

Movie S1: https://drive.google.com/open?id=1iDzOpeKgKw7jfIe4gm_A7Sr4lhwLkoR2

Movie S2: https://drive.google.com/open?id=1hy_21-Y_KIMcVFssxG5-eJ9uuDEc__Pi

Supplementary Figures

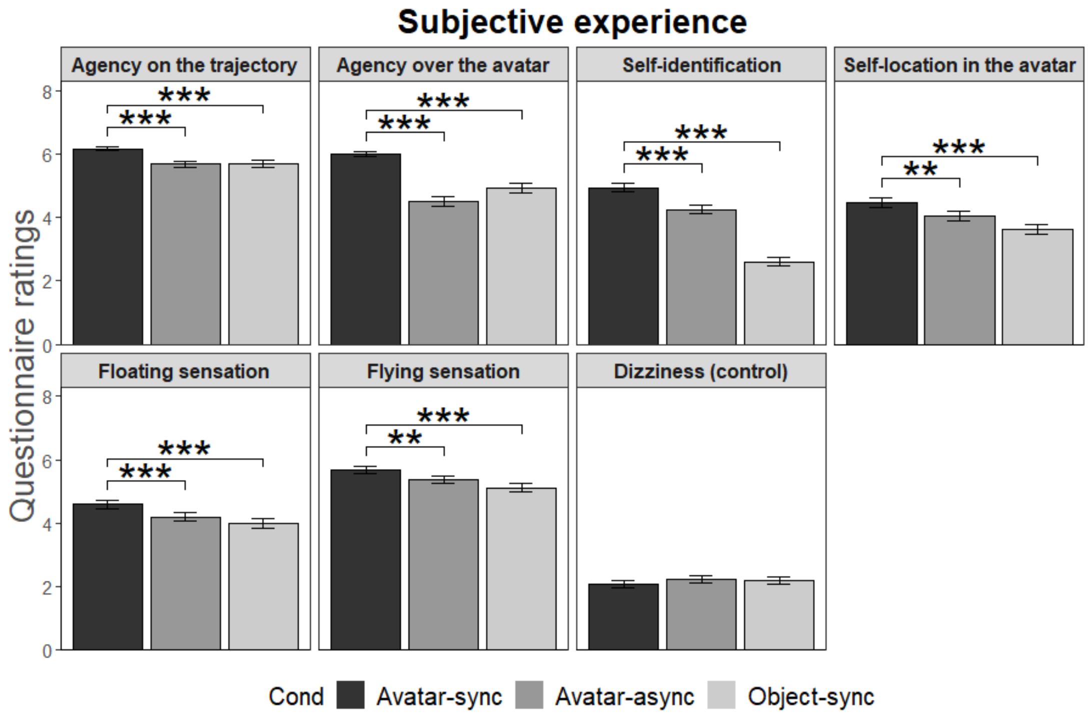

Fig S1. Questionnaire results in Study 2. ratings for each question and condition (avatar-synchronous - avatar-sync; avatar-asynchronous – avatar-async; and object-synchronous – object-sync) are shown. As ratings of the questionnaire are a Likert scale, the questionnaire data were analyzed with cumulative link mixed models with random intercepts for each participant. Results revealed that subjective ratings of agency, self-identification, and self-location (i.e., the three subcomponents of embodiment), as well as flight sensations ratings, were significantly higher in the avatar-synchronous condition as compared to the other two control conditions. Error bars represent standard error of the mean. *: p < 0.05, **: p < 0.01, ***: p < 0.001.

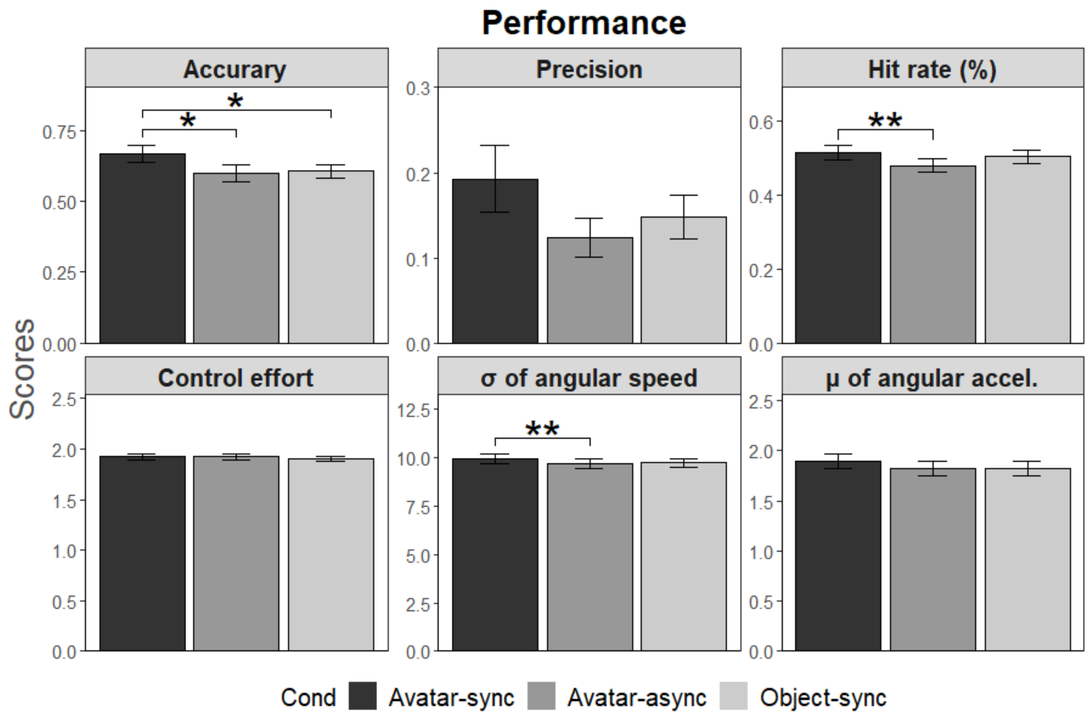

Fig S2. Flight (motor) performance in Study 2. Piloting performance for the different experimental conditions is shown. The avatar-synchronous condition results in better accuracy and hit rate as compared to two control conditions. However, the mean of angular speed in the avatar-synchronous condition was higher than the motion-asynchronous condition. Error bar represents standard error of the mean, and * and ** represent the significant difference between conditions with $p < 0.05$ and $p < 0.01$, respectively.

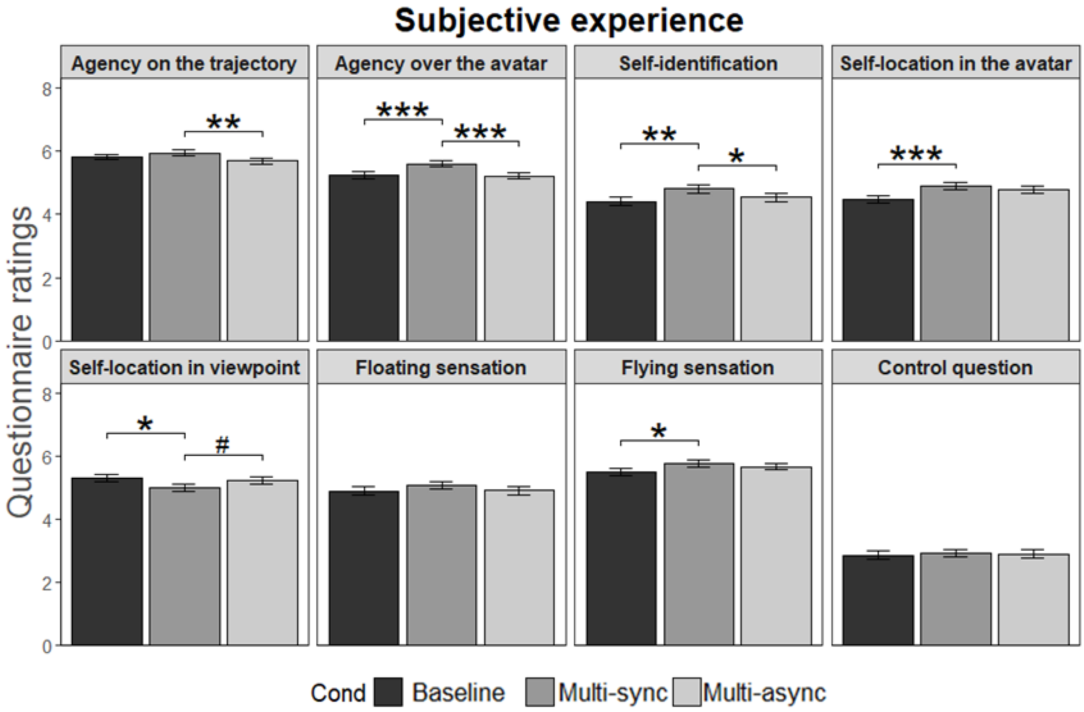

Fig S3. Questionnaire results in Study 3. Ratings for each question and condition (avatar-synchronous condition – Baseline; multisensory-synchronous condition – Multi-sync; and multisensory-asynchronous condition – Multi-async;) are shown. Error bars represent standard error of the mean. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

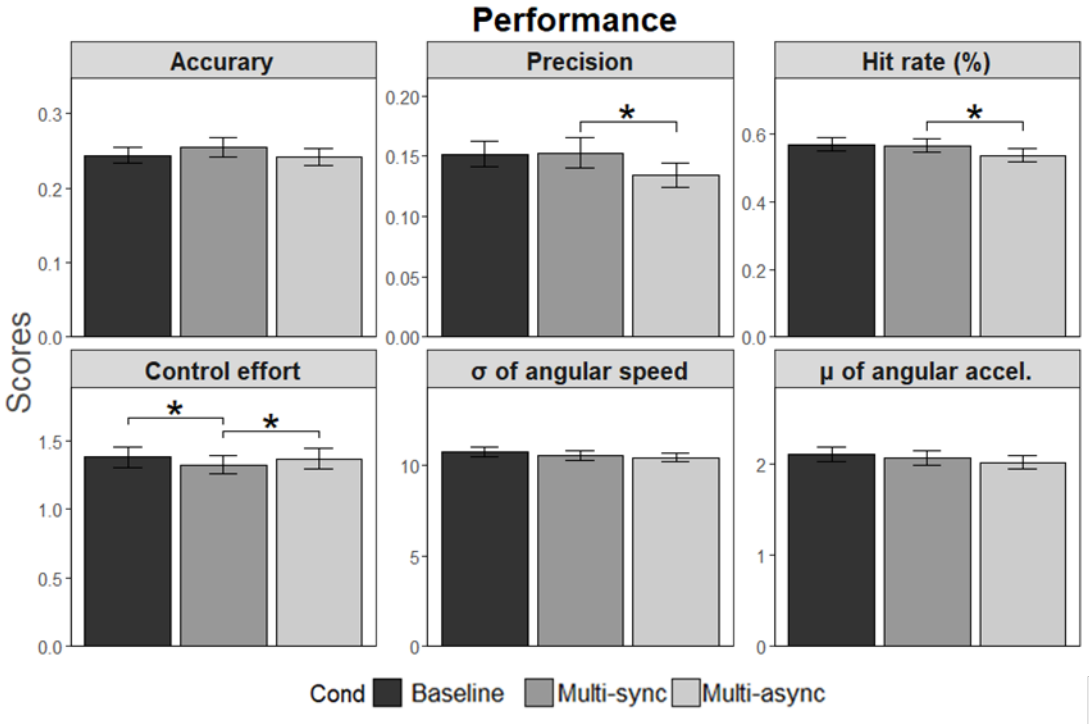

Fig S4. Flight (motor) performance in Study 3. The multisensory-synchronous condition had better precision, compared to the multisensory-asynchronous condition and less control effort relative to the other control conditions. Error bar represents standard error of the mean, and * represents the significant difference between conditions with $p < 0.05$.

