Vestibular contribution to bodily self-consciousness and multisensory cortical processing

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Abstract

How does the self relate to the body? Bodily self-consciousness, i.e. the sense of being a subject bound to a body, involves a first-person perspective (1PP), i.e. the sense of being directed at the world. Prior research suggests that bodily self-consciousness depends on brain mechanisms integrating multisensory bodily signals. However, the specific multisensory mechanisms of 1PP are poorly understood. Here, I defend the thesis that the vestibular system, i.e. the sensory system encoding rotational and linear accelerations of the head, contributes to 1PP and related multisensory processing in the brain. The first part of my thesis presents experimental evidence showing that 1PP was influenced by multisensory conflict about the direction of gravity and the location of the body. 1PP depended on integrated visual-vestibular signals and was functionally distinct from another aspect of bodily self-consciousness: self-identification, i.e. the feeling that a particular body is 'mine'. The second part of my thesis presents the electrical neural correlates by which vestibular stimulation affected somatosensory and visual cortical processing. Passive whole-body yaw rotation naturally and selectively stimulated the vestibular system while the evoked responses to somatosensory or visual stimuli were recorded by electroencephalography. Electrical neuroimaging analysis showed temporal-specific vestibular effects on somatosensory and visual evoked potentials, localized by source estimations to distinct regions of the somatosensory, visual, and vestibular cortical networks. Collectively, the results from my thesis suggest that the vestibular system contributes to 1PP and multisensory cortical processing and imply that the vestibular system should not be neglected when studying higher brain function and neurobiological mechanisms of consciousness.

Keywords: Self-consciousness; multisensory integration; first-person perspective; full-body illusion; vestibular system; semicircular canals; gravity; EEG; virtual reality; neuroscience robotics

Zusammenfassung

Was ist das Verhältnis zwischen dem Selbst und dem Körper? Körperliches Selbstbewusstsein ist die Erfahrung ein Subjekt zu sein, das an den Körper gebunden ist und die umliegende Welt von einer Ersten-Person Perspektive (1PP) wahrnimmt. Frühere Studien weisen darauf hin, dass das körperliche Selbstbewusstsein von neuronalen Mechanismen abhängig ist, die multisensorische körperliche Reizinformationen integrieren. Allerdings sind die spezifischen multisensorischen Mechanismen der 1PP bislang unbekannt. Hier verteidige ich die These, dass das Vestibuläre System, d.h. das sensorische System das Dreh- und lineare Beschleunigungen des Kopfes wahrnimmt, zu 1PP und zugehörigen multisensorischen Funktionen beiträgt. Der erste Teil meiner Dissertation präsentiert experimentelle Daten, die zeigen, dass 1PP von multisensorischem Sinnreizkonflikt bezüglich der Richtung der Schwerkraft und der Position des Körpers im Raum beeinflusst wurde. 1PP war abhängig von integrierten visuell-vestibulären Signalen und war funktional verschieden von einem anderen Aspekt des körperlichen Selbstbewusstseins: Selbstidentifikation, der Erfahrung, dass ein bestimmter Körper ‚mein' ist. Der zweite Teil meiner Dissertation präsentiert die elektrischen neuronalen Korrelate, die vestibulären Effekten auf somatosensorische und visuelle kortikale Verarbeitung zugrunde liegen. Mit passiven Rotationen des Körpers stimulierten wir auf natürliche und selektive Weise das Vestibuläre System unserer Probanden und nutzten Elektroenzephalografie um die Effekte dieser vestibulären Stimulation auf somatosensorisch- und visuell-evozierte Potentiale zu messen. Unsere Analysen ergaben zeitlich-spezifische vestibuläre Effekte auf somatosensorische und visuelle evozierten Potentiale, die mittels neuronaler Quellenanalyse in verschiedenen Regionen des somatosensorischen, visuellen, und vestibulären kortikalen Systems lokalisiert wurden. Insgesamt unterstützen die Ergebnisse meiner Dissertation die Idee, dass das Vestibuläre System zu 1PP und multisensorischer kortikaler Verarbeitung beiträgt und dass das Vestibuläre System nicht ignoriert werden sollte, wenn man höhere Hirnfunktionen und die neurobiologischen Mechanismen von Bewusstsein untersucht.

Schlüsselbegriffe: Ich-Bewusstsein; Intersensorische Integration; Erste Person-Perspektive; Ganzkörper-Illusion; Vestibuläres System; Vestibuläre Bogengänge; Gravitation; EEG; Virtuelle Realität; Neurowissenschaft-Robotik

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1 Introduction

1.1 Motivation

How does the self relate to the body? This question has fascinated humankind for centuries and continues puzzling scholars at present. Why do we experience the body, a physical object as any other object in the world, as the seat of our private experiences (Husserl, 1950)? How does this self-experience relate consciousness more generally and how does it emerge from neurobiological processes? How can we assign self-consciousness to virtual substitutes, robotic extensions, or prosthetic replacements of body parts and the entire body? In this thesis, I will argue that these questions can be approached by a cognitive neuroscience program that relates subjective first-person descriptions of phenomenal experience to third-person quantification of behavior and neurobiological processes.

Over the last decades, clinical, experimental and neuroimaging research following this approach showed that **bodily self-consciousness (BSC)**, i.e. the experience of being a subject in a body (Blanke, 2012), depends on the non-conceptual and pre-reflective integration of multisensory signals from the body (see Blanke, 2012, and Ehrsson, 2012, for reviews). This was shown for the processing of visual, tactile, proprioceptive, and interoceptive signals, which collectively affected BSC in terms of self-identification, i.e. the experience that 'I' own and belong to a body, and self-location, i.e. the experience where 'I' am located in space.

Given these encouraging previous results, the question arises whether BSC also depends on sensory information of the vestibular system (see Lenggenhager & Lopez, 2015; Lopez, Halje, & Blanke, 2008; Pfeiffer, Serino, & Blanke, 2014, for reviews). The vestibular system encodes the rotational and linear accelerations of the head in three-dimensional space and thus directly informs the brain about the movements and the orientation of the body relative to the external space. Therefore, vestibular processing might provide important information contributing to BSC in terms of **first-person perspective (1PP)**, i.e. the centeredness of subjective experience and the directedness at the world.

The reason why we know much less about vestibular contributions to BSC, and higher brain functions, might be methodological difficulties of naturally stimulating the vestibular system and concurrently recording brain data non-invasively in humans (Lopez, Blanke, & Mast, 2012; Sinha et al., 2008). Accordingly, also the mechanisms of vestibular cortical processing, in particular with respect to multisensory processing, are largely unexplored.

Given this general background from the fields of consciousness studies and the neuroimaging of vestibular processing, my thesis has the general goal to answer the following central questions:

- *How does vestibular information contribute to multisensory mechanisms of BSC, and 1PP in particular?*
- *Which spatio-temporal brain dynamics underlie vestibular contributions to multisensory processing in the visual and somatosensory system in humans?*

1.2 State of the art

BSC arguably is the most fundamental aspect of conscious experiences as a subject (Blanke, 2012). The goal of the first part of my thesis is to extend knowledge about the functional multisensory mechanisms of BSC with a particular focus on 1PP. In the following, I will review important theoretical frameworks upon which BSC is based including the specific working model of my thesis, then previous work of the experimental study of BSC and 1PP in healthy subjects will be summarized, upon which the open questions motivating my thesis research and the predicted outcomes will be formulated.

1.2.1 Consciousness, self and body: Theoretical frameworks

Consciousness has fascinated humankind and scholars for many centuries (Adam & Tannery, 1964; James, 1890; Kant, 1924). It is often described as private, unified, phenomenal experience, or awareness, of some external object or inner event. Day-to-day we witness consciousness disappearing when falling asleep and seamlessly re-appearing when waking up. In clinical practice diagnosis of the state of a patient's consciousness is often vital, e.g. discriminating between vegetative and minimally conscious states in coma or evaluating the effects of anesthetic drug administration. More than a century after the first experimental studies on consciousness were conducted (James, 1890) we still lack a unifying theory of consciousness and its neurobiological mechanisms. What exactly is consciousness? Why are we conscious? How does conscious experience emerge from neural processes? These questions, and in particular the latter, are considered by some authors too hard to be studied scientifically (Chalmers, 1996). Yet, others are much more optimistic and have embarked on an interdisciplinary endeavor to build an evidence-based neurobiological theory of consciousness (Crick & Koch, 1990).

The paper by Crick and Koch (Crick & Koch, 1990) introduced the idea of neural correlates of consciousness. Since then, numerous evidence-based models have been proposed (for a recent collection of ideas see http://open-mind.net/papers). Some accounts tend to explain consciousness by general information processing in the brain. For instance, the global workspace theory (Baars, 1988) proposes that consciousness is based on globally available information in the brain that is available to attention, memory, and language. The attention schema theory (Graziano & Kastner, 2011b) proposes that conscious experience is a representational model (i.e. a schema) about the state of attention (i.e. a information-handling process of the brain). Other models more strongly emphasize the role of integration. For instance, the binding-by-coherence hypothesis (Crick & Koch, 1990; Engel, Fries, Konig, Brecht, & Singer,

1999) proposes that consciousness is based on the binding of different representational features of a perceptual object (e.g. the smell, color, and shape of a rose), arguably instantiated by the rhythmic firing of neuronal populations encoding these distinct features. The integrated information theory (Tononi, 2008, 2012) proposes that consciousness depends on a system's ability to integrate information (i.e. being able to discriminate between a large number of different states), which includes added information beyond the sum of informational content of the system's parts.

These models about consciousness in general have been complemented by the notion that consciousness is experience made by a subject, i.e. a phenomenal self (Heidegger, 1962; Metzinger, 2003). Thus, to be able to explain consciousness, some argue, one should start with explaining what a phenomenal self is. The knowledge we have about our 'own' self spans across various layers, such as ecological, interpersonal, extended, conceptual, and private levels of description (Neisser, 1988). However, folk psychological intuitions about the self being a soul or spirit or miniature person in the theater of the head are passionately rejected by contemporary consciousness researchers (Dennett, 1991). Instead, it is commonly accepted that 'the self', as being a unit or entity that experiences something does not exist. Rather, it seems more plausible that selfhood, i.e. the sense of being a phenomenal self, is an information-integration based representational model in the brain about the organisms wherein it is located (i.e. self-model theory; Metzinger, 2003). This self-model is thought to have itself proven useful in evolution by assigning a sense of spatial unity, and of temporal constancy, to an organism that undergoes constant changes (Metzinger, 2003).

These information-integration based models, however, do not answer the question how self-consciousness relates to the brain. While we usually experience the self attached to the body, a physical object as any other object in the world (Husserl, 1950), brain damage can induce spatial dissociations between the experienced self and the physical body (Blanke, 2012; Blanke, Landis, Spinelli, & Seeck, 2004; Blanke & Mohr, 2005). Thus, another line of research has focused on the question what brain mechanisms might bind self-consciousness to the body and give rise to BSC, i.e. the non-

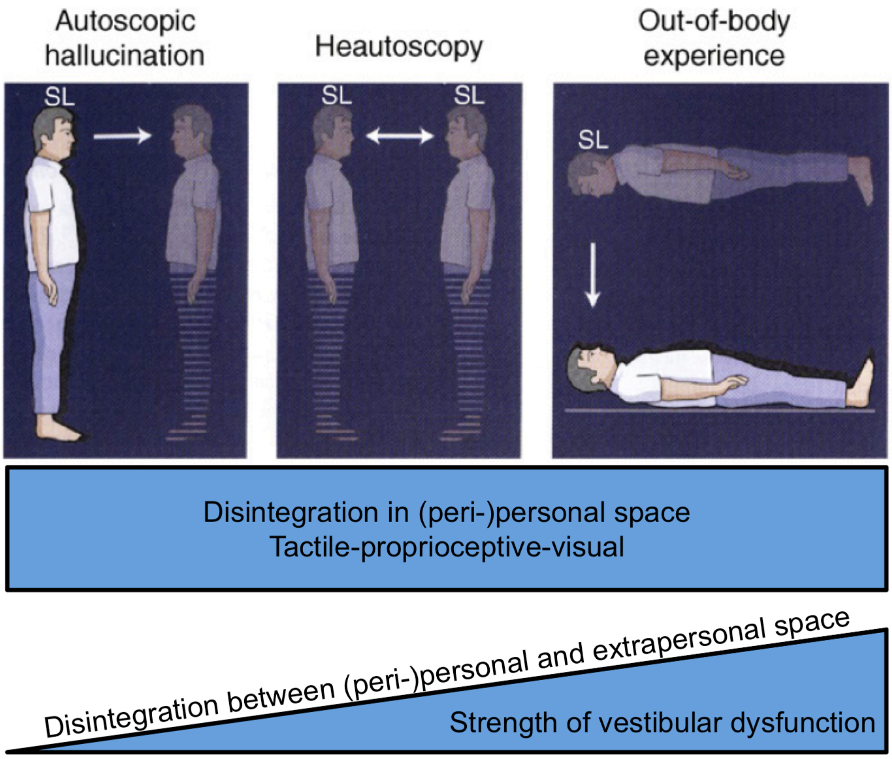

Figure 1 Autoscopic phenomena model, proposing a gradual increase of disembodiment of self-identification, self-location, and 1PP due to increasing strength of vestibular dysfunction, causing disintegration of multisensory signals between (peri-)personal and extrapersonal space, and due to disintegration of multisensory signals in (peri-)personal space (images are modified from Blanke et al., 2004, and Blanke & Metzinger, 2009).

conceptual and pre-reflective experience of being a subject inside a body. (Blanke & Metzinger, 2009; de Vignemont, 2011; Gallagher, 2005; Jeannerod, 2003). In particular, it is thought that BSC consists of self-identification (i.e. the experience that 'I' own a particular body), self-location (i.e. the experience where 'I' am in space), and 1PP (i.e. the centeredness of experience and directedness at the world)—three fundamental aspects of a minimal sense of phenomenal selfhood (Blanke & Metzinger, 2009; Metzinger, 2009, 2013).

My thesis uses BSC as conceptual framework, and follows previous clinical, neuroimaging and experimental results suggesting that BSC is based on the integration of multisensory bodily signals in the brain (Blanke, 2012). In particular, I will use the autoscopic phenomena model (**Figure 1**), that was initially based on observations in different types of neurological patients with autoscopy (i.e. patients see a hallucinated double in external space), he-autoscopy (i.e. patients experience occasional disembodiment, and bilocation, of self-identification, self-location and 1PP with respect to the hallucinated double), and **out-of-body experiences** (**OBEs**; i.e. patients experience complete disembodiment of self-identification, self-location, and 1PP anchored to the extrapersonal location of the hallucinated double; for review see Blanke et al., 2004; Blanke & Mohr, 2005). The central assumption of this model is that these distinct altered states of BSC depend on different degrees of disintegration of multisensory bodily signals within personal and peripersonal space (i.e. in particular of visual, proprioceptive, and somatosensory signals) and of disintegration of multisensory signals between personal and extrapersonal space (i.e. in particular visual and vestibular signals; Blanke, 2012; Lopez et al., 2008; Pfeiffer et al., 2014).

1.2.2 Cognitive neuroscience of bodily self-consciousness

The experimental study of BSC in healthy subjects has largely been based on the use of bodily illusions to study how conflicting multisensory signals affect perceptual processes—an approach initially introduced by James (James, 1890).

The **rubber hand illusion (RHI)** paradigm has been very influential (Botvinick & Cohen, 1998). The RHI is induced by showing to the participant a fake or virtual hand at a location within peripersonal space that differs from the location of the participant's unseen hand. Synchronous stroking of the fake/virtual hand seen by the participant and simultaneous (unseen) stroking of the participant's hand with paint brushes induces the strong feeling that touch is felt where the stroking is seen (referral of touch) and the feeling of ownership for the rubber hand, when compared to a control condition using asynchronous stroking by temporal delays or stroking of different parts of the hand (**Figure 2**; Ehrsson, Spence, & Passingham, 2004; Rohde, Di Luca, & Ernst, 2011; Tsakiris & Haggard, 2005). This illusion is constrained by several parameters, such as the maximum distance of 25 cm between the rubber hand and participant's hand (Samad, Chung, & Shams, 2015), the necessary correspondence between the locations and directions of the applied visual and tactile stroking (Tsakiris

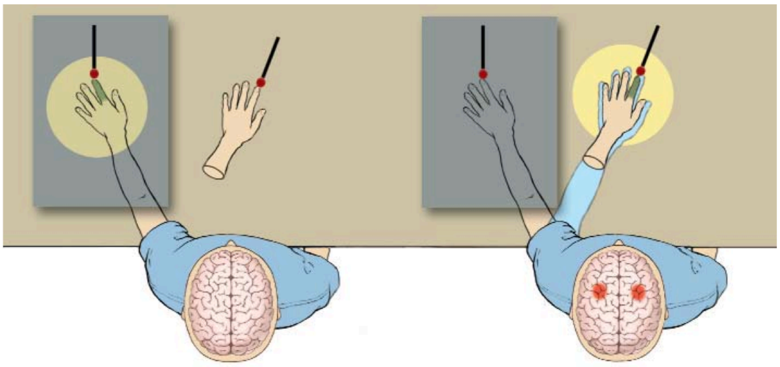

Figure 2 RHI experimental setup and experienced own-hand location (in yellow) during synchronous (left side) and asynchronous (right side) visuo-tactile stroking conditions (Botvinick, 2004).

& Haggard, 2005), a hand-like visual appearance of the rubber hand (Tsakiris & Haggard, 2005), and stroking duration of more than 10 sec (Rohde et al., 2011; Samad et al., 2015; Tsakiris & Haggard, 2005). Psychometric analysis of subjective ratings of the RHI showed that the illusion is characterized by the different types of feelings, including feeling of embodiment of the rubber hand, the loss of the own hand, movement, affect, and deafference (Longo, Schuur, Kammers, Tsakiris, & Haggard, 2008).

Objective measures of the illusion include proporiceptive drift (i.e. own-hand location judgments that systematically are biased in the direction of the rubber hand; Botvinick & Cohen, 1998), skin conductance responses to threat of the rubber hand (Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007), temperature cooling of the participant's hand (Moseley et al., 2008). Neuroimaging experiments using **functional magnetic resonance imaging (fMRI)** show that RHI experience correlates with brain activity in the insula cortex, premotor cortex, extrastriate body area, and the cingulate cortex (Ehrsson et al., 2004; Limanowski, Lutti, & Blankenburg, 2014; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007; for review see Lenggenhager & Lopez, 2015).

Some authors argue that the RHI is already a useful model for BSC, because the sense of self might be composed of an aggregation of body part representations (Ehrsson, 2012). There has been an alternative argument that the RHI does not allow manipulating more global representations of the self, especially concerning the global self-identification, self-location and 1PP related to the whole body (Lenggenhager, Tadi, Metzinger, & Blanke, 2007). Accordingly, to address these global aspects of BSC different **full-body illusion (FBI)** paradigms were developed (Ionta et al., 2011; Lenggenhager et al., 2007; Petkova & Ehrsson, 2008; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010).