Supplementary Tables

Questionnaire	
Q1	The flight trajectory was controlled by my movement
Q2	The body/object that I saw was moving in the same manner as my physical body
Q3	I felt as if the body/object that I saw was my body
Q4	I was located where I saw the body/object
Q5	I felt as if my body became lighter and I was floating
Q6	I felt as if I were flying
Q7	I felt dizzy

Table S1. Questionnaire for bodily self-consciousness and flying sensations for Study 2.

Questionnaire	
Q1	The flight trajectory was controlled by my movement
Q2	The body/object that I saw was moving in the same manner as my physical body
Q3	I felt as if the body/object that I saw was my body
Q4	I was located where I saw the body/object
Q5	I felt as if my body became lighter and I was floating
Q6	I felt as if I were flying
Q7	I felt as if I had more than one body

Table S2. Questionnaire for bodily self-consciousness and flying sensations for Study 3

2.3 Part C – Disembodied from the body: Virtual Out-of-body experience illusion

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Abstract

Out-of-body experiences (OBEs) are characterized by a feeling of being outside one's physical body, by localizing one-self seeing one's own body at an elevated perspective (Green 1968, Blanke and Mohr 2005, Lopez and Blanke 2007). Vestibular sensations such as the feeling of floating or lightness are often reported during an OBE. Neurological research suggests that OBEs are caused by impairments of multisensory integration (Blanke and Mohr 2005). The experimental induction of OBEs using virtual reality (VR) is a powerful approach to study the foundations of bodily self-consciousness (Blanke and Metzinger 2009, Blanke, Slater et al. 2015). However, previous studies using such technique could only induce mild OBE illusions and did not cover the full spectrum of OBEs (Ehrsson 2007, Lenggenhager, Tadi et al. 2007, Ionta, Heydrich et al. 2011). Here, we developed a new immersive mixed-reality (MR) system, aiming at experimentally inducing mental states that are similar to full-blown OBEs in healthy participants.

This study consists of two experiments. Thirty-six participants took part in Study 4 (pilot). They experienced three virtual OBE-like scenarios using our new MR system which combines real-time volumetric body scanning and VR. During the virtual OBE-like scenario, participants, in a supine position, were exposed to a viewpoint change from their body-centered viewpoint (BV) to an elevated viewpoint (EV). During the viewpoint change and the EV, the participants could see the observed body from a third-person viewpoint. Also, the observed body synchronously moved with the participants throughout the scenario. Autoscopy was realized in three forms (Mirror; No-mirror; upside-down). After each virtual OBE-like scenario, explicit subjective measure (questionnaire) and implicit behavioral measure of self-location (MBDT) were recorded. As a result, all OBE-like scenarios led to greater OBE-like sensations and higher elevated self-location, compared to BV. Additionally, there was a significant difference in a feeling of disconnection from the physical body between Mirror and upside-down positions.

Based on Study 4, we hypothesized that observed the body position seen from the EV can influence the OBE illusion. Also, based on the assumption that OBEs might be caused by the failure of multisensory integration, we speculated that spatial sound with respect to the viewpoint could induce the greater OBE illusion. Thirty-two healthy participants took part in Study 5 which was characterized by four virtual OBE-like scenarios (2 by 2 factorial design; observed body position (Mirror & Upside-down) and spatialization of sound cue (spatial & non-spatial sound). To investigate our questions, a ceiling fan was added to the OBE-like scenarios. The non-spatial sound condition provided a constant fan-spinning sound and the spatial sound condition introducd changes of the fan sound according to the viewpoint change. Moreover, to investigate the effects of a motor component on the OBE illusion, participants were exposed to an additional OBE-like scenario after experiencing 4 OBE-like scenarios. In the final scenario, participants saw the observed body frozen in motions during the viewpoint change and EV. The frozen condition was compared to previous OBE-like scenarios – during which participants' movements were feedback in real-time. The same measures in Study 4 were used. At the end of the experiment, participants' preference of observed body position for the OBE illusion and awareness of spatial sound were asked for exploratory analyses. As a result, all conditions were characterized by greater OBE-like sensations and higher self-location in EV, compared to BV. Also, Mirror condition led to greater disembodiment, compared to Upside-down condition. For the motor component, synchronized motor conditions induced greater disembodiment than the no-motor/frozen condition. Furthermore, exploratory analyses showed that

the preferred condition and spatial sound cues led to higher self-location and stronger vestibular sensations depending on the awareness of spatial sound, compared to other conditions.

In conclusion, we describe a new MR system able to induce a mental state including changes in disembodiment, vestibular sensations, and elevated self-location. We showed that the OBE-like mental state seems to depend on conscious multisensory and sensorimotor factors but also the preference of observed body position. Altogether this highlights the importance to consider inter-individual variabilities for future OBE studies.

Introduction

OBEs are defined as the awake experience where a person feels as being outside his/her physical body (*i.e.* disembodiment), localizes himself/herself at an elevated perspective (*i.e*. elevated self-location), and sees his/her body, as well as the world, from an elevated perspective (*i.e.* autoscopy) (Blanke, Landis et al. 2004). In addition, vestibular sensations such as floating, lightness, or flying have been frequently associated with OBEs (Blanke, Landis et al. 2004, Blanke and Mohr 2005, Lopez, Halje et al. 2008). Specifically, more than 50% of OBE patients report vestibular sensations during OBE (Blanke and Mohr 2005).

OBEs usually happen in patients with neurological or psychiatric diseases (Blanke, Landis et al. 2004), but can also occur in patients with migraine, depersonalization, or vestibular disorders (Lopez and Elziere 2018, Hiromitsu, Shinoura et al. 2019). Even 5 to 10 % of the healthy population experience OBEs, and thus among different cultures (Sheils 1978).

Although, OBEs are not that rare, its mechanisms underlying OBEsare still unclear. Many previous studies have been conduected for OBEs, based on anatomical, phenomenological, and behavioral data from patients. However, these studies have only conjectured that OBEs are caused by impairments of multisensory integration of bodily signals such as visual, auditory, somatosensory, motor, and vestibular information (Blanke and Mohr 2005, Bünning and Blanke 2005, Aspell and Blanke 2009).

Previous work showed that an OBE could be experimentally induced using two different manners. The first one is to electrically stimulate the brain over the temporoparietal junction using subdural electrodes (Blanke, Ortigue et al. 2002, Bos, Spoor et al. 2016). This technique is invasive and only applicable for patients but led to full-blown OBEs, including disembodiment, autoscopy, elevated self-location, and strong vestibular sensations.

The second manner is to use multisensory stimulations - such as visuo-tactile stimulations - to induce illusory perceptions such as the out-of-body illusion or the full-body illusion (Ehrsson 2007, Lenggenhager, Mouthon et al. 2009, Ionta, Heydrich et al. 2011). For example, Ehrsson induced the first out-of-body illusion by using visuo-tactile stimulations which led to a feeling of being outside the physical body (Ehrsson 2007). To achieve such an illusion, a participant's body was captured by a camera behind them and streamed through a head-mounted display (HMD) to the participant. With this setup, as the experimenter stroked the participant's chest and showed synchronous/congruent stroke motions in the camera, the participant felt as if they were located at the camera viewpoint behind their physical body. The illusion only happened when visuo-tactile stimulation was synchronous. If visuo-tactile stimulation was asynchronous, the illusion did not occur. This method is non-invasive and can be applied to both healthy and clinical populations. However, such paradigm only led to difference in disembodiment, without affecting other key components of OBEs: elevated self-location and vestibular sensations.

Going a step further, Lenggenhager and colleagues induced an out-of-body illusion to participants who were in a prone position and looked down at their physical body. Such paradigmshe could induce disembodiment and an elevated self-location as well as some floating sensation (Lenggenhager, Mouthon et al. 2009). Also, they found that elevated self-location was significantly and positively associated with floating sensation.

Similar OBE-like sensations were achieved using visuo-tactile stimulation and visuo-vestibular conflicts (Ionta, Heydrich et al. 2011). In that study, participants were lying in a supine position and seeing a body in a prone position.

Synchronous visuo-tactile stimulations on participants back led to vestibular sensations (floating and lightness) and half of the participants reported elevated self-location. Such illusory manipulations are usually referred to as OBE illusion. However, while we know how central are vestibular sensations in OBE, experimentally induced vestibular sensations using VR are weak and usually do not reach significance.

Here, we developed a new MR system to induce mental states that are similar to full-blown OBEs, in healthy participants. Using real-time volumetric body scanning with ten Kinects, we created a photorealistic full-size virtual body or object and projected this into the virtual environment. Therefore, participants wearing an HMD could move the photorealistic body synchronously with the physical body from a body-centered viewpoint in the virtual environment. Also, they could interact with the virtual environment as they do in the real world and experience virtual OBE-like scenarios that can be varied by modulating a trajectory and speed of visual OBEs, the form of autoscopy (observed body position), multisensory or sensorimotor stimuli.

The main aim of this study was to induce a full-blown OBE illusion by manipulating different factors such as sensorimotor and multisensory integrations to understand underlying mechanisms of OBEs. In Study 4, we explored how observed body position influenced the OBE illusion, using virtual OBE-like scenarios. In Study 5, the effects of multisensory and sensorimotor integration on the OBE illusion was tested by manipulating observed body position, sound spatialization, and sensorimotor (visuomotor) stimulation.

2.3.1 Study 4 – Virtual Out-of-Body Experience and autoscopy from (Pilot)

Methods

Participants.

Thirty-six participants took part in the experiment (age = 27.3 ± 6.3, 18 females, 33 right-handed). All participants reported no history of neurological or psychiatric illness. Experimental protocols were approved by the local ethics committee (Commission Cantonale d'Ethique de Geneve). Participants gave their written informed consent and were compensated for their time (20/30 CHF).

Materials.

The experimental setup includes an in-house real-time volumetric body scanning system, an HMD (Samsung Odyssey, AMOLED display 3.5", 1440 x 1600 per eye, 90 Hz refresh rate, 110 FOV, https://www.samsung.com), and a custom-made bed (length, width, and height; 2 meters (m) x 0.9 m x 1.1 m, **Figure 1A**). The real-time body scanning system consists of ten depth cameras (Kinect V2, Microsoft), ten client computers, one for each Kinect, and the main server computer (**Figure 1A**). Each Kinect extracts parts of a body and objects and transmits the volumetric data to the main computer. Then, the main computer calibrates the collected data from each Kinect according to predefined parameters and fully reconstructs the full environment in 3D and real-time. By placing Kinects in specific locations, Kinects' occlusions -which could happen while the body and the objects are moving- are avoided. Using this system makes possible the creation of a photorealistic virtual body or object in a mixed environment. That is, the virtual body or object is the same as the real one in appearance and its movements are synchronized. The mixed environment, as well as the visual and auditory stimuli, were created and manipulated with in-house software (ExpyVR). This was presented to participants through an HMD allowing head motion and position tracking. Also, participants reported their responses using a numpad with their left hand.

Figure 1. Experimental setup and virtual environment. Using ten Kinect cameras around a participant (**A**), appearance parameters of the body and of the objects surrounding the body are transferred to the virtual environment (**B**) as a photorealistic avatar or photorealistic virtual objects. Inside the virtual environment, the participant can see the virtual body and the virtual objects from a body-centered viewpoint (**C**). Also, movements of the virtual body are synchronized with these of the physical body. The black plate in (**B**) is the location of the virtual bed and the virtual body.

Stimulus.

During the experiment, participants lied on the bed and wore an HMD. The virtual environment was composed of a room (7.2 virtual meters (vm) x 4.3 vm x 3.7 vm) with a door (0.9 vm x 2.8 vm), a ceiling bulb (0.9 vm diameter) and a full-size bed (2 vm x 0.9 vm x 1.1 vm) (**Figure 1B & 1C**). Moreover, participants could see their own full-size body which was reconstructed by the body scanning system from a body-centered viewpoint (BV, **Figure 1C**). Movements of the virtual body were synchronized with movements of the physical body in real-time.

During the virtual OBE-like scenarios, participants experienced BV for 4 seconds (**Figure 2A**), a viewpoint change from BV to an elevated viewpoint (EV) for 15 seconds (**Figure 2B**), and EV for 8 seconds (**Figure 2C**). The trajectory of the viewpoint consisted of turning along a longitudinal axis and moving toward the ceiling. Then, the trajectory ended up 2 vm above the virtual body, with a downward viewpoint (see **Movie S1**). Also, throughout the whole experiment, white noise was played to participants through the HMD.

To investigate the role of the observed body position on the OBE illusion, at the beginning of the viewpoint change, the position of the virtual body was kept the same, changed into a left-right inverted position or changed into an up-side-down position (see **Figure 2D**, **2E**, & **2F** and **Movies S2**, **S3**, and **S4**, respectively). Thus, from EV, participants could see the virtual body in a no-mirror position, a mirror-reversal position or an upside-down position. During EV, movements of the virtual body were synchronized with the movements from the physical body. Also, participants could freely move.

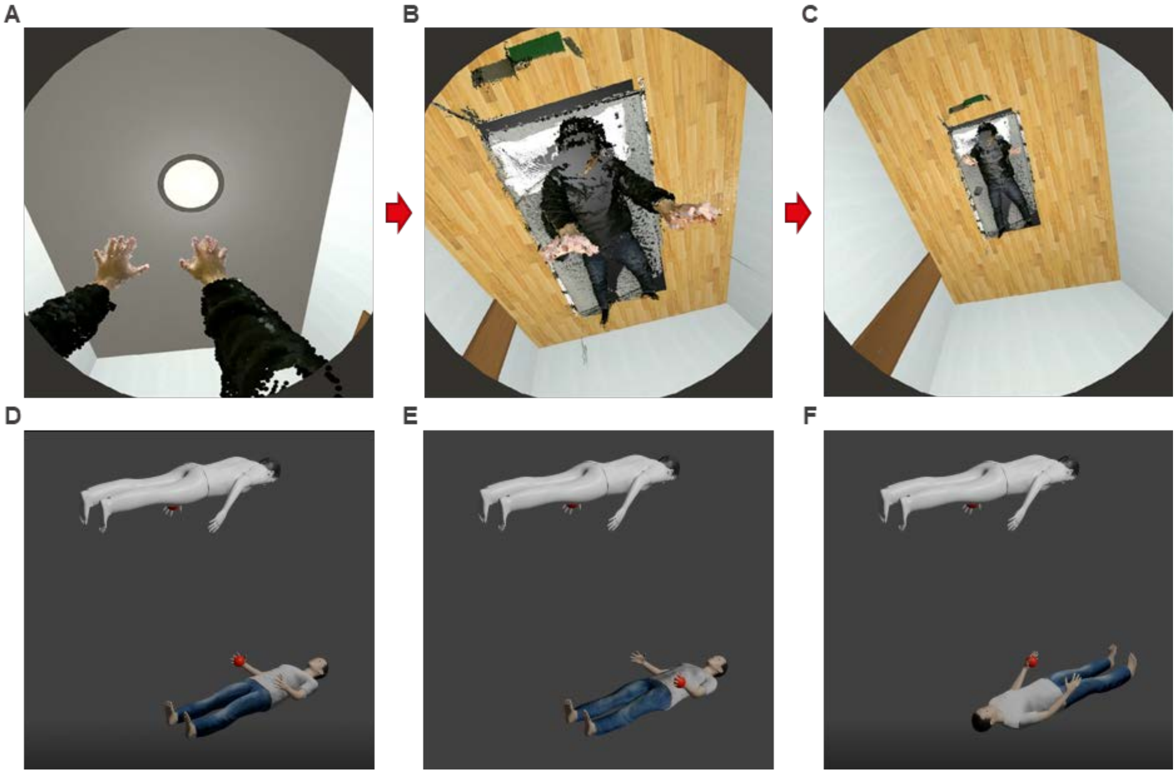

Figure 2. A sequence of virtual OBE-like scenario (A, B, and C) and different observed body positions (D, E, and F). In the beginning, a participant has a body-centered viewpoint and can move the virtual body freely as the participant does in the real world (4 seconds, **A**). When the OBE-like scenario starts, the participant is exposed to a viewpoint change from the body-centered location to an elevated location (15 seconds, **B**). Finally, when the highest viewpoint is reached, the participant maintains this elevated viewpoint (EV) for 8 seconds (**C**). From the EV, he can still see and move the observed body. There are 3 conditions related to observed body position in Study 4. The first one is a mirror position where the participant can see the observed body in a mirror-reversal position (**D**). Second, in a no-mirror condition, the participant can see the observed body in a non-reversing mirror position (**E**). Lastly, in an upside-down condition, the participant can see the observed body in an upside-down position (**F**).

Procedure.

Three groups of participants took part in the pilot experiment according to the experienced types of observed body position.

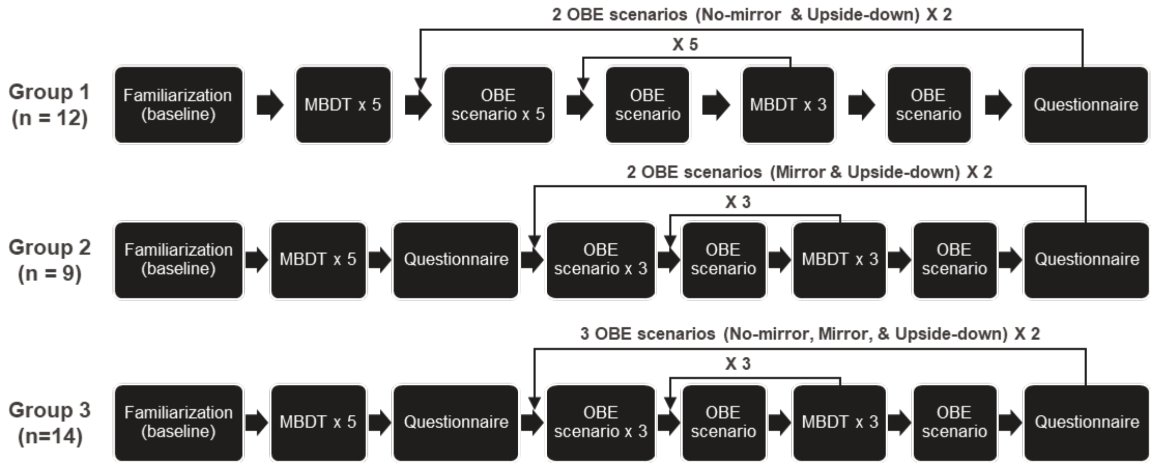

Figure 3. Experimental procedure. There are three groups of participants. Depending on the group, the participants experience different OBE-like scenarios. The participants in Group 1 experience the No-mirror and Upside-down conditions. The participants in Group 2 are exposed to the Mirror and Upside-down conditions. Lastly, The participants of Group 3 experience all conditions (Mirror, No-mirror, and Upside-down).

In the first group (the first row of **Figure 3**), the experiment started with a Baseline session. Before this session, participants practiced the Mental Ball Drop task (MBDT, see section **Mental Ball Drop task (MBDT)**). Then, participants had time to familiarize themselves with the mixed environment for 100 seconds (Step 1 of the first row in **Figure 3**). During the familiarization, wearing HMD and sitting on the bed, they looked around the virtual environment and moved their virtual body in the BV. After the familiarization, they lied on the bed and performed the MBDT (5 times) as a baseline (Step 2 of the first row in **Figure 3**). Afterward, participants of the first group were exposed to two virtual OBE-like scenarios (no-mirror and upside-down; **Figure 2E & 2F**). They repeated to experience each virtual OBE-like scenario 11 times. After each repetition, the participants waited (Step 3 of the first row in **Figure 3**) or performed the MBDT 3 times (Step 4 - 5 of the first row in **Figure 3**). Finally, after the last repetition, they filled a questionnaire in (Step 7 of the first row in **Figure 3**).

Participants from the second group (the second row of **Figure 3**) underwent two different virtual OBE-like scenarios (mirror and upside-down; **Figure 2D & 2F**) and filled the questionnaires in after the familiarization, as a baseline. The questionnaire was the same as the one used for the first group (see section **Qiestionnaires** and **Table 1**). Also, the number of repetitions for each virtual OBE-like scenario was reduced to 7 times. They waited (Step 4 of the second row in **Figure 3**) or repeated the MBDT 3 times (Step 5 - 6 of the second row in **Figure 3**) at the end of scenario repetitions. After the last repetition, they rated the questionnaire items.

Participants from the third group (the third row of **Figure 3**) underwent 3 different OBE scenarios (mirror, no-mirror, and upside-down; **Figure 2D, 2E, & 2F**). The sequence of each virtual OBE-like scenario and the questionnaire were the same as the ones from the second group.

In all groups, the order of the scenarios was randomized, and each sequence was repeated 2 times (see **Figure 3** for more details about the sequences).

Questionnaires

To obtain subjective measurements of participants' feelings related to different scenarios, participants were presented with seven items about disembodiment, vestibular sensations, self-location, and self-identification (see **Table 1**). For each of them, participants were asked to rate how much they agreed or disagreed with the presented item, using a Likert scale bar from left to right (Left = strongly disagree to Right = strongly agree, coded as 1 and 7 respectively. Numbers were hidden.)

Questionnaire
1. I felt as if I was outside my physical body
2. I felt as if I was disconnected from my physical body
3. I felt as if I became lighter
4. I felt as if I was floating
6. I felt as if the body I saw was my body
5. I felt as if I was located from where I saw the scene
7. I felt as if I had more than three bodies (control)

Table 1. Questionnaire. In the questionnaire, we asked 2 questions about disembodiment, 2 questions about vestibular sensations, each question for self-identification for the virtual body, self-location at the viewpoint, and control, respectively.

Mental Ball Drop task (MBDT)

The MBDT is an explicit behavioral measurement of self-location. During this task, a black screen was presented to participants. Subjects were instructed to close their eyes and to imagine dropping an imaginary ball from their hand to the floor when they heard a tone. They were asked to estimate the dropping time of the ball from their hand to the floor. By the first key press, participants indicated when they dropped the ball from their hand and kept pressing the key until the ball touched the floor. For each trial, the duration of the button press (*i.e.* reaction time, RT) was recorded as a sensitive indicator of elevated self-location (Lenggenhager, Mouthon et al. 2009). Whenever the tone was repeated, participants repeated this task.

Data analysis.

Each question rating and RT of the MBDT were analyzed with linear mixed models having the virtual OBE-like scenario (Baseline, mirror, no-mirror, upside-down) as a fixed effect. Intercepts for participants were included in the model as random effects. Post-hoc comparisons were computed to explore the main effect of the virtual OBE-like scenario. As this experiment was a pilot experiment, multiple comparison corrections were not applied.

Results

Reaction Times.

The linear mixed model on MBDT RTs showed a significant main effect of virtual OBE-like scenarios ($F(3,1660.3) = 3.90$, $p < 0.01$). Post-hoc comparisons showed that RTs in all virtual OBE-like scenarios were significantly higher than RTs during the baseline (Baseline: 730.26 ± 32.79 ms (estimated marginal means ± standard error); Mirror: 768.79 ± 31.00

ms, t(1660.50) = -1.96, p = 0.05 ; No-mirror: 786.68 ± 30.74 ms, t(1658.88) = -2.10, p = 0.04; Upside-down: 766.18 ± 30.22 ms, t(1655.00) = -3.33, p < 0.001, **Figure 4**).