One type of FBI consists of visually presenting a virtual or fake body in extrapersonal space and of applying visuo-tactile synchronous or asynchronous stroking to the back of the seen fake/virtual body and to the participants back (unseen by the participant, **Figure 3**a; Lenggenhager et al., 2007). After visuo-tactile stroking of about 30-120 sec, the experienced self-location is measured by blindfolded walking (Aspell, Lavanchy, Lenggenhager, & Blanke, 2010; Aspell, Lenggenhager, & Blanke, 2009; Lenggenhager, Halje, & Blanke, 2011), mental imagery measuring spatial elevation and distance from the ground (Ionta et al., 2011) and questionnaire ratings about illusion experience can be administered showing, similar to the RHI, referral of touch ratings and self-identification with a whole body (Aspell et al., 2009; Ionta et al., 2011; Lenggenhager, Mouthon, & Blanke, 2009; Lenggenhager et al., 2007). Many studies using the FBI have shown that multisensory processing is not limited to visual-tactile signals, but that the FBI depends on proprioceptive, cardiac, respiratory, and vestibular signals (Adler, Herbelin, Similowski, & Blanke, 2014; Aspell et al., 2013; Ionta et al., 2011; Palluel, Aspell, & Blanke, 2011). The FBI was induced in different postures (i.e. standing, supine and prone; Ionta et al., 2011; Lenggenhager et al., 2009; Lenggenhager et al., 2007) showing it can be reliably induced independent of a specific body orientation (**Figure 3**). Neuroimaging studies of the FBI show involvement of alpha oscillations in the premotor cortex, and processing in bilateral temporo-parietal cortex (Ionta et al., 2011; Lenggenhager et al., 2011). Other versions of the FBI (e.g. body swap illusion; Petkova & Ehrsson, 2008) in which no spatial conflict between the location of the seen virtual body and participants body was presented, showed fMRI activation in the ventral and dorsal premotor cortex and the intraparietal sulcus (Gentile, Bjornsdotter, Petkova, Abdulkarim, & Ehrsson, 2015; Petkova, Bjornsdotter, et al., 2011), which are thought to encode self-identification for

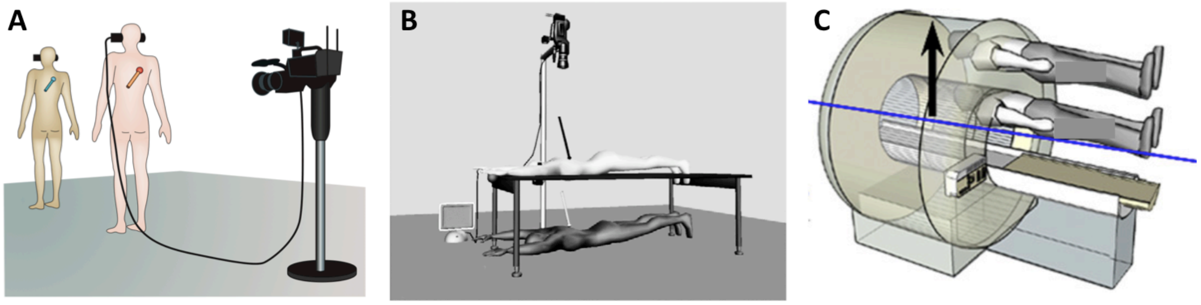

Figure 3 FBI experimental setups for the (a) standing (Lenggenhager et al., 2007), (b) prone (Lenggenhager et al., 2009), and (c) supine body postures (Ionta et al., 2011).

the body within peripersonal space (Serino et al., 2013). Collectively, the experimental and neuroimaging results of FBIs showed that also more global aspects of BSC, i.e. self-identification and self-location, depend on multisensory cortical processing.

1.2.3 1PP in cognitive neuroscience

Conscious experience as subject involves, in addition to self-identification and self-location, also 1PP, i.e. the centeredness of multimodal experience and directedness at the world (Blanke, 2012; Blanke & Metzinger, 2009; Metzinger, 2003, 2013; Newen & Vogeley, 2003). According to the minimal phenomenal selfhood model, 1PP includes a perceptual geometric representation of a central reference point of conscious experience (i.e. typically inside the body) and a spatial directedness at the world (Blanke & Metzinger, 2009; Metzinger, 2013).

The 1PP, in terms of being a non-conceptual pre-reflective phenomenal experience, has received little attention in previous cognitive neuroscience studies. Instead, most previous studies used the term *'1PP'* to refer to visual stimuli showing a visual viewpoint centered on the location of the observer, and compared these to third-person visual viewpoints centered on the location of another person (David et al., 2006; Vogeley & Fink, 2003; Vogeley et al., 2004). Such stimuli were also used to test the participant's ability to perform mental spatial transformations of the visual viewpoint to the location of another person and to judge the configuration of the spatial environment from this imagined location (Vogeley & Fink, 2003). Such mental perspective transformation abilities were related to an individual's abilities in social cognition (Hamilton, Brindley, & Frith, 2009) and autobiographical memory (Freton et al., 2013). Although these studies indicated links between mental spatial representations and higher-level representations of self and others, they do not address the non-conceptual and pre-reflective aspects of BSC, and of 1PP in particular. Furthermore, these studies almost exclusively used visual stimuli and did not address the multisensory contributions to such self-representations.

It has been proposed that 1PP is world-directed multimodal integrated experience centered on the body (Newen & Vogeley, 2003). One might argue that the idea of centeredness of experience differs from self-location, i.e. the feeling where the self is located in space, because self-location might be spatially expanded to the volume that the physical body occupies (i.e. and the space beyond bodily boundaries, see the paper I co-authored: *'Peripersonal space as the space of the bodily self'*, Appendix 3). By contrast, 1PP might be centered on a spatially unexpanded point within this spatial volume of the (experienced) body (Metzinger, 2013; Windt, 2010). The idea of centeredness of subjective experience thus relates to the notion of *'ego-centre'*, i.e. a single point where the self might be located (Bertossa, Besa, Ferrari, & Ferri, 2008; Howard & Templeton, 1966; Mitson, Ono, & Barbeito, 1976). In line with this proposal several experimental studies have asked healthy participants to localize the experienced ego- or self-center within the body using verbal inquiry or pointing tasks (Alsmith & Longo, 2014; Bertossa et al., 2008; Limanowski & Hecht, 2011). The results of visual and non-visual variants of pointing showed that healthy individuals locate their self inside the head or in the upper torso (Alsmith & Longo, 2014; Limanowski & Hecht, 2011). This suggests, that subjectively we do not experience our self homogenously distributed across the body (at least as measured by these methods), despite the feeling of self-identification with the entire body. These results lend support to the proposal that (the centeredness of) 1PP differs from self-identification—which is will addressed in more detail by the Study 1-3 of my thesis (see also General Discussion).

Although 1PP is typically experienced anchored to the body, clinical evidence suggests that body representations (e.g. the representation of the spatial dimensions and location of the body in space; Longo & Haggard, 2010) and 1PP are based on different mechanisms. Specifically, in some neurological patients interference or damage at the right **temporo-parietal junction (TPJ)** can induce OBE (Blanke, Ortigue, Landis, & Seeck, 2002; De Ridder, Van Laere, Dupont, Menovsky, & Van de Heyning, 2007). These patients have the experience that their visuo-spatial 1PP is anchored to a position outside of the bodily borders, in elevation, and is directed downward at the physical body, thus in a direction opposite to the spatial configuration of the body (Blanke et al., 2004; Blanke & Mohr, 2005; Lopez et al., 2008). Some patients further experienced distinct locations of the visuo-spatial 1PP and the audio-spatial 1PP (De Ridder et al., 2007), suggesting that 1PP experience of healthy subjects might depend on multisensory mechanisms. OBEs in these neurological patients, as well as in neurologically healthy subjects with sleep paralysis (Cheyne & Girard, 2009), but also altered 1PP experiences during FBI (Ionta et al., 2011) were associated with vestibular sensations, i.e. floating and lightness sensations, suggesting the vestibular system contributes to 1PP (Lopez et al., 2008)—however, so far no experiment has directly tested the effects of vestibular stimulation on 1PP.

Several studies have spatially separated the visuo-spatial viewpoint from the body to study the effects on own-body perception. Stratton (Stratton, 1899) was the first who by means of a portable mirror installation presented a disembodied and elevated point of view of the body (**Figure 4**a), that exposed him to a spatial conflict between visual signals and somatosensory, proprioceptive, and motor signals from the body for several days. He wrote:

"I notice [...] this reflected image as my very body itself. [...] the touch sensations were not referred to any other than their visible locality. [...] I sometimes felt myself strangely tall, as if my body had been elongated in to accord somewhat, with the apparent distance between the ground and my point of view." (Stratton, 1899, pp. 495-

496).

In a different study, Mizumoto and Ishikawa (Mizumoto & Ishikawa, 2005) installed a camera at a fixed location in a room and displayed the camera recording to a head-mounted display worn by participants who freely walked through the room. The participants reported the experience to be located at both the camera location and at the position of the seen body (Mizumoto & Ishikawa, 2005). These experiments showed that multisensory and sensory-motor spatial conflicts influence subjective own-body perceptions.

Other studies used more objective measures to quantify the effects of multisensory spatial conflict between the visual viewpoint and the body (Petkova et al., 2011; Slater et al., 2010). In an immersive virtual reality experiment Slater et al. (Slater et al., 2010) presented participants with a virtual body as seen from an egocentric viewpoint (i.e. centered on the virtual body) or from a laterally shifted allocentric viewpoint (**Figure 4**c). Participants' head movements congruently updated the virtual scenery as seen from each viewpoint, thus providing visuo-motor congruency that enhanced the level of immersion. Furthermore, participants received visuo-tactile stimulation in synchrony or asynchrony. Results showed that self-identification ratings and physiological responses (i.e. heart rate deceleration) were higher in egocentric than allocentric viewpoint conditions and that in the allocentric viewpoint condition stroking additionally modulated these dependent measures of self-identification. In a

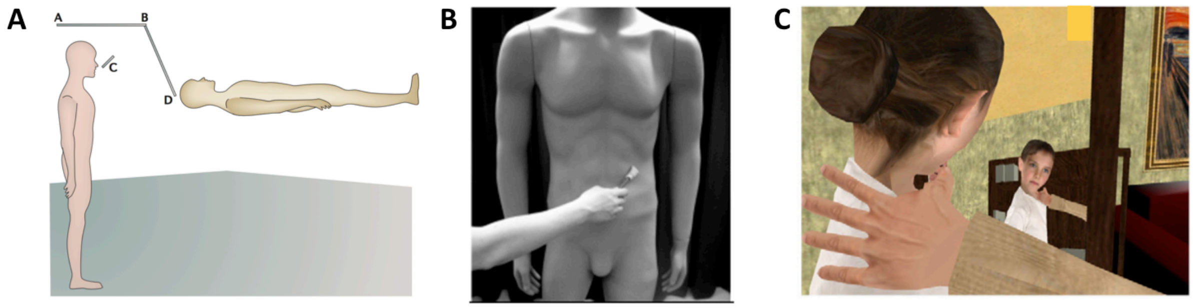

Figure 4 Different visuo-spatial viewpoint manipulations affecting self-identification with a seen body. (a) Mirror installation setup by (Stratton, 1899), figure from (Blanke, 2012), (b) visual stimulus of FBI study by (Petkova, Khoshnevis, & Ehrsson, 2011), (c) visual stimulus of virtual reality transfer study by (Slater et al., 2010).

different study by Petkova et al. (Petkova et al., 2011) the FBI was induced by presenting to participants either an egocentric or allocentric viewpoint of the abdomen of a mannequin and additional visuo-tactile stroking (again in synchronous or asynchronous fashion; **Figure 4**b). The authors found that self-identification ratings and physiological responses (here: skin conductance response to threat) were generally higher for egocentric than allocentric viewpoints, and that stroking modulated the responses only in the egocentric viewpoint condition. Slater et al. (Slater et al., 2010) and Petkova et al. (Petkova et al., 2011) thus found both that self-identification depended on the congruency between the visuo-spatial viewpoint and the physical body.

However, currently very little is known about the multisensory spatial mechanisms of 1PP and their relationship to multisensory (including vestibular) signals. Only a single study addressed this question by introducing multisensory spatial conflict about the direction of gravity. Ionta et al. (Ionta et al., 2011) induced the FBI in supine participants (i.e. veridical gravity acted toward the participants) who viewed a prone body as if seen from elevated visuo-spatial viewpoint (i.e. visual gravity acted away from the participant; **Figure 5**). This directional conflict between vestibular/somatosensory and visual gravity cues induced in half of the tested participants a downward-directed 1PP experience (i.e. down-group, N=11) whereas the remaining participants experience an upward-directed 1PP (i.e. up-group, N=11; measured by rating the question: *'Did you have the impression as if for most of the time you were looking downward at a virtual body below you or as if you were looking upward at a virtual body above you'*). These individual differences of 1PP were found despite the fact that all subjects experienced the same stimulations (**Figure 5**). Importantly in this study, 1PP experience systematically related to self-location changes during the FBI, i.e. down-group participant showed a change in self-location (i.e. comparing the synchronous with the asynchronous stroking condition) in downward direction, whereas up-group participants showed the opposite pattern (**Figure 5**). Moreover, these individual differences in 1PP and self-location, were related to neural activation difference (in fMRI) at the bilateral TPJ—a brain region functionally related to altered 1PP and self-location experience in neurological patients with OBE (Blanke et al., 2004; Blanke & Mohr, 2005; Blanke et al., 2002; Ionta et al., 2011).

1.2.4 Multisensory mechanisms of 1PP: Questions and predictions

Although previous studies showed that manipulating the visuo-spatial viewpoint can affect the experience of the body and the self—mainly with respect to self-identification (Mizumoto & Ishikawa, 2005; Petkova et al., 2011; Slater et al., 2010; Stratton, 1899)—only one study so far has investigated 1PP as dependent variable (Ionta et al., 2011). Pursuing the approach pioneered by Ionta et al. (Ionta et al., 2011), my thesis aims to extend knowledge about the multisensory mechanisms of the subjective 1PP in healthy human subjects. I will address the following questions.

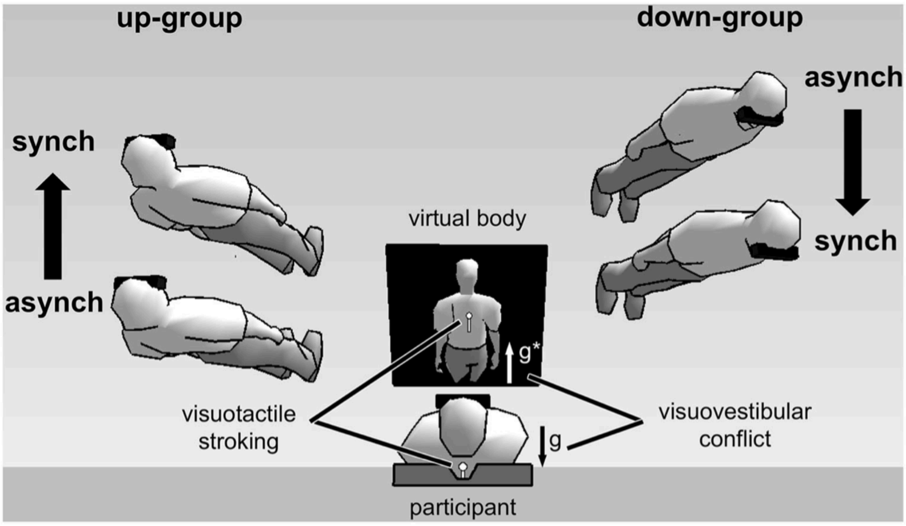

Figure 5 Experimental setup and results of FBI study by (Ionta et al., 2011) using visuo-vestibular and visuo-tactile conflict. The image center shows a participant in supine posture views a virtual body on a head-mounted display. Vestibular otolithic signals about gravity (g) are in opposite direction with respect to visual gravitational signals (g*)—thus in visuo-vestibular conflict. Results showed individual difference in 1PP experience. Virtual bodies at the left side of the figure represent subjective experiences made by up-group participants. These participants experienced an upward 1PP and showed congruent upward change in self-location during synchronous (synch) as compared to asynchronous (asynch) stroking condition. The opposite pattern was observed for down-group participants (shown at the right side of the figure; Pfeiffer et al., 2014).

1. *Question:* Can subjective 1PP experience systematically be dissociated from the body, and predictably manipulated within subjects?
   Prediction: Based on the observation that in some OBE patients the auditory and visual 1PP experiences can be spatially separated (De Ridder et al., 2007), and based on the autoscopic phenomena model (Blanke et al., 2004; Blanke & Mohr, 2005), I hypothesize that 1PP can be manipulated within-subjects by conflict between multisensory signals about personal and external space.

2. *Question:* Which sensory signals are especially relevant to 1PP?
   Prediction: Based on the association of OBE of neurological origin to vestibular sensation and cortical vestibular processing, and that experimental changes of 1PP during FBI were induced by visuo-vestibular gravity conflict (Blanke, 2012; Blanke et al., 2002; Ionta et al., 2011; Lopez et al., 2008), I hypothesize that integrated visuo-vestibular cues are particularly relevant to subjective 1PP experience.

3. *Question:* How does subjective 1PP experience relate to other aspects of BSC, self-location and self-identification?
   Prediction: Based on the observation that 1PP and self-location systematically co-varied in the study by Ionta et al. (Ionta et al., 2011) and that distinct neural structures encode self-identification and self-location (Blanke, 2012; Pfeiffer, 2015), I hypothesize that 1PP depends on distinct functional mechanisms than self-identification but that 1PP might be functionally associated with self-location.

1.2.5 Brain dynamics of vestibular contributions to multisensory processing

In the second part of my thesis, I shift focus from multisensory-vestibular mechanisms of 1PP to the neural correlates of multisensory processing in humans, with particular focus on the vestibular system. The vestibular system, the sensory system encoding linear and rotational head acceleration in three-dimensional space, not only contributes to reflexive control of gaze and posture. A growing number of behavioral and psychophysics studies suggests vestibular contributions to higher brain functions related to the perception of the body and self in space. Those include the perception of the vertical upright direction (Witkin & Asch, 1948), the localization of objects (or multisensory stimuli) and their motion in external space (Karnath, 1994; Lewald & Karnath, 2000; Zago & Lacquaniti, 2005), the perception of own-body orientation and motion (Clemens, De Vrijer, Selen, Van Gisbergen, & Medendorp, 2011; De Saedeleer et al., 2013; Graybiel & Kellogg, 1967; Indovina et al., 2013; MacNeilage, Turner, & Angelaki, 2010; Mittelstaedt, 1991; Tiliket, Ventre-Dominey, Vighetto, & Grochowicki, 1996), the perception and localization of sensory stimuli on the body (Bottini et al., 2005; Bottini et al., 1995; Ferre, Bottini, & Haggard, 2011; Ferre, Vagnoni, & Haggard, 2013; Kerkhoff et al., 2011; Lopez, Schreyer, Preuss, & Mast, 2012; Vallar, Sterzi, Bottini, Cappa, & Rusconi, 1990), pain perception (Ferre, Bottini, Iannetti, & Haggard, 2013; McGeoch & Ramachandran, 2008; McGeoch, Williams, Lee, & Ramachandran, 2008), and BSC (Lopez, Lenggenhager, & Blanke, 2010; Macauda et al., 2014). Commonly, these higher functions depend not only on vestibular, but on multisensory signals and their integration. Indeed, this behavioral and psychophysics evidence is in accord with results from electrophysiological recording in non-human primates that vestibular cortical processing is multisensory and distributed in distinct cortical regions (for review see Lopez & Blanke, 2011).