In other words, all virtual OBE-like scenarios led to higher elevated self-location, compared to the baseline. However, we did not found any difference between virtual OBE-like scenarios.

Questionnaire.

A main effect of virtual OBE-like scenarios was observed for the two disembodiment questions (Outside body: F(3,160.42) = 15.96, p < 0.001; Disconnection: F(3,1660.3) = 3.90, p < 0.001) and the floating sensation items(F(3,1660.3) = 3.90, p < 0.01). However, no main effect was observed for the control question (F(3,162.16) = 0.69, p = 0.56).

Post-hoc analyses showed that all virtual OBE-like scenarios led to greater ratings about the feeling of being outside the body, the feeling of being disconnected from the body, and about floating sensation compared to baseline (**Table 2 & Figure 4**). Participants in EV felt more as if they were outside their physical body, as if they were disconnected and separated from their physical body, and were experiencing more floating sensations in comparison to BV. Moreover, the significantly higher feeling of disconnection was observed in the upside-down position than the mirror position (t(164.23) = 1.98, p = 0.05). No difference was found for the control question (all *p*-values > 0.05)

	Baseline	Mirror	No-Mirror	Upside-down
Outside body	2.15 ± 0.36	**3.96 ± 0.31**	**4.17 ± 0.30**	**4.17 ± 0.28**
Disconnection	2.25 ± 0.37	**2.92 ± 0.31**	**3.33 ± 0.30**	**3.43 ± 0.28**
Lightness	4.26 ± 0.38	4.26 ± 0.33	4.06 ± 0.32	4.01 ± 0.30
Floating	3.21 ± 0.39	**4.25 ± 0.33**	**4.26 ± 0.32**	**4.26 ± 0.30**
Self-identification	5.57 ± 0.30	5.63 ± 0.26	5.48 ± 0.25	5.53 ± 0.23
Self-location	4.31 ± 0.38	4.33 ± 0.32	4.40 ± 0.31	4.31 ± 0.29
Control	1.49 ± 0.23	1.64 ± 0.19	1.78 ± 0.18	1.59 ± 0.16

Table 2. Estimated marginal means and standard errors for ratings of each question. Bold numbers mean significantly greater than Baseline.

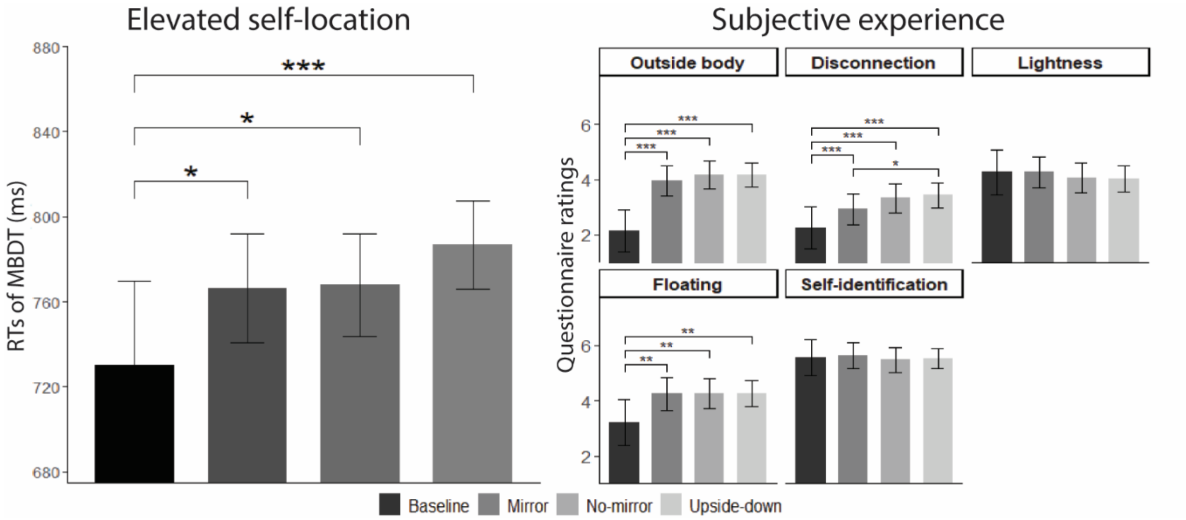

Figure 4. Elevated self-location from the MBDT and Subjective experience. The left graph shows the results of elevated self-location from the MBDT, according to conditions. Subjective experience on the right panel represents ratings of the questionnaire for each condition. 95% confidential intervals are shown in squared brackets. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

2.3.2 Study 5 – Multisensory, sensorimotor, and conscious bases of Out-of-Body Experience illusion

Study 5 was designed to identify how multisensory (audiovisual), sensorimotor, and conscious (preference and awareness) factors influence the OBE illusion. The second aim of the study was to investigate the relationship between disembodiment and vestibular sensations.

Based on our pilot (Study 4), we hypothesized that the upside-down position of the observed body could lead to a stronger OBE illusion. Also, as OBE is associated with a failure of multisensory integration (Blanke, Landis et al. 2004, Blanke and Mohr 2005, Bünning and Blanke 2005, Aspell and Blanke 2009), we speculated that audio-visual (spatial sound in respect to the viewpoint) and no sensorimotor (visuomotor) stimulations could result in greater OBE-like sensations. Lastly, we assumed that there would be a positive relationship between disembodiment and vestibular sensations.

Method

Participants.

Thirty-two healthy participants (age = 27.9 ± 4.8 years, 18 females, 29 right-handed) took part in the study. One participant was excluded as the participant could not understand the instructions. All participants reported no history of neurological or psychiatric illness. Experimental protocols were approved by the local ethics committee (Commission Cantonale d'Ethique de Geneve). Participants gave their written informed consent and were compensated for their time (20/30 CHF).

Materials.

Materials were similar to the one used in Study 4 (see section **Materials** in **Study 4**).

Stimulus.

The virtual environment consisted of a room with a door, a ceiling bulb, and a full-size bed, and a ceiling fan (0.95 vm diameter, **Figure 5**). The sequence and the trajectory of the virtual OBE-like scenarios are comprised of 8 seconds of BV, 15 seconds of viewpoint change, and 8 seconds of EV, sequentially. Also, to increase visuovestibular conflicts, smooth and small viewpoint fluctuations were added in the EV, regardless of the condition (see **Movie S5**).

To provide audiovisual stimulation, we spatialized the spinning sound of the ceiling fan. The ceiling fan's position was slightly shifted on the right side compared to the bed position. In the spatial sound condition, the fan sound was spatialized to stay congruent with the viewpoint's change (e.g. The sound moved from right to left and became louder during the viewpoint change). In the non-spatial sound condition, participants heard a constant fan sound during the entire scenario; leading to multisensory incongruency.

To investigate the effects of sensorimotor stimulation on OBE-like sensations, we created a frozen OBE-like scenario. In this scenario, participants could move their virtual body from BV. However, from the viewpoint change to EV, they could not move the observed body frozen in the last position of BV; resulting in a no-sensorimotor stimulation. This scenario included spatial sound.

Figure 5. The virtual environment of Study 5. The virtual environment consists of a room with a door, a ceiling bulb, and a full-size bed, and a ceiling fan. The ceiling fan is slightly lateralized with respect to the bed. The black plate in the figure is the location of the virtual bed and body.

Experimental design

Study 5 is designed in two parts. Part 1 was investigating the effects of observed body positions (mirror & upside-down) and spatialized sound (spatial & non-spatial) on the OBE illusion (2 by 2 factorial design, see **Movies S5 & S6**). The other part (Part 2) was demonstrating how sensorimotor stimulations influence the OBE illusion. To achieve this, we compared the OBE-like scenarios having spatial sound and sensorimotor stimulation in Part 1 of Study 5 with the scenario having spatial sound and no-sensorimotor stimulation in Part 2 of Study 5.

Procedure.

Part 1 of Study 5 was similar to group 2 and group 3 of Study 4. However, due to the increased number of conditions, we reduced the number of repetitions of the scenario to 3 (see Part 1 of **Figure 6** for details). Also, based on reports from OBE patients (Green 1968), one more item was added to the questionnaire ("I felt as if I was separated from my physical body"). The order of virtual OBE-like scenarios was randomized.

After Part 1, the participants experienced the frozen scenario if the allowed time (one and half an hour) was available for Part 2. The procedure was the same as Part 1, but there was no baseline session (Part 2 of **Figure 6**).

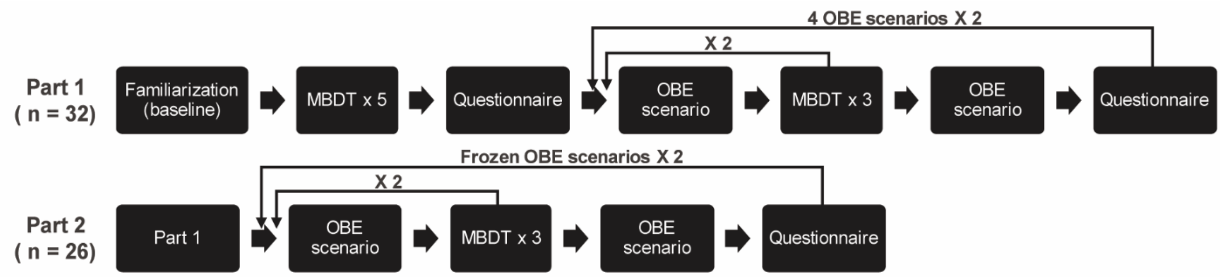

Figure 6. The procedure of Study 5. Study 5 consists of two parts. Part 1 is to investigate the effects of observed body position and spatialized sound for the OBE illusion. Part 2 is to investigate the effects of sensorimotor stimulation on the OBE illusion.

Data analysis.

Ratings of each question and RTs of MBDT were analyzed using linear mixed models with virtual OBE-like scenario as a fixed effect (Baseline, condition 1: mirror-reversal & non-spatial sound, condition 2: mirror-reversal & spatial sound, condition 3: upside-down & non-spatial sound, and condition 4: upside-down & spatial sound).

Next, the effects of observed body position and spatialization of sound on OBE illusion were investigated. Before analyzing the effects, factor analysis was performed to reduce the number of variables. Data from Part 1 and Part 2 were included for this analysis. As a result, the factor analysis found two factors based on the Kaiser criterion (Gonzalez-Franco and Peck 2018): (1) disembodiment, (2) vestibular sensations and elevated self-location (**V&E factor**). Loadings of the factor are presented in Table S1 of the supplementary section. These two factors explained 63% of the variance of our data.

Factors scores and MBDT RTs were analyzed using linear mixed models with the observed body position (Mirror and Upside-down), the spatialization of sound (non-spatial sound and spatial sound), and the interaction as fixed effects.

The relationship between disembodiment and vestibular sensations was investigated with a linear mixed model with V&E factor scores as the outcome variable and the disembodiment factor scores, the observed body position, spatialization of sound, and interactions as fixed effects.

Finally, we explored how preference for observed body position was impacting OBE-like sensation. To do so, we coded the "observed body position" variable into a new variable called 'preference' with two levels (preferred, no-preferred condition). Three participants did not have any preferred condition and were discarded from the analysis. Linear mixed models with preference, awareness of spatial sound, spatialization of sound, and the interactions as fixed effects and random intercepts for each participant were used for scores of each factor and MBDT RTs.

Lastly, linear mixed models having sensorimotor stimulation as a fixed effect were run for scores of each factor and MBDT RTs.

All models in Study 5 include random intercepts for participants and posthoc comparisons were conducted to explore significant main effects and interactions.

Results

Concerning the preference, 18 participants preferred the mirror position, 10 participants preferred the upside-down position, and 3 participants didn't prefer any positions. About the question of awareness of spatial sound, 15 participants were aware of the spatial sound and 16 participants were unaware of it.

Reaction times.

The linear mixed model on MBDT RTs showed a main effect of virtual OBE-like scenario. Post-hoc comparisons found that all virtual OBE-like scenarios had significantly higher RTs compared to baseline (Baseline: 772.55 ± 64.42; condition 1: 869.94 ± 63.27, t(1612.07) = -5.11, p < 0.001; condition 2: 876.21 ± 63.26, t(1612.05) = -5.45, p < 0.001; condition 3: 874.29 ± 63.26, t(1612.05) = -5.35, p < 0.001; condition 4: 869.00 ± 63.26, t(1612.05) = -5.11, p < 0.001; **Figure 7**). In other words, all virtual OBE-like scenarios had higher elevated self-location, compared to the baseline condition.

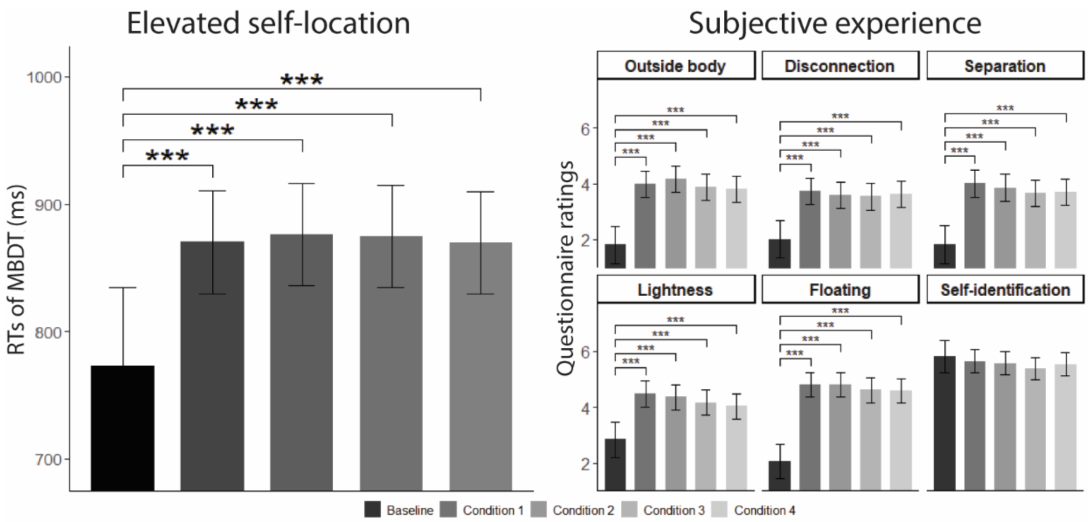

Figure 7. Elevated self-location from MBDT and subjective experience, compared with Baseline. (Left panel) RTs of the MBDT related to elevated self-location is shown for each condition. (Right panel) Ratings of a questionnaire about OBE-like sensations are represented for each condition. 95% confidential intervals are shown in squared brackets. ***: p < 0.001.

No significant effect of body position and spatialization of sound on MBDT RTs was observed (all *p*-values > 0.05). Explanatory analyses showed a main effect of preference (F(1,1271) = 11.81, p < 0.001); this effect was modulated by awareness (interaction preference* awareness F(1,1271) = 5.37, p = 0.02) and spatialization of sound (interaction preference* spatialization F(1,1271) = 16.13, p < 0.001).

The preferred condition (882.11 ± 70.25) had greater RTs than the no-preferred condition (846.88 ± 70.25, t(1277.03) = -3.43 , p < 0.001, **Figure 8A**). The interaction between preference and awareness of spatial sound showed that unaware participants had significantly higher elevated self-location in the preferred condition (870.95 ± 101.18) in comparaison with the no-preferred condition (811.96 ± 101.18, t(1277.03) = -3.97, p < 0.001, **Figure 8B**). This was not observed in the aware group (t(1277.03) = -0.81, p = 0.42). Lastly, the interaction between awareness and spatialization of sound showed that spatial sound led to higher RTs (906.21 ± 97.50) than the non-spatial ones (868.86 ± 97.50) when participants noticed the spatiality of the fan sound (t(1277.03) = -2.62, p < 0.01, **Figure 8C**). However, when participants were unaware of the fan sound spatiality, spatial sound led to lower elevated self-location, compared to non-spatial sound (spatial sound: 818.95 ± 101.18; non-spatial sound: 863.96 ± 101.18; t(1277.03) = 3.04, p < 0.01, **Figure 8C**). We did not observe a main effect of sensorimotor stimulation on MBDT RTs (F(1,1028.3) = 0.18, p = 0.67).

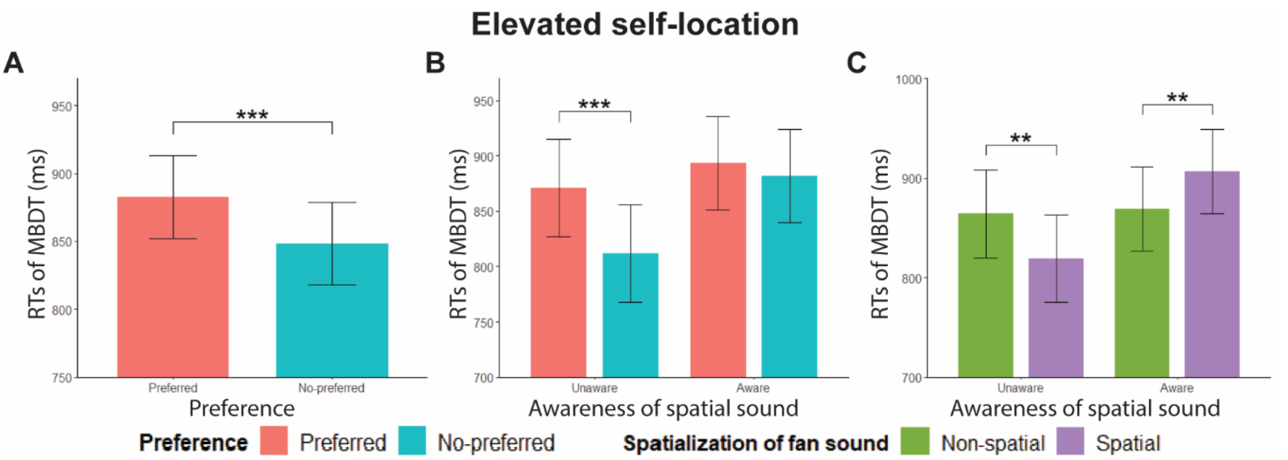

Figure 8. Effects of preference, awareness of spatial sound, and spatialization of sound on elevated self-location from MBDT. Elevated self-location measured through the MBDT are shown based on preference (**A**), preference with the awareness of spatial sound (**B**), and spatial sound with the awareness of spatial sound (**C**). 95% confidential intervals are shown in squared brackets. **: p < 0.01; ***: p < 0.001.

Questionnaire ratings.

Linear mixed models for question ratings highlighted a main effect of virtual OBE-like scenarios for the disembodiment questions (Outside body: F(4,248.03) = 23.63, p < 0.001; Disconnection: F(4,248.03) = 23.63, p < 0.001; Separation: F(4,248.03) = 23.63, p < 0.001). Moreover, a main effect virtual OBE-like scenarios for lightness (F(4,248.04) = 9.95, p < 0.001) and of floating (F(4,248.03) = 36.35, p < 0.001) sensations were observed. Post-hoc analyses revealed that all virtual OBE-like scenarios led to higher disembodiment and vestibular sensations question ratings in comparison to the baseline condition (**Figure 7 & Table 3**). Participants in EV felt more as if they were outside their physical body, as if they were disconnected and separated from their physical body, and were experiencing more lightness and floating sensations in comparison to BV.

	Baseline	Condition 1	Condition 2	Condition 3	Condition 4
Outside body	1.80 ± 0.34	**3.97 ± 0.31**	**4.16 ± 0.31**	**3.89 ± 0.31**	**3.79 ± 0.30**
Disconnection	2.00 ± 0.34	**3.74 ± 0.31**	**3.60 ± 0.31**	**3.53 ± 0.31**	**3.63 ± 0.31**
Separation	1.80 ± 0.35	**4.01 ± 0.32**	**3.85 ± 0.32**	**3.66 ± 0.32**	**3.69 ± 0.32**
Lightness	2.84 ± 0.33	**4.48 ± 0.29**	**4.35 ± 0.28**	**4.16 ± 0.28**	**4.03 ± 0.28**
Floating	2.06 ± 0.32	**4.81 ± 0.28**	**4.81 ± 0.28**	**4.61 ± 0.28**	**4.58 ± 0.28**
Self-identification	5.81 ± 0.29	5.65 ± 0.27	5.58 ± 0.27	5.38 ± 0.27	5.54 ± 0.27
Self-location	5.06 ± 0.36	4.66 ± 0.32	4.85 ± 0.32	4.63 ± 0.32	4.84 ± 0.32
Control	1.26 ± 0.14	1.38 ± 0.13	1.34 ± 0.13	1.40 ± 0.13	1.32 ± 0.13

Table 3. Estimated marginal means and standard errors for each question. Bold numbers mean significantly greater than the Baseline.

The model investigating the effects of observed body position and spatialization of sound showed a main effect of observed body position for the disembodiment factor (F(1,217.03) = 4.15, p = 0.04). Furthermore, posthoc comparisons found that the mirror position (4.01 ± 0.28) led to greater disembodiment, compared to the upside-down position (3.81 ± 0.28, t(220.07) = 2.02, p = 0.04, **Figure 9A**).

In the exploratory analyses, the linear mixed model for the V&E factor revealed a significant main effect of preference (F(1,189) = 8.04, p < 0.01). Higher scores of the V&E factor in the preferred condition (4.84 ± 0.24) were found compared to scores in the no-preferred condition (4.53 ± 0.24, t(195.2) = -2.79. p < 0.01, **Figure 9C**). Also, the model revealed an interaction between preference and awareness of spatial sound (F(1,189) = 5.65, p = 0.02). The interaction showed that the main effect of preference was mainly modulated by the spatial sound unaware group. That is, in the unaware group, the preferred condition (4.87 ± 0.35) led to higher vestibular sensations and elevated self-location scores than the no-preferred condition (4.29 ± 0.35, t(195.2) = -3.56, p < 0.001, **Figure 9D**), but such difference was not observed in the aware group.

Linear mixed models with 'sensorimotor stimulation' as a fixed effect showed a significant main effect of the sensorimotor stimulation for the disembodiment factor (F(1,147.12) = 13.04, p < 0.001). Post-hoc comparisons found the motor condition (3.89 ± 0.27) led to greater disembodiment, in respect to the no-motor condition (3.38 ± 0.29, t(148.21) = -3.60, p < 0.001, **Figure 9B**).