However, due to phylogenetic differences between non-human primates and humans a direct translation of neural correlates of vestibular cortical processing from primates to humans should be taken with caution. However, identification of neural correlates of vestibular cortical processing in the human cortex is hampered by methodological limitations and currently available non-invasive human neuroimaging methods and artificial vestibular stimulation techniques are known to induce non-vestibular sensory co-activation (Lopez, Blanke, et al., 2012).

The central aim of the second part of my thesis is to contribute to the field of human vestibular cortical neuroimaging of multisensory processes using a novel methodological approach that tries to overcome some of the methodological limitations of previous work. By combining the use of an angular whole-body motion platform to induce selective stimulation of the horizontal semicircular canals, and the use of high-density **electroencephalography (EEG)**, we study the contributions of such vestibular stimulation to multisensory cortical processing for two important sensory modalities: the somatosensory system and the visual system. These two systems were chosen based on previous literature, showing that visual and somatosensory signals contribute to various higher vestibular functions, and based on the results of my studies on 1PP from the first part of this thesis.

In the following, I will give an overview of the peripheral and central vestibular mechanisms and summarize previous work about vestibular contributions to somatosensory and visual processing, which will be the main focus of the studies of the second part of my thesis, and finally state the specific questions of the project and predictions.

1.2.6 Peripheral vestibular system

The peripheral vestibular system consists of sensory organs located in the head in the left and right inner ear. **Figure 6** shows that in each inner ear there are three semicircular canals each filled with endolymph fluid that during head rotation exerts inertial forces that bend the cupula, i.e. a conic structure attached to the inner wall of the semicircular canal, which innervates hair cells in the cupula that modulate the firing rate of vestibular nerve fibers (Fernandez & Goldberg, 1971; Goldberg & Fernandez, 1971). The roughly perpendicular arrangement of the three semicircular canals in each inner ear and the bilateral arrangement of the semicircular canals thus signals rotational accelerations of the head in three-dimensional space, i.e. yaw (by horizontal canals), pitch and roll (by different combinations of anterior and posterior canals; **Figure 6**b). However, the semicircular canals are insensitive to linear head motions. A different type of vestibular sense organs, i.e. the otoliths (utricle and saccule), code linear accelerations of the head, i.e. gravito-inertial forces from linear head motions and the constant linear gravitational force, but that are insensitive to rotational head acceleration (**Figure 6**). Hence, the semicircular canals and the otolith organs encode different aspects of head motion in three-dimensional space (Goldberg, 2012). Commonly, they function as accelerometers, i.e. they are sensitive to changes in velocity, but are insensitive to detecting constant-velocity motions (e.g. rotating in a desk chair or driving a car straight ahead in a car at constant velocity). It is worth noting that at this level of vestibular processing in the periphery, the head motion signals are encoded in a direction-specific way. For instance, head rotation in yaw to the left side increases the firing rate in the vestibular nerve of the left horizontal semicircular canal and decreases the firing rated of the right horizontal semicircular canals, while the other canals show minor or no signaling. This peripheral direction-specificity differs from the right-hemispheric dominance of vestibular cortical processing in humans (Dieterich & Brandt, 2015).

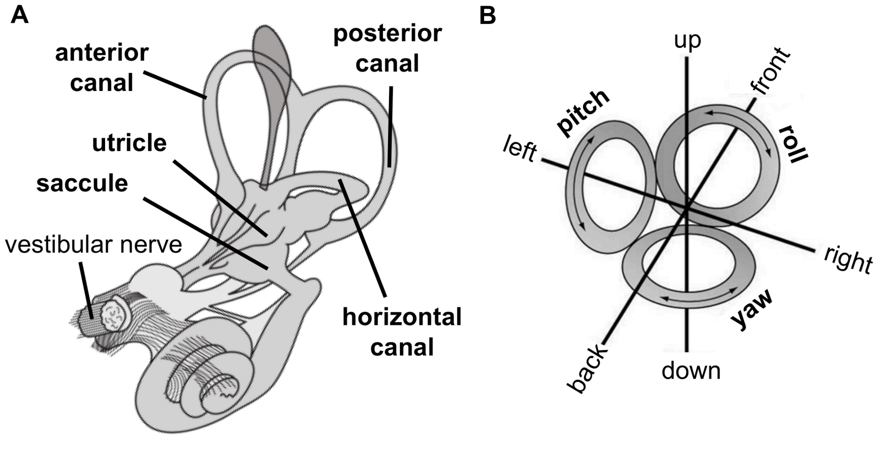

Figure 6 The human inner ear showing (a) the peripheral vestibular system and (b) encoded motions (Pfeiffer et al., 2014).

1.2.7 Central vestibular system

Vestibular information from the semicircular canals and the otolith organs are sent via the vestibular nerve to the vestibular nucleus in the brainstem. From there vestibular information is sent to the spinal cord for vestibulo-spinal reflexes for postural control, to oculo-motor nuclei in the brain stem for reflexive eye movement control and to the thalamus from where vestibular signals are further relayed to the cerebellum and the cortex (comprehensive reviews can be found in Goldberg, 2012; Lopez & Blanke, 2011).

The vestibular nucleus is the first synapse of the vestibular pathway and already here neural activity does not only depend on the peripheral signals from the vestibular sensory organs, but is also modulated by top-down projections from the cortical centers involved in visual, proprioceptive and motor processing (Angelaki & Cullen, 2008; Cullen, 2012; Lopez & Blanke, 2011; MacNeilage et al., 2010), showing that indeed the vestibular system is involved in multisensory processing at the subcortical level. Subcortical processing involving the vestibular brainstem, thalamus and cerebellum is functionally concerned with discriminating head tilt from linear motion (Angelaki, Merfeld, & Hess, 2000; Dickman & Angelaki, 2002; Perachio, Bush, & Angelaki, 1992), i.e. due to equivalence of linear head acceleration and constant gravitational acceleration (Einstein, 1907), and with integrating the sensory inputs from the bilateral semicircular canals and otolith organs to determine the direction of head motion (Dickman & Angelaki, 2002).

Current knowledge about the functional neuroanatomy of the vestibular cortex (i.e. the interconnected cortical network processing vestibular information) is mostly based on electrophysiological recordings and anatomical tracer studies in non-human primates (**Figure** 7a; Lopez & Blanke, 2011). These studies identified several distinct cortical regions receiving direct thalamo-cortical vestibular input (i.e. inner vestibular circuit) including a core input region in the posterior insula (i.e. the **parieto-insular vestibular cortex, PIVC**; Grüsser, Pause, & Schreiter, 1990a, 1990b; Guldin &

Grüsser, 1998) and two subregions within the primary somatosensory cortex, i.e. Brodmann areas 2v and 3a (Fredrickson, Scheid, Figge, & Kornhuber, 1966; Odkvist, Schwarz, Fredrickson, & Hassler, 1974). From the inner vestibular circuit, vestibular information is forwarded to temporal (dorsal medial superior temporal region), parietal (area 7, ventral intra-parietal region) and frontal (frontal eye field, supplementary eye field, area 6) cortical regions (Bremmer, Klam, Duhamel, Ben Hamed, & Graf, 2002; Bremmer, Kubischik, Pekel, Lappe, & Hoffmann, 1999; Gu, Angelaki, & Deangelis, 2008; Guldin, Akbarian, & Grüsser, 1992; Leichnetz, 1989), which are reciprocally connected to the inner vestibular circuit (Guldin et al., 1992). Thus, there are vestibular projections to all cortical lobes except the occipital lobe (**Figure** 7a). The vestibular cortex differs from any other sensory system in that no primary vestibular cortex has been identified, i.e. there is not a single cortical input region of thalamo-cortical vestibular input that processes exclusively vestibular signals, e.g. as there is V1 for the visual system, S1 for the somatosensory system, Heschl's gyrus for the auditory system (Dieterich & Brandt, 2015; Lopez & Blanke, 2011). Moreover, all vestibular cortical neurons are bimodal or trimodal and respond, in addition to vestibular signals, also to somatosensory (including proprioceptive), visual, auditory and motor signals (Bremmer et al., 2002; Grüsser et al., 1990b; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005). Based on these studies in non-human primates it is now commonly agreed that the vestibular cortex is multisensory and distributed.

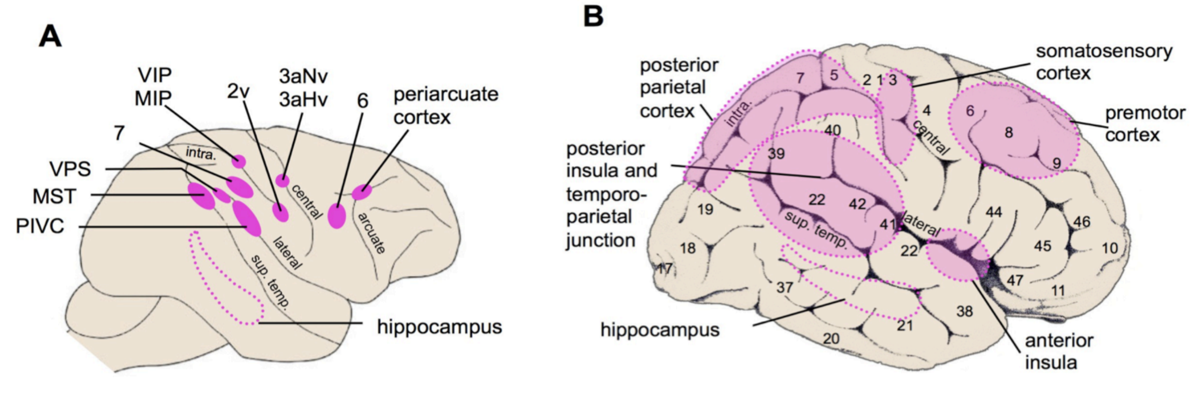

Figure 7 Vestibular cortex in (a) monkeys and (b) humans (Lenggenhager & Lopez, 2015).

As compared to non-human primates, we know considerably less about the functional neuroanatomy of the human vestibular cortex, probably due to methodological challenges involved in combined vestibular stimulation and non-invasive neuroimaging in humans (Antunes, Glover, Li, Mian, & Day, 2012; Lopez, Blanke, et al., 2012; Mian, Li, Antunes, Glover, & Day, 2013; Pfeiffer et al., 2014; Roberts et al., 2011). However, using artificial vestibular stimulation techniques (e.g. **galvanic vestibular stimulation, GVS**, caloric vestibular stimulation, auditory clicks) that allow stimulating the vestibular system in head-restrained environments, such as during fMRI, several cortical regions were identified in humans that respond to vestibular stimulation (**Figure 7**b). Indeed there are considerable differences in neural activation patterns between different vestibular stimulation methods and procedures tested (Lopez, Blanke, et al., 2012), but recent meta-analyses on such fMRI data showed a consistent overlap in of activation in the posterior insula regions (Lopez, Blanke, et al., 2012), and parietal operculum (i.e. OP2 region; zu Eulenburg, Caspers, Roski, & Eickhoff, 2012) that are thought to be the human homologue of the core vestibular input region PIVC in monkeys (i.e. for brevity I will refer to this region as human PIVC). In addition to the human PIVC, vestibular stimulation also modulated activity in the parieto-occipital (Brandt & Dieterich, 1999; Wenzel et al., 1996), post-central (Bense, Stephan, Yousry, Brandt, & Dieterich, 2001; Fasold et al., 2002), frontal, temporal, and cingulate cortical regions (Bottini et al., 1994). Several studies also showed activation modulation in the same regions for vestibular and somatosensory stimulations, i.e. in the secondary somatosensory cortex, the putamen, and the inferior parietal cortex (Bense et al., 2001; Bottini et al., 2005; Bottini et al., 1994; Fasold et al., 2002) and also between vestibular and visual stimulation, i.e. in the posterior insula, and the parieto-ocipital cortex occipital (Brandt & Dieterich, 1999; Wenzel et al., 1996). Based on these fMRI studies in humans, it seems that the human vestibular cortex shows a similarly distributed and multisensory functional neuroantomy as the animal vestibular cortex (Lopez & Blanke, 2011). However, a more precise spatio-temporal characterization of vestibular cortical processing in humans that cannot be achieved by fMRI, in particular related to natural vestibular stimulation, is highly desirable—which will be addressed by Studies 4-5 of my thesis.

1.2.8 Vestibular contributions to somatosensory and visual cortical processing

In order to extend knowledge about the spatio-temporal mechanisms of vestibular contributions to multisensory cortical processing, my thesis follows the strategy of studying vestibular effects on two (comparatively) well-studied sensory systems: the somatosensory and the visual system. These sensory systems provide a good test case to study the vestibular effects because their neural correlates have been well documented in neuroimaging studies, including EEG and evoked potentials (see below). Moreover, the visual and somatosensory sensory signals show strong functional interactions with the vestibular system, including higher perceptual functions, which I will briefly summarize below.

Somatosensory-vestibular interactions have been documented at the neuroanatomical and functional level. For instance, the monkey inner circuit of the vestibular cortex (i.e. PIVC, and primary somatosensory cortex sub regions area 2v, area 3a) and also several regions of the larger vestibular cortical network (i.e. ventral intraparietal region) host bimodal somatosensory-vestibular neurons that respond to proprioceptive signals from the neck, the limbs, and cutaneous somatosensory signals, as well as to rotational and linear vestibular stimulations (Bremmer et al., 2002; Fredrickson et al., 1966; Grüsser et al., 1990b; Guldin et al., 1992; Odkvist et al., 1974). Moreover, vestibular stimulation can ameliorate somatosensory perception deficits in brain-damaged patients (e.g. hemianaesthesia, i.e. the patient has damage in parietal cortex and does not perceive touch to the contralesional side of the body, Bottini et al., 2005; Vallar et al., 1990; tactile extinction, i.e. the patient has a parietal lesion and does not perceive touch at the contralesional side of the body when at the same time the ipilesional side is touched, Kerkhoff et al., 2011). More recently, a series of experimental studies in healthy subjects showed that vestibular stimulation can affect somatosensory perception, in terms of improving tactile thresholds for touch at the fingertips, and in terms of lowering thermal pain perception (Ferre, Bottini, et al., 2011; Ferre, Day, Bottini, & Haggard, 2013; Ferre, Kaliuzhna, Herbelin, Haggard, & Blanke, 2014; Ferre, Sedda, Gandola, & Bottini, 2011). Other studies show that vestibular sensations, such as the feeling of self-motion or body orientation in space, can be altered by somatosensory stroking or pressure cues at the participant's feet (Lackner & DiZio, 2005; Lackner & DiZio, 2000). The neural correlates of somatosensory-vestibular interactions have been studied in a small number brain damaged patients in positron emission tomography and fMRI, showing activations in the secondary somatosensory cortex, the insula, and the putamen (Bottini et al., 2005). Only one study in healthy human subjects investigated the effects of artificial vestibular stimulation on somatosensory cortical processing, using caloric vestibular stimulation and median nerve somatosensory evoked potentials in EEG (Ferre, Bottini, & Haggard, 2012) and found that in a single electrode the voltage potential at 80 ms post-stimulus onset was enhanced following vestibular stimulation. However, the spatio-temporal dynamics of such vestibular modulations of somatosensory cortical processing remain still elusive.

In addition to the somatosensory system, the visual system also strongly interacts with the vestibular system. At the neural level, in monkeys in area middle temporal, medial superior temporal, and ventral intraparietal regions there are bi- or trimodal neurons that are tuned to the motion direction of visual and vestibular signals (Chen, Deangelis, & Angelaki, 2013a, 2013b; Gu et al., 2008; Gu, DeAngelis, & Angelaki, 2007; Rosenberg & Angelaki, 2014). When the body moves, with the eyes open, the brain receives optic flow stimuli that are highly informative about self-motion and are relevant to maintain the perception of self-motion during constant-velocity movements (to which the vestibular system is insensitive). Furthermore such visual-vestibular motion signals are used to dissociate self- from object-motion (Fetsch, DeAngelis, & Angelaki, 2013). But vestibular-visual interactions are also relevant for the perception of the constant direction of gravity, for which there is evidence that the brain hosts internal models of gravity that, based on visual and vestibular gravity cues, anticipate the effects of gravity on perception and action involving one's own body and external objects (De Saedeleer et al., 2013; McIntyre, Zago, Berthoz, & Lacquaniti, 2001; Sciutti et al., 2012; Zago, McIntyre, Senot, & Lacquaniti, 2008). In humans, visual-vestibular interactions have been studied in fMRI using optokinetic visual stimuli and GVS or caloric vestibular stimulation. In these studies it was found that vestibular stimulation activated the posterior insula, the same region was deactivated by some visual stimulation patterns, which was interpreted in terms of a reciprocal visual-vestibular inhibition mechanism in line with a multisensory weighting hypothesis (Bense et al., 2001; Brandt, Bartenstein, Janek, & Dieterich, 1998; Brandt et al., 2002; Wenzel et al., 1996). However, these results do not correspond to the observation in non-human primates that during different visual and vestibular stimulations PIVC neuronal firing is not modulated by visual signals but only by vestibular stimulation. It is thus unclear whether the results in humans in fMRI for visual-vestibular cortical interactions were specific to the neuroimaging method and stimulation protocol used, or whether such interactions could be generally found in the human cortex using different stimulation methods.

1.2.9 Brain dynamics of vestibular processing: Questions and predictions

Compared to the animal literature, very little is known about the neural correlates of vestibular contributions to multisensory cortical processing in humans.

Arguably, the identification of neural correlates of vestibular cortical processing in the human cortex is hampered by methodological limitations with currently available non-invasive human neuroimaging methods and artificial vestibular stimulation techniques (Lopez, Blanke, et al., 2012; Roberts et al., 2011). Specifically, many studies on the human vestibular cortex were conducted using fMRI, which although providing an excellent spatial resolution requires subjects to keep a fixed head posture and thus does not allow for natural vestibular stimulation (Antunes et al., 2012; Mian et al., 2013; Roberts et al., 2011). The static magnetic field of the MR scanner constantly activates the vestibular sensory organs, some authors argue, making it impossible to record non-vestibular baseline conditions (Roberts et al., 2011). On the other hand, artificial vestibular stimulation methods, using thermal irrigation of the ear canals, electrical stimulation, or auditory stimuli induce sensory co-activation, make it difficult to apply natural, selective, vestibular stimulation with such techniques, and further they often unselectively activate simultaneously several of the different vestibular sensory organs (otoliths and semicircular canals).

The central aim of the second part of my thesis is to extend knowledge about the human vestibular cortex, in particular related to spatio-temporal dynamics of multisensory processing, using a novel methodological approach that aims to overcome some of the methodological limitations of previous work. By combining the use of an angular earth-vertical whole-body rotation platform, i.e. for delivering natural selective vestibular stimulation of the horizontal semicircular canals, and concurrent recording of high-density EEG, i.e. using electrical neuroimaging analyses of global electrical field (and neural source estimation), we study the contributions of such vestibular inputs to multisensory cortical processing.

Given this novel methodological approach, the goal of this thesis project is identifying the spatio-temporal neural dynamics of vestibular contributions to somatosensory and visual cortical processing. My aim is to answer the following questions

1. *Question:* Does natural selective stimulation of the horizontal semicircular canals modulate somatosensory cortical processing? Which are the spatio-temporal neural correlates?
   Prediction: Based on the animal literature showing vestibular projections to the primary somatosensory cortex (Fredrickson et al., 1966; Guldin et al., 1992; Odkvist et al., 1974) we hypothesized that the first cortical response of the median nerve somatosensory evoked potential, i.e. as early as 20 ms post-stimulus onset, would be modulated by vestibular stimulation. Furthermore, the only EEG study in humans on vestibular-somatosensory interactions observed modulation of a

later component, i.e. at 80 ms post-stimulus onset, which was hypothesized to contribute to higher-tier processing relevant to somatosensation. Here we asked whether using our setup a similarly late, i.e. more cognitive, component of the somatosensory evoked potentials would be modulated by vestibular stimulation.

2. *Question:* Can we find evidence for vestibular stimulus intensity-dependent modulation of somatosensory cortical processing?
   Prediction: According to the sensory weighting hypothesis (Brandt et al., 1998) the contribution of vestibular signals to multisensory processing underlies a weighting process. We reasoned, stronger and more intense vestibular inputs should induce stronger effects on somatosensory cortical processing, underlining their vestibular nature.

3. *Question:* Does natural selective stimulation of the horizontal semicircular canals modulate visual cortical processing? Which are the spatio-temporal neural correlates?
   Prediction: Based on the findings of visual inhibition of vestibular cortical processing in fMRI (Brandt et al., 1998), but other studies in fMRI not finding the result using different visual stimuli (Kovacs, Raabe, & Greenlee, 2008), and similarly controversial findings about visual responses in the monkey PIVC (i.e. compare Grüsser et al., 1990b, with Chen, DeAngelis, & Angelaki, 2010), we hypothesized if there is a general vestibular-visual inhibition mechanisms, we should observe such effect for combined vestibular stimulation and visual evoked potentials using static visual pattern changes.

4. *Question:* Does the vestibular effect on visual cortical processing correspond to other markers of vestibular processing identified previously?
   Prediction: Based on the literature that post-rotational vestibular stimulation follows an exponential decay (Bertolini et al., 2011; Goldberg & Fernandez, 1971; Laurens & Angelaki, 2011), and that such a temporal decay was recently found in the EEG alpha band related to vestibular stimulation (Gale, 2015), we

hypothesized that vestibular modulations of visual cortical processing, following constant-velocity vestibular stimulation protocols, should show a similar exponential temporal decay as identified previously.

1.3 Thesis outline

My thesis is divided into two parts: **Functional multisensory mechanisms of 1PP (Part A)** and **Brain dynamics of vestibular contribution to multisensory processing (Part B)**. In **Part A**, in three studies, we integrated a virtual reality and robotics platform with the FBI experimental paradigm to apply well-controlled multisensory-vestibular conflicts and to measure these effects on 1PP.

In **Study 1**, during the FBI, visual-vestibular conflicts about the direction of gravity and visuo-tactile conflicts about the location of the body were presented to participants. Our results showed that these multisensory conflicts induced individual differences in the experienced direction of 1PP and thereby replicated earlier results (Ionta et al., 2011). In addition, we showed that self-identification did not depend on the experienced direction of 1PP, whereas self-location did. Furthermore, we showed that individual differences of 1PP were related to individual differences in visual-vestibular integration related to subjective visual vertical judgments. We thus introduced measurement of 1PP as dependent variable and showed that 1PP depends on visual and vestibular graviceptive signals.

In **Study 2** we measured the effects of different visuo-spatial viewpoints on 1PP, self-location, and self-identification. Extending previous results on individual 1PP differences (i.e. Study 1, Ionta et al., 2011) we showed here that 1PP can be manipulated within-subjects and that such changes depend on visuo-spatial viewpoint and visual body information. These results show that visuo-spatial body-related cues contribute to 1PP experience.

In **Study 3** we asked whether in addition to body-related information, also contextual visual-vestibular gravity cues contribute to 1PP. Thus, during the FBI we presented additional gravity-like dynamic virtual object motion that was congruent or incongruent with the direction of veridical gravity. We showed that these visual gravity cues strongly influenced 1PP ratings, suggesting that contextual dynamic visual cues contributed to the experience of 1PP in space.

Collectively, **the studies of Part A** showed that subjective 1PP experience is malleable and influenced by the integration of multisensory signals, in particular by visual, vestibular, and tactile signals about the direction of gravity. These results also extend knowledge about the specific contributions of multisensory bodily signals to different aspects of BSC, in particular on the relationship of 1PP to self-location and self-identification.

In **Part B** (**Brain dynamics of vestibular contribution to multisensory processing,** Studies 4-5), we aimed to identify the timing and anatomical location of vestibular influences on somatosensory and visual cortical processing in humans. Because of a low temporal resolution and vestibular stimulus confounds in previous neuroimaging methods (i.e. fMRI, positron emission tomography), we here developed a novel approach that combined passive whole-body rotation and simultaneous recording of high-density EEG in response to somatosensory and visual evoked brain responses.

In **Study 4** we measured how vestibular stimulation intensity (i.e. fast versus slow rotation) as compared on non-vestibular control differentially affected somatosensory evoked potentials. We showed that vestibular stimulation affected somatosensory evoked potentials in two distinct time periods (i.e. early at 24-35 ms and late at 97-112 ms post-stimulus) and that these effects differently depended on stimulus intensity and effects on response strength and spatial configuration of the underlying neural generators (i.e. in somatosensory cortex and middle temporal cortex). Our results are important because they allowed for the first time to dissociate temporally distinct effects of vestibular stimulation on cortical processing, and thereby suggest distinct low- and high-level contributions of vestibular signals to somatosensory processing.

In **Study 5**, we analyzed the effects of vestibular stimulation on visual evoked potentials. Vestibular stimulation also modulated the response strength and the spatial configuration of the underlying neural generators in two time intervals (i.e. early at 83-119 ms and late at 178-205 ms post-stimulus). These vestibular effects on visual cortical processing were characterized by a shorter temporal decay (time constant of 4-8 sec) than vestibular-stimulation related reflexive eye movements (time constant = 11 sec), suggesting distinct contributions of subcortical vestibular processing to low-level (i.e. control of eye position) and high-level vestibular functions (i.e. modulation of visual cortical processing). Inverse solution located the vestibular effects on visual processing to different cortical regions, including a core vestibular cortical input (i.e. posterior insula) and posterior visual processing regions.

Together, **the studies of Part B** of my thesis provide evidence for temporal-specific vestibular contributions to somatosensory and visual processing in the human cortex. For the first time, to our knowledge, we achieved natural selective vestibular stimulation and high-temporal resolution electrical neuroimaging to characterize multisensory-vestibular cortical processing in humans.

1.4 Personal contributions

Papers included in my thesis

Study 1: Pfeiffer C, Lopez C, Schmutz V, Duenas J, Martuzzi R, Blanke O (2013) Multisensory origin of the subjective first-person perspective: Visual, tactile, and vestibular mechanisms. PLoS One. 8(4):e61751.
Personal Contribution: System integration of robotic device and experimental control software, experimental design, recording, analysis, writing.

Study 2: Pfeiffer C, Schmutz V, Blanke O (2014) Visuospatial viewpoint manipulation during full-body illusion modulates subjective first-person perspective. Experimental Brain Research. 232(12):4021-4033.
Personal Contribution: Experimental design, recording, analysis, writing.

Study 3: Pfeiffer C, Grivaz P, Serino A, Herbelin B, Blanke O (in preparation) Visual gravity contribution to subjective first-person perspective.
Personal Contribution: Experimental design, analysis, writing.

Study 4: Pfeiffer C, Van Elk M, Bernasconi F, Blanke O (under review) Distinct early and late effects of vestibular stimulation on somatosensory cortical processing. Under review at the Journal of Neurophysiology.
Personal Contribution: System integration of motion platform and electrical stimulator and EEG system, experimental design, recording, analysis, writing.

Study 5: Pfeiffer C, Lopez C, Blanke O (in preparation) Spatio-temporal dynamics of vestibular contributions to visual cortical processing.
Personal Contribution: Experimental design, recording, analysis, writing.

Papers in the Appendix

Appendix 1: Romano D, Pfeiffer C, Maravita A, Blanke O. (2014) Illusory self-identification with an avatar reduces arousal responses to painful stimuli. Behavioural Brain Research. 261:275-281.
Personal Contribution: Experimental design, writing.

Appendix 2: Salomon R, Lim M, Pfeiffer C, Gassert R, and Blanke O. (2013) Full body illusion is associated with widespread skin temperature reduction. Frontiers in Behavioral Neuroscience. 7:65.
Personal Contribution: Experimental design, writing.

Appendix 3: Noel J-P, Pfeiffer C, Blanke O, and Serino A. (under review) Peripersonal space as the space of the bodily self. Under review at Cognition.
Personal Contribution: Experimental design, writing.

Appendix 4: Pfeiffer C, Serino A, and Blanke O. (2014) The vestibular system: a spatial reference for bodily self-consciousness. Frontiers in Integrative Neuroscience. 8:31.
Personal Contribution: Literature research, writing.

Appendix 5: Pfeiffer C. (2015) Multisensory spatial mechanisms of the bodily self and social cognition - A commentary on Vittorio Gallese and Valentina Cuccio. In T. Metzinger & J. M. Windt (Eds.). Open MIND: 14(C). Frankfurt am Main: MIND Group.
Personal Contribution: Literature research, writing.

2 Papers

Part A: Functional multisensory mechanisms of first-person perspective

2.1 Study 1: First-person perspective during visuo-vestibular conflict

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Multisensory Origin of the Subjective First-Person Perspective: Visual, Tactile, and Vestibular Mechanisms

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Abstract

In three experiments we investigated the effects of visuo-tactile and visuo-vestibular conflict about the direction of gravity on three aspects of bodily self-consciousness: self-identification, self-location, and the experienced direction of the first-person perspective. Robotic visuo-tactile stimulation was administered to 78 participants in three experiments. Additionally, we presented participants with a virtual body as seen from an elevated and downward-directed perspective while they were lying supine and were therefore receiving vestibular and postural cues about an upward-directed perspective. Under these conditions, we studied the effects of different degrees of visuo-vestibular conflict, repeated measurements during illusion induction, and the relationship to a classical measure of visuo-vestibular integration. Extending earlier findings on experimentally induced changes in bodily self-consciousness, we show that self-identification does not depend on the experienced direction of the first-person perspective, whereas self-location does. Changes in bodily self-consciousness depend on visual gravitational signals. Individual differences in the experienced direction of first-person perspective correlated with individual differences in visuo-vestibular integration. Our data reveal important contributions of visuo-vestibular gravitational cues to bodily self-consciousness. In particular we show that the experienced direction of the first-person perspective depends on the integration of visual, vestibular, and tactile signals, as well as on individual differences in idiosyncratic visuo-vestibular strategies.

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Introduction

Recent research investigated how the processing of bodily signals modulates bodily self-consciousness and in particular *self-location* (i.e. the experience of where 'I' am in space) and *self-identification* with the body (i.e. the experience of identifying and owning a body) [1,2,3,4,5]. In these studies participants were presented with conflicting multisensory stimuli (such as visual, tactile, and proprioceptive signals) about the location and appearance of a body part (e.g. rubber hand illusion: [2]; enfacement illusion: [6,7]) or their entire body (e.g. full-body illusion: [8,9]).

Concerning the full-body illusion several paradigms have been used to investigate self-identification and self-location and their underlying brain mechanisms [10,11]. Changes in self-identification and self-location towards a virtual body have been induced in participants who were exposed to visuo-tactile mismatch between their own body and a filmed or virtual body [1,3,4,9,12] and have been associated with physiological changes [4,12], changes in visuo-tactile integration [1,13], and decreases in pain perception [14].

More recently, the effects of different visuo-spatial viewpoints on self-identification with a virtual body have been tested [15,16,17]. These studies investigated self-identification with a virtual body that was seen from a first- or third-person viewpoint and revealed stronger self-identification for first- than third-person viewpoints. Other studies have identified distinct behavioural and neural mechanisms when participants employed first-person as compared to a third-person viewpoints in perspective taking paradigms (i.e. [18,19,20]). Although these studies are important for cognitive mechanisms of perspective taking and highlight the effects of different visuo-spatial viewpoints on the strength of self-identification, they do not allow to induce changes in more subjective aspects of *first-person perspective*, that is the experience from where 'I' perceive the world [10,11].

This was achieved in a recent study where changes in the experienced direction of the first-person perspective were induced in the absence of any overt visual changes that were present in all previous works on the first-person perspective. The participants in the study by Ionta et al. [21] were lying supine on a robotic device with their head oriented upwards and their arms outstretched next to their body. They wore a head-mounted display (HMD) and saw the back of a virtual body as if seen from an elevated and downward looking perspective (Fig. 1A left panel and Fig. 1B). Participants were thus exposed to strong visuo-vestibular conflict. All participants received robot-controlled visuo-tactile stimulation. Yet, despite identical visuo-tactile stimulation, there were individual differences in the direction of the experienced first-person perspective. Half of the participants experienced looking upwards to the virtual body ('Up-group'), whereas the other half experienced looking downwards to the virtual body ('Down-group'). These individual differences in the experienced direction of the first-person perspective were associated with congruent patterns of self-location.

Ionta et al. [21] argued that these individual differences in the experienced direction of the first-person perspective were related to individual differences in multisensory integration of visual and vestibular signals related to gravity. Thus, participants in that study viewed a visual image on the HMD that contained a conflict between the visual gravitational cues of the seen body and the gravitational acceleration coded by the participant's vestibular and somatosensory receptors [22,23,24,25]. This may have caused differences in the experienced direction of the first-person

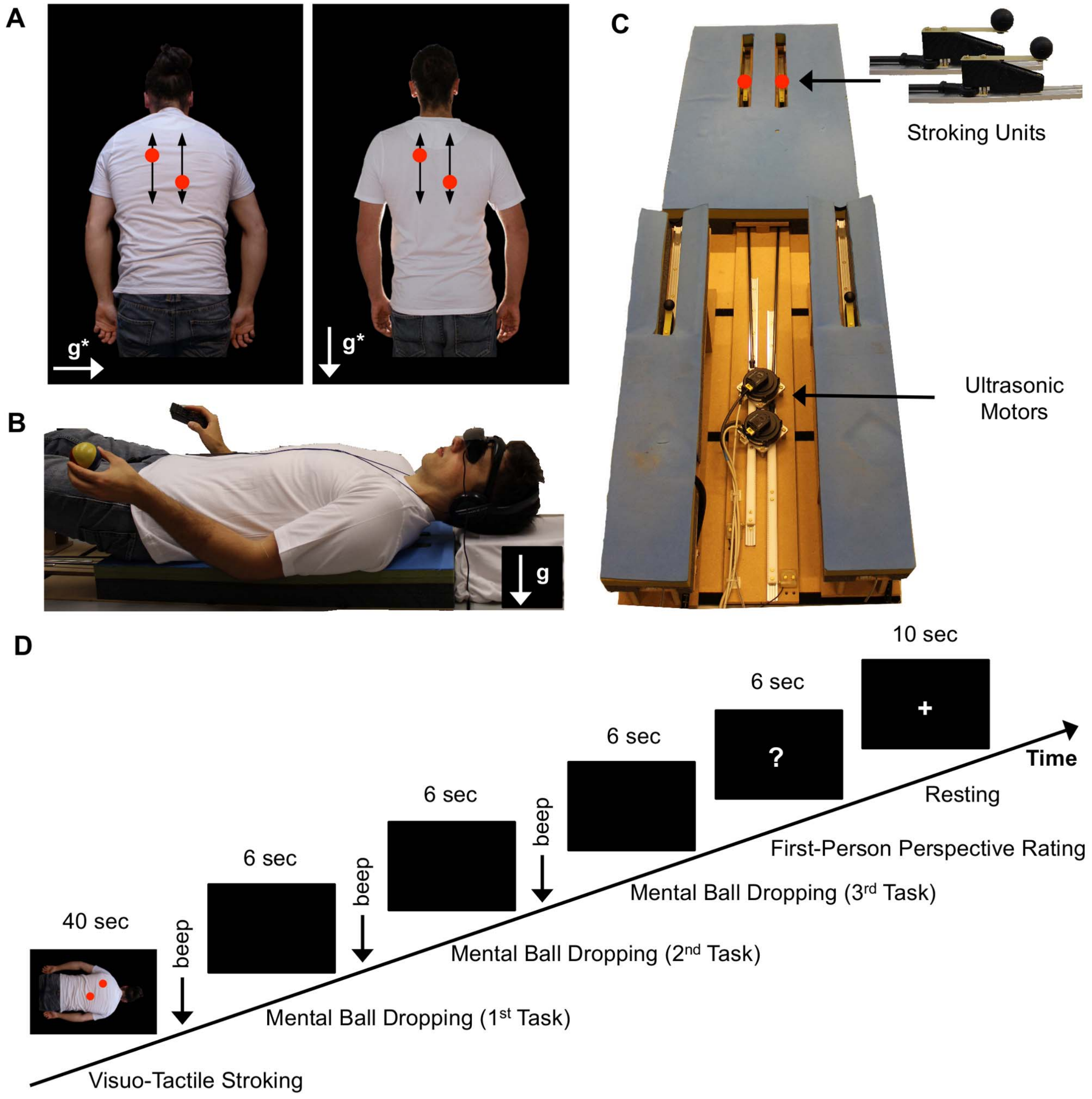

Figure 1. Experimental stimuli, setup, and procedure. (A) Visual stimuli showing a virtual body in prone posture from an elevated downward perspective used during the strong Visuo-Vestibular Conflict condition (left panel) and the same body standing used during the weak Visuo-Vestibular Conflict condition (right panel). Visual implied direction of gravity in each panel is indicated by a white arrow and 'g*' label. Visual stroking was presented by red dots (trajectory indicated by black arrows). (B) Participant lying supine, equipped with a ball to facilitate mental imagery during Mental Ball Dropping task, a button response device, and a head-mounted display. Direction of veridical vertical is indicated by a white arrow and 'g' label. (C) Robotic device used for tactile stimulation of the participants' back. Stroking units (in red color) were actuated by ultrasonic motors. (D) Sequence of events in an experimental trial.

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perspective, with participants from the Up-group relying more strongly on vestibular cues (indicating gravitational acceleration directed towards the participants' body) than on visual gravitational cues from the seen virtual body (indicating gravitational acceleration away from the participants' body), whereas participants from the Down-group showed the opposite pattern. However, individual differences in visuo-vestibular integration and their relevance for first-person perspective and other aspects of bodily self-consciousness have not yet been tested.