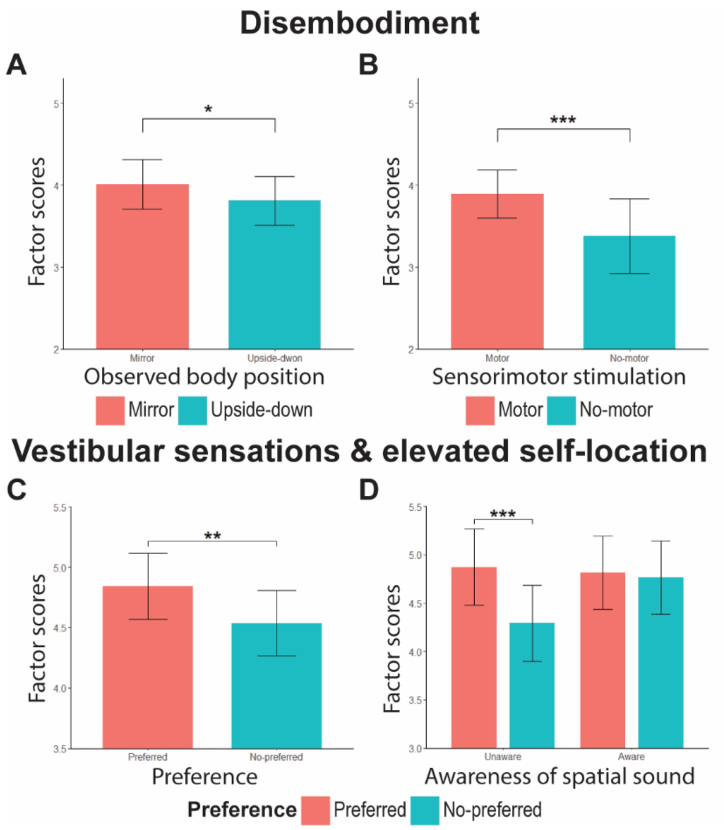

Figure 9. Results of subjective experience from factor analysis in Study 5. Factor scores about disembodiment and vestibular sensations & elevated self-location (V&E) are shown based on observed body position (**A**), sensorimotor stimulation (**B**), preference (**C**), and preference with the awareness of spatial sound (**D**). 95% confidential intervals are shown in squared brackets. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Relationship between disembodiment and vestibular sensations.

The linear mixed model with V&E factor as outcome highlighted a significant main effect of disembodiment factor ($F(1,220.78) = 22.56$, $p < 0.001$): V&E factor was positively associated with disembodiment (regression coefficient = 0.34, **Figure 10**)

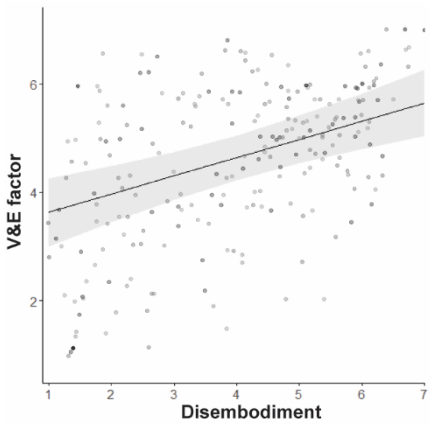

Figure 10. A positive relationship between disembodiment and vestibular sensations & elevated self-location. Each data point indicates the factor scores for each OBE-like scenario, participant, and trial. X-axis and Y-axis represent scores of the disembodiment factor and scores of the V&E factor, respectively. Grey shadow represents 95% confidence intervals.

Discussion

Several studies tried to induced OBE illusions (Ehrsson 2007, Lenggenhager, Mouthon et al. 2009, Ionta, Heydrich et al. 2011, Pfeiffer, Lopez et al. 2013, Pfeiffer, Schmutz et al. 2014, Pfeiffer, Grivaz et al. 2016). However, the OBE illusions in these experiments were mild or did not cover the whole spectrum of OBEs (disembodiment, autoscopy, elevated self-location, and vestibular sensations). Here, we have strived to achieve a realistic and full-blown OBE illusion. Also, we have investigated how various factors influence the OBE illusion to understand the mysterious mechanisms of OBEs. For these purposes, we developed a new MR system and created a variety of virtual OBE-like scenarios. As a result, we observed five main findings.

First, we showed that our virtual OBE-like scenarios could induce greater OBE-like sensations such as disembodiment, elevated self-location, and floating sensation, compared to the experience of BV. These results were in line with previous studies related to the OBE illusions (Ehrsson 2007, Lenggenhager, Mouthon et al. 2009, Ionta, Heydrich et al. 2011). Moreover, we found that stronger visuo-vestibular conflict led to vestibular sensations, based on a feeling of lightness. This result was similar to previous studies demonstrating that stronger visuo-vestibular conflict resulted in higher elevated self-location (Pfeiffer, Lopez et al. 2013, Pfeiffer, Schmutz et al. 2014, Pfeiffer, Grivaz et al. 2016).

Our second main finding was that the OBE illusion did not depend on observed body positions. Actually, concerning observed body position, we found contradictory results between Studies 1 and 2. In Experiment 1, the upside-down position led to a greater feeling of disconnection with the physical body, compared to the mirror position. However, the mirror position resulted in greater disembodiment than the upside-down position in Experiment 2. Of course, due to the factor analysis, the question about disconnection in Experiment 1 was integrated into the disembodiment factor. So, we could not say these two variables are the same. Moreover, through the exploratory analyses, it seemed more likely that the preference for observed body position contributed to the OBE illusion rather than observed body position per se. Our results are in line with previous claims (Brugger 2002) and suggest that there might not be a dominant observed body position in OBEs. In detail, Brugger (2002) explained that, among autoscopic phenomena, autoscopic hallucination (AH) and heautoscopy (HAS) have dominant observed body position (AH – mirror-reversal position & HAS – Non-revering mirror position), but there is little explicit information about observed body position during OBEs. In the absence of this information, our result might imply no dominant observed body position.

Our third finding was the effects of multisensory and conscious factors on the OBE illusion. The exploratory analyses revealed that preference and spatial sound led to higher elevated self-location and greater vestibular sensations depending on the awareness of spatial sound. However, there is one controversial point in these results. While participants who were aware of spatial sound showed an enhancing effect of spatial sound on elevated self-location, unaware participants showed an inhibiting effect of spatial sound on self-location. Such results can be explained in two ways. First unaware participants' immersion to VR could have been unconsciously broken due to the incomprehensible sound changes. A second explanation would be expectancies for experiment results (Lush 2020). In other words, if participants have expectancies for the results, these can induce a voluntary top-down control of phenomenologies like bias or prior. Therefore, in future studies, the experiment should include proper ways to control for expectations and difficulties of imaginative suggestion (Lush 2020).

Fourth, we found that the synchronous sensorimotor stimulation led to greater disembodiment than the no-sensorimotor stimulation. However, such a result contradicts previous results from the literature (Bourdin, Barberia et al. 2017). Bourdin and colleagues showed that the virtual OBE-like scenario with sensorimotor stimulation led to a higher feeling of connection with the observed body than the other scenario with no-sensorimotor stimulation. However, there were two conjectures which could explain such discrepancies. First, in addition to the sensorimotor stimulation, Bourdin's study included synchronous visuo-tactile stimulations to maximize the connection between the physical body and the observed body. Second, although the question between the two experiments may seem the opposite, it may not be so or even be the same. To feel disembodiment, firstly the connection with the body must be at the base to some extent. However, if there is no connection at all, there is no reason to feel disembodiment. In fact, Bourdin's study reported a positive correlation between self-identification and connection, but our study showed a positive relationship between self-identification and disembodiment (Refer to Table S1 of the supplementary session).

Lastly, our study confirms and extends the knowledge regarding OBE-like sensations. Using a factor analysis, we confirmed the positive relationship between elevated self-location and vestibular sensations, in line with previous work (Lenggenhaga, Mouthon et al. 2009). Furthermore, we found a positive relationship between disembodiment and vestibular sensations. These results were in line with previous studies supporting that vestibular signals importantly contribute to anchoring the self to the body (Ferrè, Lopez et al. 2014, Deroualle, Toupet et al. 2017, Lopez and Elziere 2018). Even this extends these studies by suggesting that distorting to anchor the self to the body (disembodiment) might lead to vestibular sensations.

Although we induced greater OBE-like sensations in comparison to BV, we cannot be sure that the OBE-like sensations in our study are the same as the experience of OBE in patients. Therefore, future work should induce OBE illusion in OBE patients or in people who experienced OBEs before.

Altogether, we strived to induce a mental state similar to full-blown OBEs and we investigated how different factors affect OBE illusions to get insights into the underlying mechanisms of OBEs. As a result, we showed that audio-visual, sensorimotor, and conscious factors contributed to the OBE illusion. Further work should consider the contribution of new factors (e.g. dynamic vestibular feedback using a motion platform) and inter-personal differences such as preference or visual field dependency to OBE illusions. Such studies will not only help understanding OBEs but will also expand knowledge about bodily self-consciousness.

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Supplementary materials

Supplementary Movies

Movie S1: https://drive.google.com/open?id=1iQG3BJtvdrI6HMaiP1x67Fy44Yj4K4ya

Movie S2: https://drive.google.com/open?id=1iBZl27E6szjkadzqks-Tnbcs5UVY1rd7

Movie S3: https://drive.google.com/open?id=1i7pYxu8UQ80jR6tI6KaJ12WfbICNdQG7

Movie S4: https://drive.google.com/open?id=1i2uBk05eTqeiOqTRBXLCRodrVSN2nb-1

Movie S5: https://drive.google.com/open?id=1iEgxK2Ce9JzSFaYAnKTEPF__jdKpJnc9

Movie S6: https://drive.google.com/open?id=1iPC9Ws_9ImWvIzoH4Oj1y8Sk46FNNcI7

Supplementary Table

Question	Factor 1	Factor 2
1. I felt as if I was outside my physical body	0.843	0.104
2. I felt as if I was disconnected from my physical body	0.949	
3. I felt as if I was separated from my physical body	0.929	
4. I felt as if I became lighter	0.167	0.717
5. I felt as if I was floating	0.152	0.785
6. I felt as if I was located from where I saw the scene	-0.195	0.827
7. I felt as if the body I saw was my body	0.195	
8. I felt as if I had more than three bodies (control)		

Table S1. Loadings of factor analysis on questionnaire data from Study 5

Chapter 3 General discussion

3.1 Summary of results

The overall aim of my research was to modulate embodiment and investigate the effects of altered embodiment on vestibular sensation. To modulate embodiment, I utilized sensorimotor and multisensory stimulation methods from cognitive neuroscience. Also, I combined these methods with aviation robotics, a flight simulator, and VR to develop new paradigms to induce the vestibular sensations and to investigate its relationship with embodiment

Study 1 demonstrated embodiment of an observed body in a remote place by identifying PPS around the observed body – an objective, and implicit measure. In detail, observing a body from a third-person viewpoint and moving the body in the synchronized way with movements of a physical body can induce embodiment of the observed body (Sensorimotor FBI). During the FBI, I measured PPSs around both the viewpoint and the observed body. As PPS appears when an object or a system is embodied, I could objectively suggest that the observed body was embodied. However, just observing the body without movements did not show PPS around the observed body. In other words, to induce embodiment of the observed body in a remote place, just seeing a static body image is not enough, but correct sensorimotor stimulation is required.

In Study 2, I found that manipulating embodiment could influence vestibular sensations by extending the FBI from Study 1 into a flight simulator. Participants experienced flight simulation on the interactive flight simulator (Birdly) while seeing a virtual avatar from a third-person viewpoint. The movements of the avatar were synchronized with the movements of participants. The FBI set-up induced embodiment of the virtual avatar and better flight sensations, compared with other conditions where the avatar movements were not synchronized or there was a virtual box instead of the avatar. Mediation analysis showed the causal relationship from embodiment of flight sensations. Furthermore, improved embodiment also boosted piloting performance and learning.

In Study 3, I showed that combining sensorimotor and multisensory stimulation could further enhancement of embodiment compared to Study 2. Also, although we could not see the difference in flight sensations between the combined stimulation and the other control conditions, we could see the steeper positive relationship embodiment and flight sensation than Study 2. I combined the paradigm in Study 2 with a new wearable haptic device. This haptic device provided synchronized visuo-tactile stimulation corresponding to the movements of the physical body. The multisensory FBI led to better embodiment of the virtual avatar, but a mismatch between visuo-tactile stimulation and movements did not show such improvement. As in Study 2, enhanced embodiment mediated better flight sensations. Moreover, although better embodiment did not result in better piloting performance it induced faster-learning speed.