In the present series of experiments, we used a robotic full-body illusion paradigm and studied the multisensory mechanisms of self-identification, self-location and, in particular, of the experienced direction of the first-person perspective. In Experiment 1, we investigated whether different degrees of visuo-vestibular conflict have a distinct impact on self-identification, self-location, and the experienced direction of the first-person perspective. In Experiment 2, we investigated whether individual differences in the experienced direction of the first-person perspective that we observed in Experiment 1 for strong visuo-vestibular conflicts could also be quantified in repeated judgments of first-person perspective. In Experiment 3, we investigated whether individual differences in the experienced direction of the first-person perspective during the full-body illusion correlated with idiosyncratic differences in visuo-vestibular integration as quantified in a classical task of visuo-vestibular integration (i.e. visual vertical judgments).

Ethics Statement

All experimental protocols were approved by the local ethics committee–La Commission d'Ethique de la Recherche Clinique de la Faculté et de Medicine de l'Université de Lausanne–and each experiments was conducted in line with the Declaration of Helsinki. The person on the photographs of Figure 1 has given written informed consent, as outlined in the PLOS consent form, to publication of their photograph. Participants gave written informed consent to participate in the experiment before inclusion in the experiment.

Experiment 1

In Experiment 1, we investigated whether and how different levels of visuo-vestibular conflict during the full-body illusion, and thus additional visuo-tactile stimulation, influence bodily self-consciousness, in particular the experienced direction of the first-person perspective. For this, we used a modified version of the robotic device, that was used by Ionta et al. [21], and virtual reality technology to precisely control visuo-tactile stroking. We manipulated visuo-vestibular conflict by presenting participants with visual cues about the direction of gravity, which did not match the direction of veridical vertical (Fig. 1A–B). We hypothesized, first, that visuo-tactile stroking modulates self-identification (i.e. [1,4,9,12]) and that visuo-tactile stroking, together with visuo-vestibular conflict, would modulate self-location and the experienced direction of the first-person perspective. Following Ionta et al. [21] we used first-person perspective ratings to divide the participants sample into two subgroups that differed in terms of their predominantly experienced direction of the first-person perspective (Up- versus Down-group participants, see below). Based on findings by Ionta et al. [21], we hypothesized, second, that self-location but not self-identification would reflect individual differences between first-person perspective groups.

Methods

Participants. Twenty-six students from the Ecole Polytechnique Fédérale de Lausanne participated participated (12 female; mean age: 21 years, range: 18–28 years). All participants were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological or psychiatric impairment. Each participant was debriefed about the experimental purpose and received 30 CHF after the experiment.

Experimental setup. The experiment was conducted in complete darkness. A custom-made robotic device was installed on a table at 90 cm above the floor. The robotic device had 200 cm×90 cm×10 cm dimensions (for a detailed description see [26]). Figure 1B–C illustrates the experimental setup with a participant lying on the robotic device.

The robotic device stroked the back of the participant with two stroking units. A stroking unit consisted of an ultrasonic motor (Shinsei, USR60-E3N, Japan, http://www.shinsei-motor.com) delivering rotatory motion, a carbon stick that translated rotatory in linear motion, and a sliding unit with a plastic sphere mounted that touched the back of the participant. The stroking units stroked the left and right upper back of participants. Soft foam covered the robotic device to allow participants to comfortably lie during prolonged periods. The foam included gaps permitting the plastic spheres to directly touch the back of the participant. Participants wore a cotton T-shirt in order to reduce frictions between the plastic sphere and their back.

Visual stimuli were presented to participants on a head-mounted display (HMD, Virtual Realities, Virtual Viewer 3D, www.vrealities.com/virtualviewer3d.html) with a resolution of 800×600 pixels, representing about 35° of visual angle. Headphones presented white noise to participants to mask acoustic cues from robotic stroking. In-house software (ExpyVR, http://lnco.epfl.ch/expyvr) was used for visual stimulus presentation, real-time synchronization of visual stroking with robotic stroking, and for recording responses of the participant. Participants gave their responses with their right hand on a serial keypad (Targus Numeric Keypad AKP10US, www.targus.com).

Visual and tactile stimuli. Participants were presented with conflicting visuo-tactile stroking to induce the full-body illusion. '*Visual stroking*' consisted of projecting two red dots on the back of a virtual body seen in the HMD. The red dots moved along predefined stroking paths (illustrated by black arrows in Fig. 1A). *'Tactile stroking'* consisted of moving two plastic spheres along the back of a participant lying on the robotic device (Fig. 1C).

The sequences of visual stroking (seen on the HMD) and tactile stroking (felt on the participant's back) were either synchronous or asynchronous. Four stroking profiles were created before the experiment. Each profile consisted of a random sequence of positions in 0–20 cm distance range, 2–12 cm/s velocity range, and 40 s duration. The stroking profiles varied randomly in length, speed, direction, and inter-stroke-intervals (0–1.5 s), thus when simultanously executed they were incongruent. During the experiment, either two times the same profile or two incongruent profiles were randomly assigned to a stroking unit (touching the back of the participant) and the corresponding red dot (on the HMD), which resulted in visuo-tactile synchronous or asynchronous stroking.

Participants saw on the HMD a virtual body filmed from its back at 2 m distance, who wore a white T-shirt and blue jeans. All visual information around the virtual body was removed and replaced by black color in order to exclude visual cues about absolute distance to the environment. Either a male or female virtual body was shown to match the participant's gender. Male and female virtual body size was matched, as well as overall luminance in the images. We were careful to match the limb configuration of participants, who were lying on the robotic device, to the limb configuration of the virtual body, seen in the HMD. Participants' arms were positioned next to their trunk on the soft foam and their limbs were outstretched on the robotic device.

In addition to visuo-tactile stroking we manipulated visuo-vestibular conflicts about the direction of linear gravitational acceleration. We presented in the HMD images that showed a virtual body (seen from the back) in different postures with respect to visual gravity. Visual gravity cues were gravitational pull on hair, clothes, and the posture of the shoulders of the virtual body [27,28]. In addition, we chose a distribution of light on the front and back of the virtual body that was congruent with a light following the direction of visual gravity.

The first image (Fig. 1A, right panel) showed a virtual body in prone posture on which linear gravitational acceleration acted along an axis through the virtual body's back and chest. This image gave the impression of looking downwards at the virtual body. The second image (Fig. 1A, left panel) showed the same virtual body in standing posture on which linear gravitational acceleration acted along a vertical axis from the virtual body's head and feet. This image gave the impression of looking in front at the virtual body. The two images (i.e. looking downwards, looking in front) were respectively in strong and weak visual-vestibular conflict with the participant posture lying on the back on the robotic device and looking upwards (Fig. 1B). For the first image (strong conflict), the conflict was of 180° and for the second image (weak conflict) it was of 90°.

Experimental procedures and data collection. Each participant completed 32 trials in 4 experimental runs of 8 trials each. For each experimental run the 8 trials were from the same condition, but the stroking profiles were randomly selected for each trial. Fig. 1D illustrates the organization of each trial. Each trial began with the presentation of visual stroking on the virtual body in the HMD while tactile stroking was applied on the back of the participant for 40 s. After that, participants were shown a blank screen for a fixed inter-stimulus interval of 1 s. An acoustic beep was presented for 200 ms that instructed participants to perform the Mental Ball Dropping task within 6 s.

The Mental Ball Dropping task (adapted from [3,21]) was used to measure self-location. Before the experiment proper, participants performed a training session with at least 20 trials to be familiarized with the experimental procedures and the materials. Participants were asked to imagine dropping a ball from their hand to the floor (Fig. 1B). First, they pressed a button with their right index finger when they imaged dropping a ball from their hand, which was at the level of their body lying supine. Participants held the button depressed during the imagined time of ball dropping and released the button at the moment they imagined the ball hit the floor. The duration of button press (response time, RT) was shown to be a sensitive estimate of the participant's height, or self-location, above the floor [3]. Participants executed three Mental Ball Dropping tasks successively, then a white fixation cross was presented for 20 s, indicating a pause before the next experimental trial.

After having completed 8 trials of an experimental run participants answered a short version of the full-body illusion questionnaire (adapted from [3,21,29]. Questions were presented separately on the HMD along with a visual analogue scale, i.e. a continuous visual scale from left to right with either two or 11 levels, on which participants indicated their response. The questions measured (1) self-identification, by rating their agreement with the statement *"It felt as if the body I saw was me"* using a 11-point visual analogue scale ranging from 1 (= weak feeling) to 11 (= strong feeling); (2) illusory touch, by rating their agreement with the statement *"I had the feeling as if the touch I felt was located where I saw the stroking"* using a 11-point visual analogue scale ranging from 1 (= weak feeling) to 11 (= strong feeling); (3) and the experienced direction of the first-person perspective, by answering the question *"Did you have the impression as if you were looking upwards/downwards at a body above/below you?"* with a forced-choice categorical response format labeled 0 (= "*upwards*") and 1 (= "*downwards*").

Data analysis. Individual answers to question 3 regarding the experienced direction of first-person perspective were used to assign participants to two groups. Following the methods of Ionta et al. [21], who reported individual differences in first-person perspective and self-location, participants were assigned to the Up-group, if less than 2 out of the total 4 ratings were downward direction of the experienced first-person perspective (N = 15). Participants were assigned to the Down-group, if at least 2 out of 4 ratings were downward direction of the first-person perspective (N = 9). The Group (Up-group, Down-group) was used as a between-participants factor for subsequent statistical analyses.

Questionnaire scores for self-identification (question 1), illusory touch (question 2), and first-person perspective (question 3) were analyzed using separate 2×2×2 mixed model ANOVAs with one between-participants factor Group (levels: Up-group, Down-group) and two within-participants factors Visuo-Vestibular Conflict (levels: strong, weak) and Stroking (levels: synchronous, asynchronous).

For the Mental Ball Dropping task (i.e. self-location measure), we excluded trials that contained no response and trials with response times shorter than 200 ms or longer than 4 s. We excluded the data from two participants from further analysis because more than 10% of their trials had to be excluded. For the remaining 24 participants, we removed response times that exceeded 2 standard deviations of the grand average. We calculated then, for each participant, trial-wise averages across three repetitions of the Mental Ball Dropping task and used this data to calculate condition-wise averages for the four experimental conditions. Mean response times were analyzed with a 2×2×2 mixed model ANOVA with one between-participant factor Group (levels: Up-group, Down-group) and two within-participant factors Visuo-Vestibular Conflict (levels: strong, weak) and Stroking (levels: synchronous, asynchronous).

Post-hoc comparisons were performed with an a priori alpha level of.05. As post-hoc comparisons were conducted only the basis of significant interactions in ANOVAs, there was no correction for multiple comparisons.

Results

Questionnaire scores. Statistical analysis of self-identification ratings (question 1) revealed a main effect of Stroking ($F(1, 22) = 24.06$, $p < .001$, $\eta^2 = .52$). Participants rated on average 5.9 ($SE = .5$) points for synchronous Stroking and 2.9 ($SE = .4$) points for asynchronous Stroking. This main effect reflects that synchronous visuo-tactile Stroking increased self-identification with a virtual body and shows that we induced the full-body illusion with a novel robotic device. In addition we found a main effect of Visuo-Vestibular Conflict on self-identification ($F(1, 22) = 16.25$, $p = .001$, $\eta^2 = .43$). Participants rated 3.1 ($SE = .5$) points for strong Visuo-Vestibular Conflict and 4.7 ($SE = .4$) points for weak Visuo-Vestibular Conflict, suggesting that our manipulation of visuo-vestibular conflict had an influence on self-identification and that a strong visuo-vestibular conflict decreases self-identification with the virtual body. Furthermore, we found a significant interaction of Visuo-Vestibular Conflict×Stroking regarding self-identification ($F(1,22) = 9.35$, $p = .006$, $\eta^2 = .30$, Fig. 2A). Self-identification with the virtual body decreased during strong Visuo-Vestibular Conflict in the synchronous conditions (post-hoc paired t-test, $t(23) = -4.8$, $p < .001$), but not in the asynchronous control conditions. There were no main effect and interactions involving the between-participant factor Group (all F values <1), reflecting that individual differences in the direction of first-person perspective had no influence on self-identification.

Statistical analysis of illusory touch ratings (question 2) showed a main effect of Stroking ($F(1,22) = 152.69$, $p < .001$, $\eta^2 = .87$). Participants rated illusory touch on average with 9.0 (SE = .2) points for synchronous Stroking and 2.6 (SE = .5) points for asynchronous Stroking. This main effect shows that synchronous Stroking induced stronger illusory touch sensation. No other main effects and interactions were significant ($F < 1$).

Response times. Statistical analysis of response times of the Mental Ball Dropping task revealed an interaction of Stroking × Group, $F(1,22) = 4.85$, $p = .038$, $\eta^2 = .18$ (Fig. 2B). Up-group participants' response times were on average 901 (SE = 149) ms for synchronous Stroking and 834 (SE = 130) ms for asynchronous stroking. By contrast, for the Down-group participants, the pattern of response times was reversed and averaged 1214 (SE = 192) ms for synchronous Stroking and 1260 (SE = 167) ms for asynchronous Stroking. Post-hoc tests revealed a marginally significant difference between response times of the two Groups for asynchronous Stroking (independent samples t-test, $t(22) = 2.0$, $p = .056$). These results corroborate data by Ionta et al. [21] and reveal that those participants who experience mostly an upward direction of the first-person perspective showed longer response times in the synchronous versus asynchronous Stroking condition (indicating a drift in self-location towards the seen virtual body). This was different in participants experiencing mostly a downward direction of the first-person perspective who showed the opposite drift (i.e. a decrease in response times). In both groups, we observed a drift in self-location towards the seen virtual body. No other effects were significant.

First-person perspective ratings. Following the methods of Ionta et al. [21], we used first-person perspective ratings to divide the total sample of participants into Up-group (N = 15) and Down-group (N = 9) (see Data analysis section).

Statistical analysis of first-person perspective ratings (question 3) only revealed a main effect of Group, $F(1,10) = 94.3$, $p < .001$, $\eta^2 = .81$, which is a direct consequence of our method using question 3 rating to assign the datasets into two Groups. Up-group participants rated on average.08 (SE = .04) points and Down-group participants rated.75 (SE = .05) points. These scores reflect average frequency of participants rating *"downwards"* direction of first-person perspective (i.e. because we assigned the value 0 for an *"upwards"* rating and the value 1 for a *"downwards"* rating). The main effect reflects lower frequency of *"downwards"* rating for the Up-group and a higher frequency of *"downwards"* rating for the Down-group. No other main effect and no interaction reached statistical significance ($F < 1$), reflecting that Stroking and Visuo-Vestibular Conflict did not influence first-person perspective.

Discussion

In Experiment 1, we investigated how different degrees of Visuo-Vestibular Conflict modulate self-identification, the experienced direction of first-person perspective, and self-location during the full-body illusion. To this end, we used a novel robotic device [26] to administer visuo-tactile stimulation and manipulated the degree of Visuo-Vestibular Conflict and the synchrony of Stroking.

Regarding self-identification (question 1), we found, as expected, an increase in self-identification with the virtual body for synchronous stroking, supporting several earlier video and virtual reality studies applying visuo-tactile stroking manually [1,4,6,9,12,30]. We also confirmed that self-identification does not depend on the experienced direction of the first-person perspective [21]. A new finding was that self-identification additionally depended on the degree of Visuo-Vestibular Conflict,

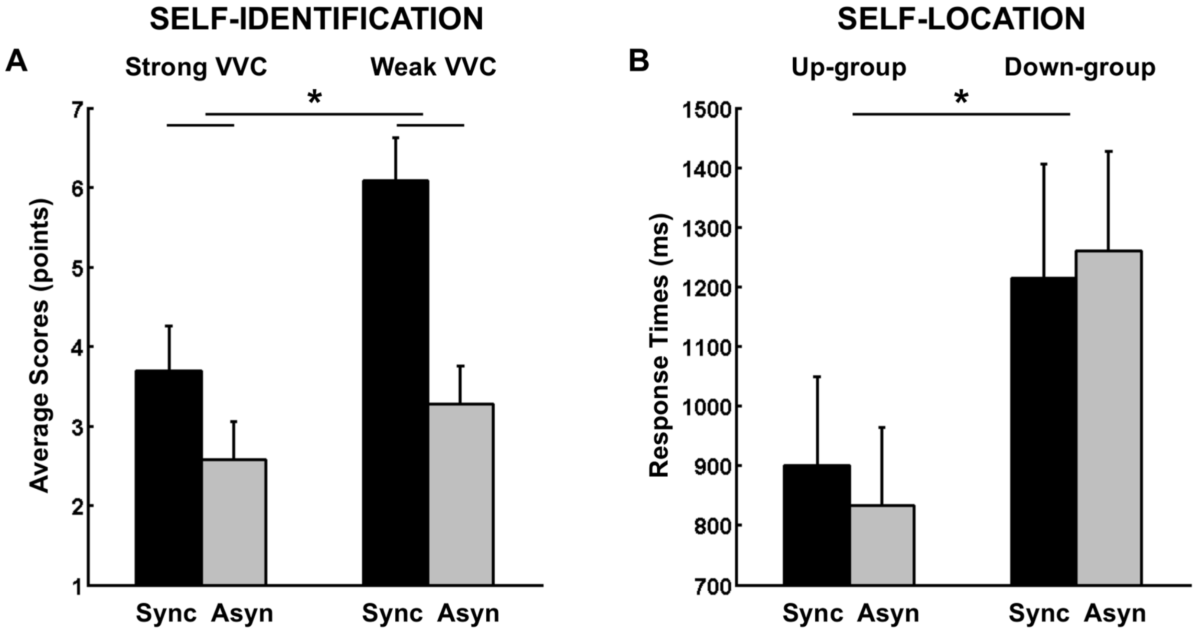

Figure 2. Results of Experiment 1. (A) Average self-identification ratings for the synchronous (Sync) and asynchronous (Asyn) visual-tactile stroking and for the strong and weak visual-vestibular conflict (VVC). (B) Self-location results showing average response times in the Mental Ball Dropping task. Error bars indicate standard errors of the mean.
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with strong conflict decreasing self-identification, an effect found only for the illusion condition (during synchronous visuo-tactile stimulation). These data show that under conditions of illusory self-identification with the virtual body strong Visuo-Vestibular Conflict decreases illusory self-identification, suggesting that the visuo-vestibular compatibility between the participant's body posture and position and those of the virtual body interfere with self-identification (see General Discussion).

Concerning the first-person perspective, we asked participants to rate their experienced direction once at the end of each experimental condition. Similarly to Ionta et al. [21], we found individual differences in Up- and Down-group participants. Using a slightly modified robotic platform, different experimental conditions, and a different participants sample we also observed for Up-group (respectively, Down-group) participants that response times increased (decreased) during the synchronous versus asynchronous Stroking condition, indicating a more elevated (lower) self-location in the illusion condition. These self-location data corroborate the presence of individual differences in first-person perspective and demonstrate a directional congruence between the experienced direction of the first-person perspective and the direction of the drift in self-location. However, these subjective ratings did not depend on the tested visuo-vestibular conflict or on visuo-tactile stroking. Therefore, they did not support our hypothesis that visuo-vestibular conflict, as manipulated here, is of relevance for the experienced direction of the first-person perspective.

In conclusion, Experiment 1 revealed that self-identification depends on visuo-vestibular and visuo-tactile mechanisms, whereas self-location and first-person perspective were only modulated by visuo-tactile stimulation. We confirmed the presence of individual differences in self-location and first-person perspective and the dependence of self-location on the experienced direction of the first-person perspective.

Experiment 2

In Experiment 1, we measured the direction of the first-person perspective once at the end of multiple repeated trials for the same condition. Using this procedure we may have not been able to detect more subtle changes in first-person perspective. Whereas in Experiment 1 trial order was randomized at the level of experimental runs (i.e. all trials within an experimental run were from the same experimental condition), in Experiment 2 trial order was randomized trial-by-trial. Participants were presented with the virtual body in strong visuo-vestibular conflict to be consistent with the study by Ionta et al. [21], and we collected the experienced direction of the first-person perspective after each experimental trial. In addition, we measured self-identification and self-location in a control condition where no body was shown (as in Ionta et al., [21]).

Methods

Participants. Twenty-three students participated (11 female; mean age: 22 years, range: 18–30 years). All participants were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological or psychiatric impairment. Each participant was debriefed about the experimental purpose and received 30 CHF after the experiment.

Experimental setup and stimuli. We used an identical experimental setup and the same visuo-tactile stroking stimuli as in Experiment 1. Self-identification, self-location, and the experienced direction of the first-person perspective were tested by presenting in a HMD a virtual body in strong Visuo-Vestibular Conflict (i.e. body condition) or a control condition in which the stroking was shown on a black background (i.e. no-body condition). In contrast to Experiment 1, participants judged their experienced direction of their first-person perspective repeatedly during the full-body illusion.

Experimental design and procedures. The full-body illusion was tested in 4 experimental conditions: 2 Object conditions (levels: body, no-body)×2 Stroking conditions (levels: synchronous, asynchronous), which were presented in a pseudo-randomized order. Participants completed 8 trials for each of the 4 experimental conditions. Each trial began with visuo-tactile Stroking for 40 s. Immediately after, all visual stimuli were removed from the display, and after 1 s, an acoustic beep was presented for 200 ms. Participants executed a single Mental Ball Dropping task within 6 s (identical procedure as for Experiment 1). After the Mental Ball Dropping task, they judged the direction of their first-person perspective. In the HMD the question *"Orientation?"* was presented in white color along with a two-choice response scale showing *"upwards"* and *"downwards"*. Participants were instructed to judge after each trial the direction of the first-person perspective experienced during the preceding stroking period. They gave their judgment within 6 s by pressing either a button with their right index finger to indicate an experienced upward direction of the first-person perspective, or by pressing a button with their middle finger to indicate an experienced downward direction of the first-person perspective. A white fixation cross was presented on the HMD for 20 s, indicating a pause before the next trial. In contrast with Experiment 1, participants executed the Mental Ball Dropping task only once and gave a first-person perspective judgment at the end of each experimental trial. In this way, we obtained a measure of self-location and first-person perspective for each experimental trial. After having completed the experiment, participants answered a short-version of the full-body illusion questionnaire separately for synchronous and asynchronous stroking (see Experiment 1).

Data analysis. Individual answers to question 3 regarding the experienced direction of first-person perspective (collected once at the end of the experiment) were used to assign participants to two groups (see Experiment 1 for details). We considered participants as Up-group participants when they experienced an upward direction of first-person perspective for both synchronous and asynchronous stroking (Up-group, $N = 12$). Down-group participants were those who experienced a downward direction of first-person perspective for synchronous and/or asynchronous stroking (Down-group, $N = 11$). The rationale for this procedure was to balance group size by lowering the threshold for classification. In Experiment 2, the downward direction of the first-person perspective was less frequently reported than upward direction.

Scores for self-identification (question 1) and illusory touch (question 2) were analyzed with separate 2×2 mixed model ANOVAs with one between-participant factor Group (levels: Up-group, Down-group) and one within-participant factor Stroking (levels: synchronous, asynchronous). No self-identification ratings were collected for the no-body condition.

Response times for the Mental Ball Dropping task (i.e. self-location measure) were analyzed as in Experiment 1. Condition-wise average response times for each participant were analyzed using a 2×2×2 mixed model ANOVA with the between-participant factor Group (levels: Up-group, Down-group) and two within-participant factors Object (levels: body, no-body) and Stroking (levels: synchronous, asynchronous).

Judgments of the direction of the first-person perspective given after each trial were analyzed after excluding trials where participant did not give a judgment within 6 s (<10%). We coded *"upwards"* responses as 0 and *"downwards"* responses as 1. Individual frequencies of *"downwards"* rating were calculated for each condition (i.e. sum of the values across the repetitions of each condition divided by the total number of valid judgments per condition). We thus obtained, for each participant and each condition, a frequency value of *"downwards"* rating ranging from 0 (i.e. never judged *"downwards"*) to 1 (i.e. always judged *"downwards"*). These frequencies were analyzed with a 2×2×2 mixed model ANOVA with the between-participant factor Group (levels: Up-group, Down-group) and two within-participant factors Object (levels: body, no-body) and Stroking (levels: synchronous, asynchronous).

Results

Questionnaire scores. Statistical analysis of self-identification (question 1) revealed a main effect of Stroking (F(1, 21) = 11.9, p = .002, $\eta^2 = .36$), reflecting higher self-identification for synchronous stroking (mean ± SE: 4.3±.5) than for asynchronous stroking (2.8±.4). There was no difference between the two Groups and no interaction (all F values <1). As for Experiment 1, visuo-tactile synchrony influenced self-identification with a virtual body and individual differences in the experienced direction of first-person perspective did not modulate self-identification.

Statistical analysis of illusory touch (question 2) showed a main effect of Stroking (F(1, 21) = 35.0, p<.001, $\eta^2 = .63$). Illusory touch was higher for synchronous stroking (6.2±.4) than for asynchronous stroking (4.0±.5). There was no difference between the Groups and no significant interaction (all F values <1).

Response times. Statistical analysis of response times of the Mental Ball Dropping task revealed an interaction between Stroking and Group (F(1,21) = 6.87, p = .016, $\eta^2 = .25$, Fig. 3C). For Up-group participants response times were on average 1025 (SE = 104) ms for synchronous Stroking and 1007 (SE = 107) ms for asynchronous Stroking (paired-sample t-test, p>.1), whereas for Down-group participants response times were 926 (SE = 108) ms in the synchronous and 996 (SE = 110) ms in the asynchronous Stroking condition (paired sample t-test, t(10) = −2.4, p = .04). Thus, we confirmed that the pattern of self-location (as measured through response times) is congruent with individual differences in the experienced direction of the first-person perspective. Up-group participants showed an upward drift in self-location (a slight increase in response times during the illusion) congruent with the upward direction of the first-person perspective, By contrast, Down-group participants show a downward drift in self-location (a decrease in response time during the illusion) congruent with the experienced downward direction of the first-person perspective.

The analysis also revealed a marginally significant effect of Object (F(1,21) = 4.1, p = .057, $\eta^2 = .16$) with longer response times for the body condition (M = 992, SE = 76 ms) when compared to the no-body control condition (M = 974, SE = 76 ms). This suggests that independently of visuo-tactile Stroking, self-location tended to be more elevated if a body in strong Visuo-Vestibular Conflict was presented as compared to a no-body control condition. There was no significant effect of Group and no interaction (all F values <1).

First-person perspective ratings. Statistical analysis of first-person perspective ratings collected after each trial revealed a significant main effect of Stroking (F(1,21) = 6.23, p = .021, $\eta^2 = .23$, Fig. 3A). The frequency of *"downwards"* ratings was higher during asynchronous (M = .48, SE = .03) than synchronous Stroking (M = .38, SE = .03). Furthermore, the analysis showed a main effect of Group (F(1,21) = 5.88, p = .024, $\eta^2 = .22$, Fig. 3B), with an average *"downwards"* rating frequency of.35 (SE = .04) for the Up-group and.48 (SE = .04) for the Down-group. There was no significant main effect of Object and no significant interactions (all F values <1). These results confirm the consistency between final ratings of first-person perspective in the full-body illusion questionnaire (i.e. on which grouping was based) and trial-wise ratings for first-person perspective during the experiment. However, they also show that trial-wise ratings fluctuated for all participants and that a downward direction of the first-person perspective was more likely associated with asynchronous visuo-tactile stimulation.

Discussion

The data on self-identification and self-location corroborate those of Experiment 1 and previous work in a different participant sample. We found that self-identification and illusory touch were higher in the synchronous Stroking condition and that the degree of self-identification was not related to individual differences in the experienced direction of first-person perspective. Self-location was found to be Stroking- and first-person perspective-dependent and we again observed a relative elevation in self-location towards the seen virtual body for Up-group participants and a relative lowering in self-location for Down-group participants. In Experiment 2, the order of the trials was randomized to control for habituation and training effects. This differed from previous studies (Experiment 1, [21]), further underlining the consistency of these changes in self-location and self-identification.

Self-location results are consistent across three experiments–the study by Ionta et al. [21] and the present Experiments 1 and 2. The asynchronous Stroking condition induced significantly higher self-location for Down-group participants when compared to Up-group participants. Subjective first-person perspective was most frequently rated *"downwards"* in the asynchronous Stroking condition (Experiment 2), although self-identification was low ([21]; Experiments 1–2). Furthermore, the body condition, where a virtual body was presented in strong visuo-vestibular conflict, was associated with higher self-location than the no-body condition. Together these results suggest that asynchronous stroking and the presentation of a virtual body in strong visuo-vestibular conflict induced a response pattern congruent with the visually-implied direction of gravity: high self-location, downwards direction of the subjective first-person perspective, and low self-identification.

In Experiment 2, participants indicated their experienced direction of the first-person perspective after each 40-second period of visuo-tactile stimulation. Analysis of trial-wise ratings confirmed those ratings of the first-person perspective collected at the end of Experiment 2. Although this reveals consistency of ratings given in the full-body illusion at different time points, the first-person perspective data from Experiment 2 also showed that participants that were classified as Up- or Down-group may also have experienced quite frequently a direction of the first-person perspective that was 180° inverted with respect to their most frequently experienced perspective. This may be compared to effects found in bistable perception in which identical physical stimuli evoke two perceptual states that alternate spontaneously [31,32,33].

Moreover, our analysis revealed an influence of visuo-tactile Stroking on the frequency of downward direction of the first-person perspective. We found a higher frequency of downward direction of the first-person perspective during asynchronous Stroking conditions as compared to synchronous Stroking conditions. Ionta et al. [21] found that self-location depended on both first-person perspective and visuo-tactile stroking. In this study, Down-group participants showed higher self-location in the

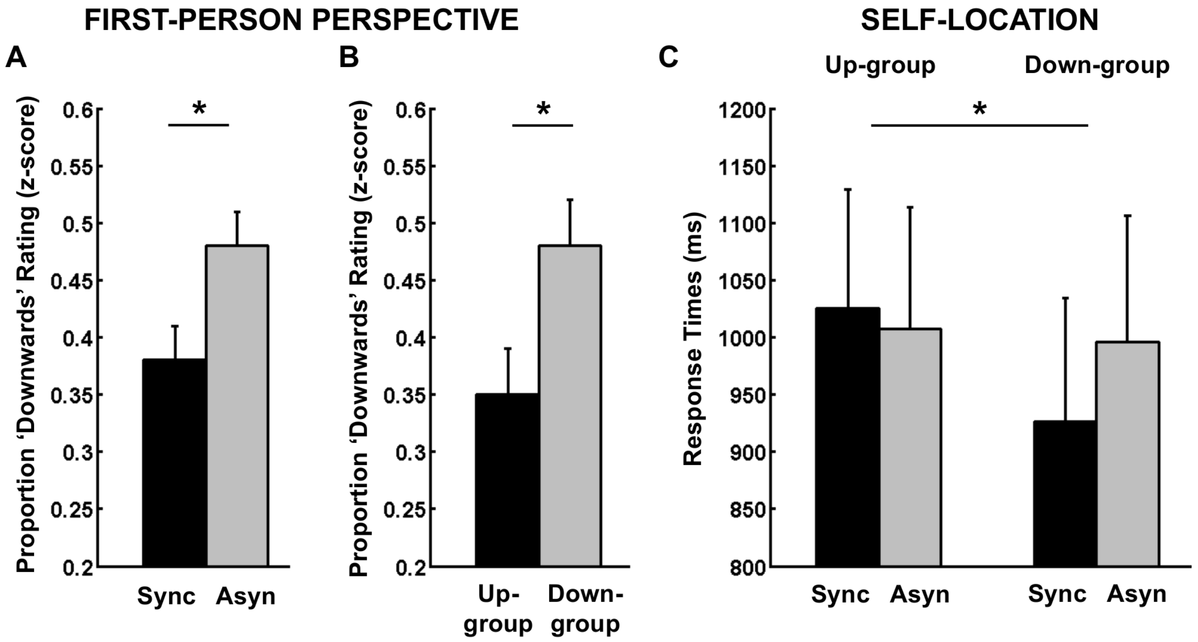

Figure 3. Results of Experiment 2. Frequency of *"downwards"* ratings for the experienced direction of the first-person perspective showing the main effect of Stroking (A) and Group (B). (C) Self-location results showing average response times in the Mental Ball Dropping task. Error bars indicate standard error of the mean.
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asynchronous than in the synchronous stroking condition, reflecting that self-location decreased or drifted towards the seen virtual body (in line with the downwards direction of subjective first-person perspective). Thus, during asynchronous stroking, an association of a downwards direction of the subjective first-person perspective with a high level of self-location was found [21]. The same participants reported in the same asynchronous condition floating sensations, sensations of being elevated and of touching the ceiling, compatible with more elevated self-location. Thus, first-person perspective ratings, self-location measures, and spontaneous verbal reports were strongly related during asynchronous visuo-tactile stroking. In Experiment 2, we found an association between asynchronous visuo-tactile Stroking and a downward direction of the experienced first-person perspective, not only for Down-group participants, but for all participants.

In conclusion, Experiment 2 shows that within participants the synchrony of visuo-tactile Stroking affected the first-person perspective, resulting in the highest frequency of downward direction of the first-person perspective for asynchronous Stroking. Furthermore, self-location was elevated above a no-body baseline condition level when a virtual body was shown in strong visuo-vestibular conflict from an elevated viewpoint. Finally, we confirmed the results of individual differences in self-location and first-person perspective from Experiment 1 and by Ionta et al. [21]. Together, these results suggest that both visuo-tactile integration and individual differences can affect the experienced direction of the first-person perspective.

Experiment 3

In Experiment 3, we investigated whether individual differences in first-person perspective are associated with idiosyncratic strategies for solving visual-vestibular conflicts. Individual differences and strategies for processing visual-vestibular mismatch have traditionally been approached by tasks requiring visual vertical judgments. Visual vertical judgments require the integration of vestibular signals (informing about the direction of gravity), somatosensory signals (informing about the position of the body segments) and visual signals (informing about the orientation of the visual environment) [34]. Typically, participants are required to align a visual line with their internal representation of the vertical [35]. The influence of visual signals on vertical perception has been investigated by manipulating the orientation of the visual background relative to the veridical vertical to induce visual-vestibular conflicts. In the widely used rod and frame test, participants judge the orientation of a mobile rod that is embedded in a tilted square frame [35]. The perceived visual vertical is typically deviated in the direction of the frame tilt. However, the amplitude of this deviation is strongly variable across subjects and depends on the degree to which participants rely on visual references. Two groups of participants have usually been dissociated [23,24,35,36,37]. Visual Field-Dependent (FD) participants present strong deviations of the perceived vertical in the direction of the frame tilt, indicating that they rely strongly on visual signals. By contrast, visual Field-Independent (FI) participants present smaller deviations of the perceived vertical, indicating that they rely more on vestibular and somatosensory signals. It has been argued that visual field dependence-independence is a stable trait, which shows a high robustness throughout life [38,39]. As the rod and frame test is a well-established way to measure individual differences in visuo-vestibular integration, the present experiment directly investigates how visual field dependence-independence relates to the experienced direction of the first-person perspective. We hypothesize that FD participants, in contrast with FI participants, are more likely to experience a direction of the first-person perspective that is congruent with that visually shown in the HMD. Data from Experiment 1 suggest that these participants should be more prone to rely on the visually conflicting gravitational information when exposed to strong Visuo-Vestibular Conflict. Thus, in the present case, FD participants observing a body lying in a prone position should experience more frequently a downward direction of the first-person perspective.

Methods

Participants. Twenty-nine students participated (11 female; mean age: 23 years, range: 18–30 years). All participants were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological or psychiatric impairment. Each participant was debriefed about the experimental purpose and received 40 CHF after the experiment.

Methods for the rod and frame test. Participants were comfortably seated in front of a computer screen (Philips 150S6FS, TFT, 1024×768 resolution, 60 Hz refresh rate) at 60 cm eye-to-screen distance. The screen was covered with a black circular frame in order to restrict the visual field to a circular area (36 cm in diameter, subtending 34° of the visual field) and to exclude any vertical and horizontal references from the visual surrounding (for similar methods see [40]). A chinrest was used to maintain the participants' line-of-gaze aligned with the center of the screen. Participants wore custom-made goggles to occlude any visual cue surrounding the circular-shaped screen.

A grey dotted line (18 cm long, subtending 17° of the visual field) was presented on the screen. This line was surrounded by a square frame (22×22 cm, subtending 29° of the visual field), which was either vertical or tilted by 20° in the clockwise or counterclockwise direction. This amplitude of the frame tilt has been shown to evoke large deviations of the perceived visual vertical towards the frame tilt [24,34,41]. Participants performed visual vertical judgments by pressing a left or right response button to rotate the line in a clockwise or counterclockwise direction until they judged the line vertically oriented. They were instructed to ignore the surrounding frame and to perform accurate and unspeeded judgments. The initial position in which the line was shown was either clockwise (6 trials) or counterclockwise (6 trials) at pseudo-random offset of ±12°, ±6°, and ±3° from veridical vertical. We used the same frame orientation for six consecutive trials before another frame orientation was presented. Each frame orientation was presented twice, and a total of twelve measurements were obtained per condition. For each participant, we calculated the average subjective visual vertical for each frame orientation (20° counterclockwise, 20° clockwise, vertical frame). Subjective visual vertical was analyzed with repeated-measures ANOVA with the Frame orientation as a within-participants factor (levels: clockwise, counterclockwise, and vertical frame).

Methods for the full-body illusion. After having completed the rod and frame test, participants were tested with the full-body illusion paradigm. The procedures were identical to that of Experiment 2, except for one aspect. In order to validate the robustness of the response times during the Mental Ball Dropping task, participants performed this task during and after the stroking.

We used a 2 Object (levels: body, no-body control) ×2 Stroking (levels: synchronous, asynchronous) design. We measured self-location by recording response times in the Mental Ball Dropping task and asked participants to indicate their experienced direction of first-person perspective after each experimental trial (online first-person perspective judgment) and after each experimental block (final first-person perspective judgment). After the experiment, participants filled in a questionnaire about the full-body illusion separately for the synchronous and asynchronous Stroking conditions. Self-identification was not rated for the no-body control condition.