In Study 4, I developed a new MR system to induce a full-blown OBE illusion. Using the system, participants could see a photorealistic avatar from a BV in a mixed environment. During a virtual OBE-like scenario, they could experience a viewpoint change from a BV to an elevated viewpoint and could observe their body from an elevated viewpoint. I could modify several factors in the virtual OBE-like scenario such as observed body position and multisensory or sensorimotor stimuli. As a pilot experiment, I investigated the effects of observed body position (mirror, no-mirror, and upside-down) on OBE illusion. Through the experiment, I found all OBE-like scenarios with different observed body positions showed greater disembodiment, greater floating sensation, and higher elevated self-location compared to BV, by using an MBDT and a questionnaire. Also, there was a significant difference in disembodiment between the mirror position and the upside-down position.

Lastly, in Study 5, I found contributions of conscious, multisensory, and sensorimotor factors to OBE illusion and a positive relationship between disembodiment and vestibular sensations. Based on Study 4 and previous studies linking OBE to impairments of multisensory integration, I created different OBE-like scenarios including observed body position, audio-visual (spatial sound) stimulation, and sensorimotor stimulation. Also, conscious factors such as preference and awareness of spatial sound were considered for the OBE illusion. By comparing virtual OBE-like scenarios based on these factors, I showed that preferred body position, spatial sound, and synchronized sensorimotor stimulation led to greater OBE-like sensations and higher elevated self-location, compared to the other factors. Furthermore, regardless of the factors, the study demonstrates a positive relationship between disembodiment and vestibular sensations.

3.2 Embodiment and peripersonal space

In line with my hypothesis, Study 1 showed the FBI using active sensorimotor stimulation led to PPS around an observed body in a distant location. In other words, we objectively confirmed that participants embodied the observed body through PPS, which is one of the measures of embodiment. However, PPS around the observed body was not found without active sensorimotor stimulation. The results were in line with previous studies demonstrating that the FBI only occurs when there is correct multisensory or sensorimotor stimulation (Lenggenhager, Tadi et al. 2007, Maselli and Slater 2013, Kokkinara and Slater 2014, Debarba, Bovet et al. 2017). Also, my results confirmed the existence of PPS around the viewpoint, as shown in previous studies in humans (Serino, Noel et al. 2015) and monkeys (Fogassi, Gallese et al. 1996). Thus, near the viewpoint and for looming visual stimuli, the responses to the tactile stimuli were sped up by integrating tactile and visual stimuli.

Study 1 is the first study to show distinct PPS around the observed body in a remote place. Most previous studies have focused on behavioral and physiological changes around the visual viewpoint (physical body), although questionnaire results revealed that the FBI made participants embody the observed body. For example, after induction of the FBI, Lenggenhager and her colleagues (2007) showed that self-location of the physical body drifted towards the observed body position. Another study identified that embodiment of the observed body reduced arousal responses of the physical body to painful stimuli (Romano, Pfeiffer et al. 2014). Moreover, although there was a study to measure PPS after FBI induction, this study also investigated only around the physical body (Noel, Pfeiffer et al. 2015). This study showed that the FBI induced an extension of PPS in the front-space of the physical body towards the observed body and a shrink of PPS in the back-space of the physical body. There had been no clue about what happens in PPS around the observed body after the FBI, but only one study investigated PPS in a remote place (Teneggi, Canzoneri et al. 2013). Teneggi investigated PPSs around the physical body and a third person when participants interacted with the third person. Similar to the FBI, PPS around the physical body extended towards the third person after a cooperative interaction, but PPS around the third person was not found. That is, a temporal social interaction with a third person could transform PPS around the body like the FBI, but it is not enough to induce embodiment of the third person. Therefore, Study 1 was the first showing embodiment of the observed body in a separate location through the existence of PPS

Another novelty of Study 1 is to objectively show that healthy participants can be located in two different bodies simultaneously, as described in the case of a heautoscopy. Active sensorimotor stimulation led to the creation of distinct PPSs around both the viewpoint and the observed body. This could be a behavior marker of a duplication of the self, a crucial feature of heautoscopies (Blanke, Landis et al. 2004). Several studies have suggested the duplication of the self in healthy participants using different experimental manipulations (Stratton 1899, Mizumoto and Ishikawa 2005, Aymerich-Franch, Petit et al. 2016). Especially, Stratton (1899) and Mizumoto and Ishikawa (2005) demonstrated that double representations could be induced by similar sensorimotor stimulation. However, the result was only based on subjective reports such as an interview and a questionnaire. Therefore, my results firstly suggested the double representations of the self objectively using the behavioral measure of multisensory integration.

On the other hand, the results of Study 1 do not fit with Noel's study (Noel, Grivaz et al. 2015). Noel measured PPS around the physical body while walking and standing without seeing the observed body. Although the experimental setup was similar to Study 1, the study found an extension of PPS in the walking condition, compared to standing. However, it might be due to the difference in embodiment. In Study 1, participants saw their observed body to induce embodiment of the observed body while they walked forward, but the study of Noel, Grivaz et al. (2015) did not manipulate such embodiment. Also, it might be due to the small number of participants.

Due to the lack of data on subjective experience from a questionnaire, the result cannot confirm relationships between the subjective experience and PPS properties. Therefore, further research is needed to establish relationships by adding a questionnaire in the experiment.

There are three possible applications of Study 1 in the research of bodily self-consciousness. First, my study could provide a new experimental paradigm to study the mechanisms of heautoscopy by inducing a heautoscopy illusion in healthy participants. Second, Study 1 opens the possibility to investigate the roles of visual viewpoint on embodiment and PPS. As Study 1 used a drone for the experimental set-up, it is possible to select any viewpoint during FBI induction. Lastly, the paradigm can be exploited to investigate visuo-vestibular interaction. PPS is depending not only on the visual and tactile information but also on the vestibular information (Bufacchi and Iannetti 2016). Therefore, by utilizing conflicts between visual inputs and vestibular inputs, it is possible to find how visual information, vestibular information, and their interaction contribute to embodiment and PPS. This is also related to the first-person perspective of bodily self-consciousness.

3.3 Embodiment, flight simulators, and VR

The results from Study 2 and Study 3 showed that insights and methodologies from cognitive neuroscience, especially related to bodily self-consciousness and embodiment, could be transferred to a flight simulator for better realism, better performance, and faster learning. First, I confirmed that the FBI could be achieved using sensorimotor or multisensory stimulation in a flight simulator. This is an extension of existing research of embodiment (Stratton 1899, Farrer, Franck et al. 2003, Jeannerod 2006, Lenggenhager, Tadi et al. 2007, Serino and Haggard 2010, Blanke 2012, Blanke, Slater et al. 2015, Debarba, Bovet et al. 2017). Also, as well as the previous studies, the induction of embodiment of a virtual body was achieved only while synchronous sensorimotor or multisensory stimulation was applied and participants saw a virtual body, but not a virtual object (Lenggenhager, Tadi et al. 2007, Debarba, Bovet et al. 2017).

Moreover, Study 2 found that the modulation of embodiment through the FBI influenced flight sensations. This result is in line with previous studies showing that alterations of embodiment caused by neurological disease are linked with vestibular hallucinations, illusory self-motion, and abnormal self-location (out-of-body experiences and heautoscopy (Blanke and Mohr 2005, Heydrich and Blanke 2013)). Similarly, this is consistent with some studies revealing that the FBI in healthy participants induced vestibular sensations and changed vestibular perception (Lenggenhager, Mouthon et al. 2009, Ionta, Heydrich et al. 2011, Nesti, Rognini et al. 2018). Generally, these studies suggest that vestibular information is important to link the self to the physical body, but if embodiment is manipulated by neurological disease or the FBI, the contribution of vestibular inputs becomes weaker than the contribution of visual inputs and it decreases the link between the self and the body. I speculate that my result of flight sensations might share similar mechanisms of visuo-vestibular integration. At the same time, the new relationship between embodiment and flight sensations is another novelty of Study 2 and 3. Previous studies also tried to investigate this relationship in flight simulation, but could not reveal one (Amato, Perény et al. 2019, Zhang, Riecke et al. 2019). This is directly linked with the main question of my thesis.

Also, Studies 2 and 3 showed that better embodiment led to better piloting performance and higher learning rates. These results are compatible with previous studies about flight simulators and drone piloting. These studies developed new human-machine interfaces to improve realism in flight simulation or drone piloting by providing more intuitive control methods (Cherpillod, Mintchev et al. 2017, Miehlbradt, Cherpillod et al. 2018, Yoon, Lee et al. 2018). As a result, the new interfaces achieved better piloting performance and faster learning like Study 2 and 3. Similarly, recent research in fields of VR, neuroprosthetics, and robotics attempted to improve embodiment, motor performance, and learning by providing various sensory feedback (Brizzi, Peppoloni et al. 2017, Makin, de Vignemont et al. 2017, Stephens-Fripp, Alici et al. 2018, Seinfeld, Feuchtner et al. 2020).

Studies 2 and 3 provide cognitive guidelines for a new generation of flight simulators and VR technologies. Current development in flight simulators and VR only focuses on providing realistic feedback and minimizing sensorimotor latencies (Elbamby, Perfecto et al. 2018). However, without considering multisensory bodily stimulation and cognitive aspects, it will be stuck in the uncanny valley of technology (Berger, Gonzalez-Franco et al. 2018). That is, just developing a system that can give multimodal and accurate feedback could make the subjective experience worse unless it considers multisensory bodily integration or a cognitive (causal) explanation about the feedback. Therefore, I suggest that multisensory stimulation and cognitive aspects should be included when a new flight simulator or VR system is designed.

Due to the FBI paradigm, the preferred viewpoint for gaming, and the similarity to OBE, Study 2 and 3 used a third-person viewpoint for the experimental setups. However, because of this, it was beyond the scope of this study to compare the results with a first-person viewpoint that is the usual viewpoint in daily life. Therefore, future studies should take into account including a first-person viewpoint flight simulator and the way to integrate multisensory and sensorimotor stimulation into the flight simulator with the first-person viewpoint.

Moreover, I suggest that it is possible to extend these manipulations of embodiment into other fields where embodiment and vestibular sensations are playing an important role. For example, VR games including water or space as a background could exploit the paradigms to give more realistic vestibular sensations. Also, the application of these manipulations in sports training could lead to better learning of motor skills. So far, although there has been no research between embodiment and learning in sports training, one study showed that embodiment in firefighter training led to a sense of embodied identify mobility boosting motivation for learning and achievement (Yarnal, Hutchinson et al. 2006). Also, another study showed that embodiment in the learning of physics content led to better retention of certain types of knowledge (Johnson-Glenberg, Megowan-Romanowicz et al. 2016). In line with these studies, I would suggest that it is possible to induce better learning of sports by inducing embodiment.

3.4 Multisensory, sensorimotor, conscious basis of OBE illusion

In Study 4, I developed a new mixed reality (MR) system to induce a full-blown OBE illusion that is strong and covers the whole characteristics of OBE. Through the MR system, it was possible to create a variety of virtual OBE-like scenarios. Studies 4 and 5 showed that virtual OBE-like scenarios could induce OBE-like sensations such as disembodiment, vestibular sensations, and elevated self-location. These results are similar to previous studies about OBE illusion using multisensory stimulation (Lenggenhager, Mouthon et al. 2009, Ionta, Heydrich et al. 2011, Bourdin, Barberia et al. 2017). Moreover, the factor analysis from Study 5 revealed the positive relationship between elevated self-location and vestibular sensations and this confirms the previous finding from the study of Lenggenhager and her colleagues (Lenggenhager, Mouthon et al. 2009).

Furthermore, Study 5 provides new insight into the relationship between disembodiment and vestibular sensations. That is, the more participants feel to be disembodied from the physical body, the stronger vestibular sensations were felt. This result is in line with previous studies supporting that vestibular signals significantly work by anchoring the self to the body (Ferrè, Lopez et al. 2014, Deroualle, Toupet et al. 2017, Lopez and Elziere 2018). Even this extends these studies by implying that impairing the anchoring of the self to the body (disembodiment) might result in vestibular sensations. This is in line with the main question of the current thesis: how modulation of embodiment influences vestibular sensations.