Experimental procedures. Each experimental trial began with the presentation of visuo-tactile stroking for 40 s. In contrast to Experiments 1 and 2, participants performed the Mental Ball Dropping task twice during the stroking and twice after the stroking period. We modified the timing of the Mental Ball Dropping task to investigate the possibility to use the Mental Ball Dropping task as an online measure during stroking. An acoustic beep was presented for 200 ms, cueing participants to perform the Mental Ball Dropping task within 6 s, and response times were recorded as the duration of button press. After the stroking, all visual stimuli were removed from the display and the stroking stopped. After the last Mental Ball Dropping task, participants indicated their experienced direction of first-person perspective by a button press. The phrase "*Orientation?*" was presented in the HMD together with three response categories (category 1: "*As if I was looking up at a body above me*"; category 2: "*As if I was looking in front at a standing body*"; category 3: "*As if I was looking down at a body below me*"). Participants indicated their judgments by button press with the right index (for *"upwards"*), middle (for *"front"*), or ring finger (for *"downwards"*). Immediately after, a fixation cross was presented for 10 s, indicating a resting period.

After the experiment, participants gave a final rating of first-person perspective, considering the experiment as a whole, and indicated their most frequently experienced direction of first-person perspective in a forced-choice two-response format (category 1: "*As if I was looking up at a body above me*"; category 2: "*As if I was looking down at a body below me*"). Participants answered the full-body illusion questionnaire separately for the synchronous and the asynchronous stroking condition (11 items, visual presentation of the questions together with a 11-point visual analogue scale, adapted from [3]).

Data analysis. As in Experiments 1 and 2, participants were asked for a final rating of their overall experienced direction of first-person perspective. We used this rating to classify participants into Up-group and Down-group. Each item of the full-body illusion questionnaire was analyzed separately using a 2×2 mixed model ANOVA with a between-participants factor Group (levels: Up-group, Down-group) and a within-participant factor Stroking (levels: synchronous, asynchronous).

Response times for the Mental Ball Dropping task were averaged after excluding trials (less than 10%) with responses shorter than 200 ms and longer than 4 s as well as response times that exceeded 2 standard deviations of the grand average. For each trial, we calculated averages of 4 Mental Ball Dropping tasks. These data were analyzed using a mixed model ANOVA with the between-participants factor Group (levels: Up-group, Down-group) and two within-participant factors: Object (levels: body, no-body control), and Stroking (levels: synchronous, asynchronous).

Analysis of trial-wise ratings of first-person perspective-direction included calculation of frequency scores for "downwards" ratings by summing all non-"upwards" ratings (i.e. "downwards" and "front") per condition and dividing this value by the total number of trials per condition. Because both the "front" and "downwards" response categories were similar in that they indicated deviation from the participants' physical body orientation (looking "upwards"), we decided to collapse the "front" and "downwards" judgments into a single score reflecting deviation from "upwards". This resulted in a comparable ratio of Up-group versus Down-group participants as in the previous experiments where no "front" category was used. Thus, frequency scores ranged from 0 (i.e. never "downwards" and never "front") to 1 (i.e. always "downwards" or "front"). Individual frequency scores for "downwards" first-person perspective were subjected to a mixed model ANOVA with the between-participant factor Group (levels: Up-group, Down-group) and the within-participant factors Object (levels: body, no-body control) and Stroking (levels: synchronous, asynchronous).

Field dependence-independence classification and analysis. We analyzed the relationship between field dependence-independence and the experienced direction of the first-person perspective in two ways. First, across all participants we conducted a linear correlation analysis between continuous values for subjective visual vertical bias (average across left and right frame tilt condition) and the frequency of downward first-person perspective (average across experimental conditions).

Second, comparing subgroups of participants we performed a binominal correlation analysis (see below) on classification-based labels for field dependence-independence (FI-group, FD-group) and individual difference in first-person perspective (Up-group, Down-group). Data processing involved calculating baseline-corrected averages of subjective visual vertical for each participant by subtracting the perceived vertical measured with the vertical frame to the perceived vertical for the clockwise and counterclockwise frame orientations (see [24] for similar approach). We used an ascending hierarchical classification, i.e. a standard procedure for processing rod and frame test data, to classify participants into two groups of visual field dependent (FD) and field independent (FI) participants (see [24,42] for similar methods). Ascending hierarchical classification was performed on these data with SPSS 13.0 (IBM corporation, New York, US). The clustering method took into account individual average subjective verticality ratings for left-, and right-frame conditions. The method evaluated similarities between individual ratings of different participants by calculating Euclidean distance between participants. Based on Euclidean distances, the hierarchical clustering algorithm grouped participants into clusters using the Ward's aggregation method. Ward's aggregation linked pairs of participants, who were close, into binary clusters forming a hierarchical tree. Finally, separating the hierarchical tree at the maximum of dissimilarity provided two distinct clusters of participants with low (cluster 1, FI-group) or high (cluster 2, FD-group) deviations of perceived vertical induced by the tilted frame (Fig. 4E).

In order to investigate the relationship between labels for visual field dependence-independence and labels for first-person perspective-direction for each participant, we used the phi coefficient as a binominal non-parametric test of correlation [43]. The phi coefficient indicates whether two binominal categorical variables correlate, and in which direction they are associated.

Results

Rod and frame test. The ANOVA revealed a significant main effect of the frame orientation ($F(2,27) = 12.0$, $p < .001$, $\eta^2 = .47$, Fig. 4D) with a counterclockwise bias for the frame tilted counterclockwise ($M = -1.01°$, $SE = .39°$), a clockwise bias for the frame tilted clockwise ($M = .78°$, $SE = .38°$), and no bias for the vertical frame ($M = .02°$, $SE = .21°$). The analysis of the visual field dependence by an ascending hierarchical classification revealed a group of 13 FD participants (subjective vertical: $M = 1.70°$, $SE = .30°$) that presented significantly larger deviations of the visual vertical than a group of 16 FI participants (subjective vertical: $M = .70°$, $SE = .10$) when the frame was tilted by 20° (Fig. 4E).

Field dependence-independence correlates with first-person perspective. Linear correlation analysis between continuous data for subjective visual vertical bias and experienced direction of the first-person perspective showed no significant correlation ($R = .107$, $p = .578$), suggesting that across the entire participant sample there was no linear relationship between these measures.

Binominal correlation analysis between field dependence-independence and individual differences of the first-person perspective correlated significantly ($N = 29$, Phi coefficient $= -.442$, $p = .017$). Fig. 4F shows that there were proportionally more FI participants in the Up-group (12 out of 16) than in the Down-group (4 out of 13). Conversely, there were proportionally more FD participants in the Down-group (9 out of 13) than in the Up-group (4 out of 16). This result confirms our hypothesis that FD participants rely more on the visual information about the direction of gravity that was contained in the videos depicting a body lying in a prone position. Furthermore, this results shows a relationship between field dependence-independence and first-person persepective on the level of individual differences.

Self-identification and self-location. The ANOVA showed a significant effect of stroking for self-identification (question 1). Self-identification was higher during synchronous ($M = 4.9$ points, $SE = .6$ points) than asynchronous stroking ($M = 2.9$ points, $SE = .4$ points) ($F(1,28) = 12.3$, $p = .002$, $\eta^2 = .31$, Fig. 4A). Similarly, illusory touch (question 2) was higher for the synchronous ($M = 8.0$ points, $SE = .4$ points) as compared to the asynchronous stroking condition ($M = 4.3$ points, $SE = .5$ points) ($F(1,27) = 40.4$, $p < .001$, effect size $= .60$). There were no group differences (i.e. between Up- and Down-group of first-person perspective) in all questionnaire items.

Although, the pattern of Mental Ball Dropping response times was similar to those obtained in Experiment 1 and 2 (Fig. 4C), statistical analysis of the response times revealed no significant main effect and interaction. Inspection of the data shows that Up-group participants showed longer response times in the synchronous ($M = 850$ ms, $SE = 65$ ms) versus asynchronous Stroking condition ($M = 828$ ms, $SE = 59$ ms), whereas Down-group participants did not show the expected changes in response times (synchronous: $M = 666$ ms, $SE = 72$ ms; asynchronous: $M = 670$ ms, $SE = 65$ ms).

Regarding online ratings of the first-person perspective, the ANOVA revealed a significant main effect of Object ($F(1,27) = 8.8$, $p = .006$, $\eta^2 = .25$), with higher frequency of *"downwards"* ratings in the body condition ($M = .43$, $SE = .04$) as compared to the no-body condition ($M = .30$, $SE = .05$) (Fig. 4B). These results show that *"downwards"* ratings were more frequent in the condition in which a body was shown (i.e. in strong visuo-vestibular conflict) as compared to a no-body control condition, where no visual cues about the direction of vertical were provided. In addition, the statistical analysis revealed a main effect of Group with a lower frequency of *"downwards"* ratings for the Up-group ($M = .14$, $SE = .05$) as compared to the Down-group ($M = .59$, $SE = .06$) ($F(1,27) = 5.7$, $p < .001$, $\eta^2 = .55$). This result confirms the consistency between online and final ratings of first-person perspective and is also consistent with data from Experiment 2. There were no other main effects or interactions.

Discussion

Results of the rod and frame test showed that oriented visual references resulted in a predicted bias of visual vertical judgment. Experiment 3 thus replicates with a 2-dimensional computer-adaptation of the rod and frame test earlier findings obtained with the classical 3-dimensional rod and frame test [35,44]. As noted previously, biases of visual vertical judgments that are measured with a 2-dimentional rod and frame test are weaker, but nonetheless significant (review in [44]). In the present experiment, we classified participants into two groups of FD and FI participants [23,24,36] that differed in term of the perceptual bias evoked by a tilted frame. This result reveals individual differences in solving visual-vestibular conflict during the rod and

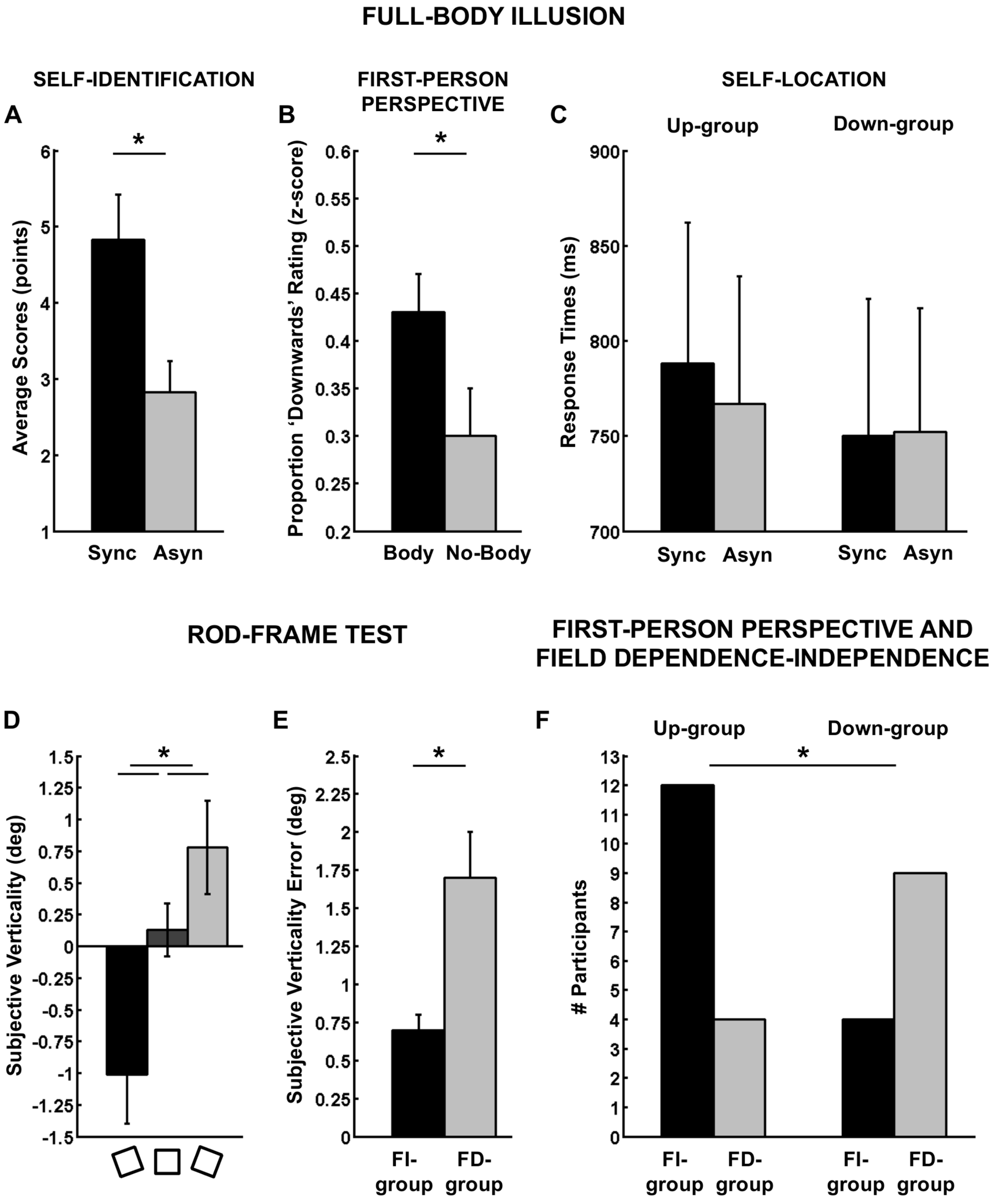

Figure 4. Results of Experiment 3. (A) Main effect of synchrony of visual-tactile Stroking on self-identification. (B) Average frequency of *"downwards"* rating for the experienced direction of the first-person perspective for the virtual body and no-body control condition. (C) Self-location results showing a similar pattern as Experiment 1 and 2. (D) Average subjective verticality rating for different frame orientations. Negative (positive) values denote counterclockwise (clockwise) deviations of the subjective verticality. (E) Average subjective verticality error in field independent (FI-group) and field dependent (FD-group) participants. Error bars denote standard errors of mean. (F) Association between Field dependence-independence and direction of the first-person perspective.
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frame test. These differences, also referred to as perceptual styles or sensory strategies, have been related to idiosyncratic selection of spatial frames of reference for spatial perception and orientation [45]. According to this view, we predicted that FD participants will rely mostly on an allocentric (i.e. visual) frame of reference, whereas FI participants will rely mainly on an egocentric (i.e. body-centered) frame of reference. The correlation between the visual field dependence-independence and the experienced direction of first-person perspective is discussed in the General Discussion.

As in previous experiments, self-identification with the virtual body was modulated predictably by visuo-tactile stimulation. Regarding self-location, we did not find any significant effect within or between experimental conditions or participant groups, although the general pattern was similar. For Experiment 3, we changed the timing of the Mental Ball Dropping task to include responses during the stroking and this may have affected responses. Thus, participants performed the Mental Ball Dropping without knowing exactly when the acoustic cue will be presented, resulting in shorter preparation time for the mental imagery procedure than in Experiments 1 and 2. Secondly, participants performed the Mental Ball Dropping task 6 s earlier as compared to participants of Experiments 1 and 2, allowing less time for the illusion to develop. Finally, we note that the effect size of earlier work and the present Experiments 1 and 2, revealing a modulation of self-location by first-person perspective and visuo-tactile stroking were not very large, making it likely that across several different subjects samples, these effect do not reach significance (averaging data across all three Experiments, we did observe a significant interaction of Group×Stroking).

Regarding the first-person perspective, we confirmed the results of Experiment 2, indicating consistency between online ratings given during the experiment and the final rating of overall first-person perspective-direction. In addition, there was a main effect of Object, with higher frequency of downward direction of the first-person perspective in the body condition than in the no-body, control, condition. This suggests that in the no-body condition participants relied more on vestibular signals, whereas in the body condition (in strong visuo-vestibular conflict), participants were more influenced by the visual information indicating a downward direction of gravity.

General Discussion

We investigated how multisensory stimulation influences three important aspects of bodily self-consciousness: *self-identification* (i.e. how much 'I' identify with a virtual body), *self-location* (i.e. where 'I' am located), and *first-person perspective* (i.e. from where 'I' perceive the environment). We found three main results. First, self-identification does not depend on the experienced direction of the first-person perspective, whereas self-location does. Second, bodily self-consciousness strongly depends on visual gravitational signals. Third, individual differences in the experienced direction of first-person perspective correlate with individual differences in visuo-vestibular integration, i.e. with idiosyncratic sensory strategies.

First-person Perspective, Viewpoint, and Self-identification

Results of the present three experiments confirm that self-identification with a virtual body depends on visuo-tactile stimulation and increases during synchronous stroking as observed by previous authors [1,4,9,12]. Whereas in these previous full-body illusion studies the first-person perspective was not altered, we here show that changes in the experienced direction of the first-person perspective did not modulate the strength of self-identification, We thus confirm the data of Ionta et al. [21] in a different subjects sample, using a different stroking robot, in three experiments performed outside the MRI scanner. Whereas our data and those of Ionta et al. [21] suggest that illusory self-identification does not depend on the experienced *direction* of the first-person perspective, previous studies showed that self-identification depends on the *viewpoint* from where the environment is presented to the participants. Thus, Petkova et al. [16] showed that a first-person (i.e. body-centered) viewpoint, but not a third-person viewpoint (i.e. displaced 75 cm to the side), induces stronger illusory self-identification with an artificial body. The data by Petkova and Ehrsson [4] and Slater et al. [17] are also compatible with this observation. These data converge in showing that perceptual changes in the visual direction of the viewpoint modulate self-identification, whereas subjective changes in the direction of the first-person perspective do not, a finding compatible with different brain mechanisms for viewpoint versus first-person perspective changes.

Next, we found that strong visuo-vestibular mismatch diminishes experimentally-induced changes in self-identification. Thus, in Experiment 1, we found that a strong visuo-vestibular conflict (i.e. when observing a body lying on the stomach and seen from an elevated viewpoint) decreases illusory changes in self-identification compared to that obtained with a weak visuo-vestibular conflict (i.e. when observing a body in a standing upright posture seen from a standing viewpoint). These data demonstrate for the first time that visuo-vestibular conflict influences self-identification. They also suggest that the central nervous system extracts visual information about the gravitational influence on body structure and shape, such as gravitational pull on hair, clothes, and shoulder, and modulations in light distribution on the body, suggesting a postural configuration relative to natural light sources. This visual information modulates accordingly the way we identify with fake or virtual bodies seen under the present experimental conditions. Indeed, there is substantial evidence that the visual system is highly tuned to interpret postural configurations in relation with gravity [40] and that the orientation of seen bodies with respect to the apparent direction gravity strongly influences body configuration and body motion processing [46,47,48]. This evidence suggests that the central nervous system has internalized the expected influence of gravity on body configuration and structure [40,49], most likely through mostly preconscious internal models of gravity [50]. Several studies have demonstrated that the vestibular nuclei and the vestibular cortex (such as the temporo-parietal junction) can detect the congruence of visual orientation and the motion of objects with respect to the physical laws of gravity [51,52,53]. Thus, in the case of strong visual-vestibular conflict used in the present experiments, these neural systems could detect that the apparent gravitational force acting on the virtual body is incongruent with the physical forces acting on the participant's body. Such visuo-vestibular conflict may decrease self-identification through a different cortical system than that involved in the visuo-tactile conflicts classically tested, but may involve the temporo-parietal cortex (i.e. [21]). In addition, we note that several related studies demonstrated that pictorial cues about gravitational orientation in a visual scene (which can be artificially tilted or reversed) outweigh orientation information from the physical gravity and the participant's body [54]. This suggests that visual information about the orientation and direction of gravity strongly constraints the participants' perception of their own body and the environment.