Studies 4 and 5 investigated influences of observed body position on OBE illusion, but the studies showed opposite results for each other. Through exploratory analyses, it seems that preference for observed body position contributes to OBE illusion rather than observed body position per se. In other words, I suggest observed body position per se does not influence OBE illusion, but preference plays an important role in OBE illusion. Moreover, the data might answer a question from Brugger’s study (Brugger 2002). He explained that, among autoscopic phenomena, there had not been clear data about observed body position during OBE, whereas autoscopic hallucination (AH) and heautoscopy (HAS) have dominant positions of the observed body (autoscopy, AH – mirror-reversal position, HAS – Non-reversing mirror position). According to my data, I can speculate that there might be no dominant observed body position in OBE.

Study 5 also extends the findings of previous studies about OBE illusion. These studies mainly focused on effects of visuo-tactile and visuo-vestibular stimulation on OBE illusion (Ehrsson 2007, Lenggenhager, Mouthon et al. 2009, Ionta, Heydrich et al. 2011, Pfeiffer, Lopez et al. 2013, Pfeiffer, Schmutz et al. 2014, Pfeiffer, Grivaz et al. 2016). However, my study focused on the roles of other multisensory factors such as audio-visual and sensorimotor stimulation and conscious factors such as preference and awareness of spatial sound. Most results from these factors were consistent with and expanded the existing evidence of OBE. However, sensorimotor stimulation led to contradictory result to the claims of Bourdin and his colleagues (Bourdin, Barberia et al. 2017). In his study, synchronized sensorimotor stimulation between the physical body and the observed body resulted in higher connection compared to no visuomotor stimulation, whereas Study 5 showed that synchronized visuomotor stimulation induced higher disconnection compared to no sensorimotor stimulation. There are two speculations that could account for such discrepancies. First, Bourdin's study included not only sensorimotor stimulation but also visuo-tactile stimulations to maximize the connection between the physical body and the observed body. Second, although the question between the two experiments may seem the opposite, it may not be so or even be the same. To feel disembodiment, firstly the connection with the body must be at the base to some extent. However, if there is no connection at all, there is no reason to feel disembodiment. In fact, Bourdin's study reported a positive correlation between self-identification and connection, but our study showed a positive relationship between self-identification and disembodiment (Refer to Table S1 in Study 5).

However, I cannot confirm if the OBE-like sensations in Studies 4 and 5 are the same with OBE in patients. I identified the sensations during virtual OBE-like scenarios were higher than these during the experience of the body-centered viewpoint. Although the sensations covered the whole characteristics of OBE, the sensations could be different from those of OBE patients. Thus, future study should include OBE patients or healthy participants who had spontaneous OBE in these virtual OBE-like scenarios and compare the experience with their previous OBE. As well as Study 1, measures of PPS can be used to investigate and understand OBE illusion as PPS reflects embodiment and multisensory properties, especially vestibular characteristics (De Vignemont 2011, Bufacchi and Iannetti 2016, Serino 2019). For example, measuring PPS during virtual OBE-like scenarios can objectively demonstrate if participants are disembodied from the physical body. Also, it could clarify whether OBE illusion is just depending on visual stimulation or considering vestibular and other multisensory integrations. Moreover, another line of future research should integrate dynamic vestibular stimulation using a motion platform. So far, all OBE illusion studies utilized a conflict between dynamic visual inputs and static vestibular inputs. However, for clearer understanding and investigating multisensory aspects of OBE, I suggest that considering dynamic vestibular inputs would be necessary.

As my study is creating a full-blown OBE illusion in a healthy population, measuring neural correlates using electroencephalography (EEG) or functional magnetic resonance imaging (fMRI) during the OBE illusion could provide insights about brain mechanisms of OBE. Studies about neurological patients have suggested that OBEs are caused by the failure of multisensory integrations (Lopez, Halje et al. 2008). Thus, it could be possible to provide evidence for the speculation or new insights by investigating neural activations in important areas for OBE such as TPJ, the posterior superior temporal gyrus, the angular gyrus and multisensory cortices such as the ventral intraparietal region and the medial superior temporal region (Blanke, Ortigue et al. 2002, Ionta, Heydrich et al. 2011, Pfeiffer, Serino et al. 2014).

3.5 Conclusion

Throughout the current thesis, I have strived to answer a question: “how does modulation of embodiment influence vestibular sensations?”. To answer this question, I developed new experimental setups using aviation robotics, a flight simulator, and VR. Besides, I modulate embodiment with sensorimotor and multisensory stimulation. Collectively, my studies show that embodying a flying avatar and being disembodied from the physical body leads to stronger vestibular sensations compared to embodying the avatar less and being less disembodied from the body. I suggest that these embodiment modulations might induce a reduction in the contribution of vestibular input. Thus, future research should investigate changes in the contribution of vestibular input during modulations of embodiment. For example, if embodiment is modulated with a conflict between dynamic visual stimuli and dynamic vestibular stimuli by using a motion platform, it is possible to calculate to changes of relative weights of visual stimuli and vestibular stimuli.

At the same time, I investigated the effects of embodiment modulation for behaviors and perception such as PPS, motor performance, learning, and height perception. Relationships of embodiment with behaviors and perceptions have been interesting topics in the fields of Robotics, Neuroprosthetics, VR, and teleoperation (Brizzi, Peppoloni et al. 2017, Makin, de Vignemont et al. 2017, Stephens-Fripp, Alici et al. 2018, Seinfeld, Feuchtner et al. 2020). My thesis also supports and extends previous studies in these fields by emphasizing consideration of sensorimotor and multisensory aspects.

Studies from my thesis corroborate and extend our current understanding of embodiment and interaction between embodiment and the vestibular system. Also, my thesis showed that technological advances in aviation robotics and VR can provide new paradigms or methodologies to investigate cognitive neuroscience, especially bodily self-consciousness and, at the same time, insights and methodologies from bodily self-consciousness can also improve the quality of engineering fields such as flight simulators. However, as discussed in the previous section, there are still many scientific questions that need to be answered and many possibilities to apply the knowledge and methods of cognitive neuroscience engineering disciplines and their technical challenges. Therefore, the scientific community should continue the endeavor of understanding underlying mechanisms of embodiment and translating that knowledge into practical ways such as implementing immersive virtual experience and improving motor performance.

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Abbreviations

ACME	Average causal mediation effect
ADE	Average direct effect
AH	Autoscopic hallucination
BSC	Bodily self-consciousness
BV	Body-centered viewpoint
EEG	Electroencephalography
EV	Elevated viewpoint
FBI	Full-body illusion
fMRI	Functional magnetic resonance imaging
HAS	Heautoscopy
HMD	Head-mounted display
m	Meter
MBDT	Mental ball drop task
OBE(s)	Out-of-body experience(s)
PPS	Peripersonal space
RHI	Rubber hand illusion
RT	Reaction time
rTPJ	Right temporal-parietal junction
V&E factor	Vestibular sensations & elevated self-location factor
VLI	Virtual leg illusion
vm	Virtual meter
VR	Virtual reality

Curriculum Vitae

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EDUCATION

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2016 – present **EPFL (École polytechnique fédérale de Lausanne), Lausanne, Switzerland**
Ph.D. student in *Neuroscience from May. 2016*
- Thesis: Flight of mind: Sensorimotor and multisensory embodiment with aviation robotics, flight simulator, and virtual reality

2008 – 2015 **KAIST (Korea Advanced Institute of Science and Technology), Daejeon, Korea**
B.S. in Dept. of *Bio and Brain Engineering Feb. 2015*
- Graduate with Magna Cum Laude
- Double major: Business and Economics Program
- National Science and Engineering Scholarship (2008-2015, $1,524 per semester)

WORK & RESEARCH EXPERIENCES

==

2016 – present **Laboratory of Cognitive Neuroscience**, EPFL, Doctoral student
Supervisor: Prof. Olaf Blanke, Laboratory of Cognitive Neuroscience (LNCO)
- Inducing out-of-body experience in healthy subjects with virtual reality
- Enhancing embodiment in flight simulation with sensorimotor and multisensory stimulation to improve flight sensation and piloting performance
- Teaching assistantship in bachelor's courses on Neuroscience

2016 **Hyprsense**, 2-month software engineer intern
Supervisor: Jungwoon Park, Ph.D. (Co-Founder and CSO, Hypersense, South Korea)
- Using a depth camera, develop a program and which automatically collects data about face land-marks from a real subject

2015 **Center for Cognition and Sociality,** Institute for Basic Science (IBS), Research assistant
Supervisor: Shin Hee-Sup, MD, Ph.D. (IBS, South Korea)
- Inducing social behavior and modeling cooperation with wireless deep brain stimulation
- Investigating the role of the thalamic reticular nucleus in absence seizure of a mouse model with single-unit recording

2013 & 2015 **ybarin(Seoul, Korea),** Researcher
- Simultaneous recording of electroencephalogram (EEG) during transcranial direct-current stimulation (tDCS) in human
- EEG and Behavior analysis with SPSS & MATLAB: Dynamics & connectivity analysis
- Electrocorticography (ECoG) experiment on Beagle with tDCS stimulation

2014 **Shimojo Psychophysics Laboratory,** Caltech, Summer research student
Supervisor: Shinsuke Shimojo, Ph.D. (Computation & Neural Systems, Caltech, USA)
- With EEG hyperscanning and motion tracking, investigating interpersonal neural and behavioral synchronization after social activities
- Leading to sound-induced visual illusion using audio-visual stimulation
- Fund: $4,800 from Dept. of Bio and Brain Engineering (KAIST)

2011 – 2013 **Military service,** Republic of Korea Army
- Discharged upon completing military service as a sergeant
- Combat intelligence army in Command and Control Center in Republic of Korea Army to guard Military Demarcation Line

PUBLICATIONS

==

M Song, Y Shin, K Yun, "Beta frequency EEG activity increased during transcranial direct current stimulation", Neuroreport. 2014;25(18):1433-6.

M. Song, G. Rognini, A. Cherpillod, A. Nesti, P. Grivaz, D. Floreano & O. Blanke, Flight of mind: Embodiment of the flying avatar improves flight sensations and piloting performance (in preparation)

M. Song, P. Grivaz, O. A. Kannape, M. Perrenoud, G. Rognini, J. B. Ruiz, D. Floreano, A. Serino & O. Blanke, Superposition of the self: Peripersonal space dynamically remaps around two distinct locations (in preparation)

M. Song, S. Betka, F. Lance, O. A. Kannape, B. Herbelin, O. Blanke, Disembodied from the body: virtual Out-of-body experience illusion (in preparation)

SKILLS

==

Software skills: C/C++, C#, Python, Java, MATLAB, R, LabVIEW, Blender, and COMSOL
Virtual reality: Unity, Motion tracking and a virtual avatar reconstruction with Kinect, Hand tracking with leap motion
Hardware design: Arduino
Neuroimaging: Acquisition and analysis of EEG in human / ECoG in beagle / EEG, local field potential (LFP), and single unit in mouse
Bioinstrumentation: Measuring interoceptive signals with BIOPAC, Motion tracking using Vicon system, Eye-tracking using Eyelink

EXTRACURRICULAR ACTIVITIES

==

2013 – 2014 Founder and President of KAIST Dep. Cocktail Association "Secret Bar"
2008 – 2009 Member of KAIST Student Robot Association: "Microrobot Research (Mr)"

LANGUAGES

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Korean	**Mother tongue**
English	**Fluent**
	Summer research program in Caltech
	4th year PhD student in EPFL
French	Basic knowledge

PERSONAL INFORMATION

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National Technology of Certificate for Craftsman Bartender in Korea (2013)
Korean and Swiss (type B) driver's licenses

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