Common Multisensory Mechanisms Underlying Self-location and the Experienced Direction of the First-person Perspective

Another main finding of the present results is the close association between self-location and the direction of first-person perspective. Self-location depended both on the synchrony of visuo-tactile stroking and on individual differences in the experienced direction of the first-person perspective. In two out of three experiments, we found that the drift changes in self-location were congruent with the experienced direction of first-person perspective, although visuo-tactile and visuo-vestibular stimulation parameters were identical. These data suggest that these two spatial aspects of bodily self-consciousness are associated in terms of function, multisensory, and likely brain mechanisms [11]. Such a close association between self-location and first-person perspective has also been reported during paroxysmal full-body illusions of neurological origin, such as out-of-body experiences, when the abnormal experience of being located out-of-the body is tightly associated with the experience of perceiving the environment from a disembodied and elevated self-location and perspective [55,56,57,58]. As the commonality between both spatial aspects has been discussed extensively in a recent review, we will not discuss it further here [11].

Another important finding of the present experiments is the influence of visual gravitational signals on the experienced direction of first-person perspective and self-location. We note that, to date, almost all previous behavioral and neuroimaging studies on bodily self-consciousness have used conflicts between visual, tactile, proprioceptive, and motor signals [2,9,12,15,59,60]. Therefore, most previous studies neglected to study the contributions of a major sensory system for one's experience of spatial location and self-motion perception: the vestibular system [58]. In the present study, we did not manipulate vestibular signals directly, but the visual information about the direction of gravity was manipulated, to be congruent or not with the experienced direction of gravity coded by the vestibular sensors. The significant changes in self-location and in the experienced direction of the first-person perspective that we observed in a situation of strong visual-vestibular conflict demonstrated the importance of visual gravitational information for both spatial aspects of bodily self-consciousness. These data are in agreement with previous studies showing that immersion of participants in tilted or inverted visual environments strongly influences the perceived directions of up and down and the perception of the vertical [61,62]. The vestibular and multisensory nature of the first-person perspective is compatible with data from neurology, vestibular physiology, and abnormal own body perceptions [11,55,56,58]. First, several authors have noted that abnormal forms of the first-person perspective and self-location (such as in out-of-body experiences), occurring in neurological patients and healthy subjects, depend on body position and are more frequent in subjects that are lying supine and still than in subjects sitting or standing upright [63,64]. This could be related to the decreased sensitivity of otolithic vestibular receptors in the lying position, together with the decrease in motor and somatosensory signals in this position, which could relatively enhance the importance of visual graviceptive signals [65]. Second, observations performed in environments where gravity is strongly reduced (microgravity) or temporarily cancelled (parabolic flights) are associated with strong alterations of self-location. In these conditions, astronauts have reported striking illusions such as body-inversion illusions and room-tilt illusions (e.g. [66]). Likely, such gravitational vestibular manipulations may alter sensory integration in multimodal brain regions [67], decreasing the impact of vestibular, and increasing the importance of visual, tactile and proprioceptive signals. Finally, vestibular brain regions are mostly located at the posterior end of the Sylvian fissure, in close proximity to the temporo-parietal junction, inferior parietal lobule and the intraparietal sulcus [68,69]. Interestingly, these vestibular regions overlap with the temporo-parietal junction, whose activity has been showed to reflect the experimentally-induced changes in self-location and the experienced direction of the first-person perspective in the full-body illusion [21]. Altogether, these observations indicate that visual and vestibular signals and their integration play a crucial role in the experience of self-location and the subjectively experienced first-person perspective [10].

Visuo-vestibular Integration and the Experienced Direction of the First-person Perspective

The third main finding of the present experiments regarding the multisensory mechanisms of bodily self-consciousness is that visual-field dependence (measured by the rod and frame test) correlates with the experienced direction of the first-person perspective during the full-body illusion. We found that significantly more visual FD participants experienced a downward (or front) direction of first-person perspective (Down-group) during the full-body illusion while lying supine and being presented with a strong visuo-vestibular conflict. This result suggests an association between a visually dominant style (more deviations of the subjective visual vertical in the rod and frame test) and the subjectively experienced first-person perspective of our participants during the full-body illusion. FD participants rely mostly on an allocentric frame of reference [36,45] and have been shown to be more unstable than FI participants [22,23]. We found that the experienced downward direction of the first-person perspective is a relatively unstable perspective. Down-group participants, who experienced mostly a downward direction of the first-person perspective, showed fluctuations of their judgments and only rarely reported to experience a constant downward direction of first-person perspective. This was different for the up-looking participants, who had more stable first-person perspective judgments. Accordingly, it was proposed that FD participants use visual references not only for visual vertical perception, but also to determine their full-body orientation and regulate their balance [23]. Here, we showed that in the full-body illusion FD participants relied more strongly on the gravitational information depicted in the body posture (indicating a dorsal to ventral gravitational acceleration) and adapted the direction of their first-person perspective accordingly (i.e. down-looking). Thus, in this subpopulation, we showed that vision seems to trump vestibular perception for the spatial aspects of bodily self-consciousness, extending previously utilized perceptual paradigms (e.g. [42,70]) to the first-person perspective. Conversely, we found that more visual FI participants experienced an upward direction of first-person perspective (Up-group) during the full-body illusion under the same experimental conditions. These participants were thus less influenced by visual graviceptive cues and experienced (accurately) that their body was in a supine position and looking upward. FI participants are generally weakly influenced by visual references and have a better balance [23,36]. It is assumed that they rely mainly on an egocentric (i.e. body-centered) frame of reference and thus presumably rely more strongly on vestibular and somatosensory signals. Indeed, manipulations of proprioceptive signals by head tilts induce stronger deviations of the subjective visual vertical in FI participants [38].

Visuo-vestibular perceptual styles such as visual FD and FI have been described so far during simple visual tasks such as perception of line orientation [71]. The present data suggest that visuo-vestibular styles are also of importance for bodily self-consciousness. Previous studies established connections between visual field dependence-independence and postural control [23], indicating that the reliance upon visual signals constrains one's body orientation and stabilization. Each individual can refer his body orientation and stabilization to several references frames and this referral depends on a continuous selection along life and environmental constraints [45,72,73]. However, no previous studies to date had investigated the contribution of visual field dependence-independence and perceptual styles to higher-level phenomena such as the experienced direction of the first-person perspective. Our data are important because they reveal that the interpretation of the experienced direction of first-person perspective that humans experience continuously and that is a cornerstone of consciousness studies (i.e. [10,74,75] depends on sensory strategies, or perceptual styles [45]. The neurobiological understanding of such strategies may allow important insights into the neural mechanisms of self-consciousness.

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Author Contributions

Conceived and designed the experiments: CP CL RM OB. Performed the experiments: CP VS JAD. Analyzed the data: CP CL VS JAD. Contributed reagents/materials/analysis tools: CP CL JAD RM. Wrote the paper: CP CL OB.

References

1. Aspell JE, Lenggenhager B, Blanke O (2009) Keeping in touch with one's self: multisensory mechanisms of self-consciousness. PloS one 4: e6488.
2. Botvinick M, Cohen J (1998) Rubber hands 'feel' touch that eyes see. Nature 391: 756.
3. Lenggenhager B, Mouthon M, Blanke O (2009) Spatial aspects of bodily self-consciousness. Consciousness and cognition 18: 110–117.
4. Petkova VI, Ehrsson HH (2008) If I were you: perceptual illusion of body swapping. PloS one 3: e3832.
5. Tsakiris M, Haggard P (2005) The rubber hand illusion revisited: visuotactile integration and self-attribution. Journal of experimental psychology Human perception and performance 31: 80–91.
6. Sforza A, Bufalari I, Haggard P, Aglioti SM (2010) My face in yours: Visuo-tactile facial stimulation influences sense of identity. Social neuroscience 5: 148–162.
7. Tsakiris M (2008) Looking for myself: current multisensory input alters self-face recognition. PloS one 3: e4040.
8. Ehrsson HH, Wiech K, Weiskopf N, Dolan RJ, Passingham RE (2007) Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. Proceedings of the National Academy of Sciences of the United States of America 104: 9828–9833.
9. Lenggenhager B, Tadi T, Metzinger T, Blanke O (2007) Video ergo sum: manipulating bodily self-consciousness. Science 317: 1096–1099.
10. Blanke O, Metzinger T (2009) Full-body illusions and minimal phenomenal selfhood. Trends in cognitive sciences 13: 7–13.
11. Blanke O (2012) Multisensory brain mechanisms of bodily self-consciousness. Nature Neuroscience Reviews (accepted).
12. Ehrsson HH (2007) The experimental induction of out-of-body experiences. Science 317: 1048.
13. Palluel E, Aspell JE, Blanke O (2011) Leg muscle vibration modulates bodily self-consciousness: integration of proprioceptive, visual, and tactile signals. Journal of neurophysiology 105: 2239–2247.
14. Hänsel A, Lenggenhager B, von Kanel R, Curatolo M, Blanke O (2011) Seeing and identifying with a virtual body decreases pain perception. European journal of pain 15: 874–879.
15. Petkova VI, Bjornsdotter M, Gentile G, Jonsson T, Li TQ, et al. (2011) From part- to whole-body ownership in the multisensory brain. Current biology : CB 21: 1118–1122.
16. Petkova VI, Khoshnevis M, Ehrsson HH (2011) The perspective matters! Multisensory integration in ego-centric reference frames determines full-body ownership. Frontiers in psychology 2: 35.
17. Slater M, Spanlang B, Sanchez-Vives MV, Blanke O (2010) First person experience of body transfer in virtual reality. PloS one 5: e10564.
18. Vogeley K, Fink GR (2003) Neural correlates of the first-person-perspective. Trends in cognitive sciences 7: 38–42.
19. Vogeley K, May M, Ritzl A, Falkai P, Zilles K, et al. (2004) Neural correlates of first-person perspective as one constituent of human self-consciousness. Journal of cognitive neuroscience 16: 817–827.
20. Corradi-Dell'acqua C, Ueno K, Ogawa A, Cheng K, Rumiati RI, et al. (2008) Effects of shifting perspective of the self: an fMRI study. NeuroImage 40: 1902–1911.
21. Ionta S, Heydrich L, Lenggenhager B, Mouthon M, Fornari E, et al. (2011) Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. Neuron 70: 363–374.
22. Golomer E, Cremieux J, Dupui P, Isableu B, Ohlmann T (1999) Visual contribution to self-induced body sway frequencies and visual perception of male professional dancers. Neuroscience letters 267: 189–192.
23. Isableu B, Ohlmann T, Cremieux J, Amblard B (1997) Selection of spatial frame of reference and postural control variability. Experimental brain research Experimentelle Hirnforschung Experimentation cerebrale 114: 584–589.
24. Lopez C, Lacour M, Magnan J, Borel L (2006) Visual field dependence-independence before and after unilateral vestibular loss. Neuroreport 17: 797–803.
25. Young LR, Oman CM, Watt DG, Money KE, Lichtenberg BK (1984) Spatial orientation in weightlessness and readaptation to earth's gravity. Science 225: 205–208.
26. Duenas J, Chapuis D, Pfeiffer C, Martuzzi R, Ionta S, et al. (2011) Neuroscience robotics to investigate multisensory integration and bodily awareness. Conference proceedings : Annual International Conference of the IEEE Engineering in Medicine and Biology Society IEEE Engineering in Medicine and Biology Society Conference 2011: 8348–8352.
27. Lipshits M, McIntyre J (1999) Gravity affects the preferred vertical and horizontal in visual perception of orientation. Neuroreport 10: 1085–1089.
28. Matin L, Fox CR (1989) Visually perceived eye level and perceived elevation of objects: linearly additive influences from visual field pitch and from gravity. Vision research 29: 315–324.
29. Lenggenhager B, Halje P, Blanke O (2011) Alpha band oscillations correlate with illusory self-location induced by virtual reality. The European journal of neuroscience 33: 1935–1943.
30. Slater M, Perez-Marcos D, Ehrsson HH, Sanchez-Vives MV (2008) Towards a digital body: the virtual arm illusion. Frontiers in human neuroscience 2: 6.
31. Blake R, Wilson H (2011) Binocular vision. Vision research 51: 754–770.
32. Bremmer F (2011) Multisensory space: from eye-movements to self-motion. The Journal of physiology 589: 815–823.
33. Kim CY, Blake R (2005) Psychophysical magic: rendering the visible 'invisible'. Trends in cognitive sciences 9: 381–388.
34. Lopez C, Mercier MR, Halje P, Blanke O (2011) Spatiotemporal dynamics of visual vertical judgments: early and late brain mechanisms as revealed by high-density electrical neuroimaging. Neuroscience 181: 134–149.
35. Witkin HA, Asch SE (1948) Studies in space orientation; further experiments on perception of the upright with displaced visual fields. Journal of experimental psychology 38: 762–782.
36. Luyat M, Ohlmann T, Barraud PA (1997) Subjective vertical and postural activity. Acta psychologica 95: 181–193.
37. Marendaz C, Brenet F, Ohlmann T, Raphel C (1988) Solving the rod-and-frame test in a tachistoscopic presentation: effects of stimulus size and perceptual style. Perception & psychophysics 44: 445–450.
38. Golomer E, Guillou E, Testa M, Lecoq C, Ohlmann T (2005) Contribution of neck proprioception to subjective vertical perception among experts in physical activities and untrained women. Neuroscience letters 381: 31–35.
39. Hagberg B, Samuelsson G, Lindberg B, Dehlin O (1991) Stability and change of personality in old age and its relation to survival. Journal of gerontology 46: P285–291.
40. Lopez C, Bachofner C, Mercier M, Blanke O (2009) Gravity and observer's body orientation influence the visual perception of human body postures. Journal of vision 9: 1 1–14.
41. Zoccolotti P, Antonucci G, Goodenough DR, Pizzamiglio L, Spinelli D (1992) The role of frame size on vertical and horizontal observers in the rod-and-frame illusion. Acta Psychol (Amst) 79: 171–187.
42. Lopez C, Lacour M, Ahmadi AE, Magnan J, Borel L (2007) Changes of visual vertical perception: a long-term sign of unilateral and bilateral vestibular loss. Neuropsychologia 45: 2025–2037.
43. Cramer H (1946) Mathematical methods of statistic. Princeton: Princeton University Press.
44. Isableu B, Gueguen M, Fourre B, Giraudet G, Amorim MA (2008) Assessment of visual field dependence: comparison between the mechanical 3D rod-and-frame test developed by Oltman in 1968 with a 2D computer-based version. Journal of vestibular research : equilibrium & orientation 18: 239–247.
45. Ohlmann T, Marendaz C (1991) Vicarious processes involved in selection/control of frames of reference and spatial aspects of field dependence-independence. In: Wapner S, Demick J, editors. Field dependence-independence: Cognitive style across the life Span. New Jersey: Hillsdale. 105–129.
46. Reed CL, Stone VE, Bozova S, Tanaka J (2003) The body-inversion effect. Psychological science 14: 302–308.
47. Schwabe L, Lenggenhager B, Blanke O (2009) The timing of temporoparietal and frontal activations during mental own body transformations from different visuospatial perspectives. Human brain mapping 30: 1801–1812.
48. Troje NF, Westhoff C (2006) The inversion effect in biological motion perception: evidence for a "life detector"? Current biology: CB 16: 821–824.
49. Bonnet C, Paulos C, Nithart C (2005) Visual representations of dynamic actions from static pictures. Perception 34: 835–846.

50. McIntyre J, Zago M, Berthoz A, Lacquaniti F (2001) Does the brain model Newton's laws? Nature neuroscience 4: 693–694.
51. Indovina I, Maffei V, Bosco G, Zago M, Macaluso E, et al. (2005) Representation of visual gravitational motion in the human vestibular cortex. Science 308: 416–419.
52. Miller WL, Maffei V, Bosco G, Iosa M, Zago M, et al. (2008) Vestibular nuclei and cerebellum put visual gravitational motion in context. Journal of neurophysiology 99: 1969–1982.
53. Bosco G, Carrozzo M, Lacquaniti F (2008) Contributions of the human temporoparietal junction and MT/V5+ to the timing of interception revealed by transcranial magnetic stimulation. The Journal of neuroscience : the official journal of the Society for Neuroscience 28: 12071–12084.
54. Zago M, La Scaleia B, Miller WL, Lacquaniti F (2011) Coherence of structural visual cues and pictorial gravity paves the way for interceptive actions. Journal of vision 11: 13.
55. Blanke O, Landis T, Spinelli L, Seeck M (2004) Out-of-body experience and autoscopy of neurological origin. Brain : a journal of neurology 127: 243–258.
56. Blanke O, Ortigue S, Landis T, Seeck M (2002) Stimulating illusory own-body perceptions. Nature 419: 269–270.
57. Heydrich L, Lopez C, Seeck M, Blanke O (2011) Partial and full own-body illusions of epileptic origin in a child with right temporoparietal epilepsy. Epilepsy & behavior : E&B 20: 583–586.
58. Lopez C, Halje P, Blanke O (2008) Body ownership and embodiment: vestibular and multisensory mechanisms. Neurophysiologie clinique = Clinical neurophysiology 38: 149–161.
59. Ehrsson HH, Spence C, Passingham RE (2004) That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. Science 305: 875–877.
60. Tsakiris M, Hesse MD, Boy C, Haggard P, Fink GR (2007) Neural signatures of body ownership: a sensory network for bodily self-consciousness. Cerebral cortex 17: 2235–2244.
61. Dyde RT, Jenkin MR, Harris LR (2006) The subjective visual vertical and the perceptual upright. Experimental brain research Experimentelle Hirnforschung Experimentation cerebrale 173: 612–622.
62. Jenkin HL, Dyde RT, Jenkin MR, Howard IP, Harris LR (2003) Relative role of visual and non-visual cues in determining the direction of "up": experiments in the York tilted room facility. Journal of vestibular research: equilibrium & orientation 13: 287–293.
63. Blanke O, Mohr C (2005) Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin Implications for neurocognitive mechanisms of corporeal awareness and self-consciousness. Brain research Brain research reviews 50: 184–199.
64. Green CE (1968) Out-of-body experiences. London: Hamish Hamilton.
65. Lopez C, Lenggenhager B, Blanke O (2010) How vestibular stimulation interacts with illusory hand ownership. Consciousness and cognition 19: 33–47.
66. Lackner JR (1992) Spatial orientation in weightless environments. Perception 21: 803–812.
67. Cheron G, Leroy A, De Saedeleer C, Bengoetxea A, Lipshits M, et al. (2006) Effect of gravity on human spontaneous 10-Hz electroencephalographic oscillations during the arrest reaction. Brain research 1121: 104–116.
68. Lopez C, Blanke O (2011) The thalamocortical vestibular system in animals and humans. Brain research reviews 67: 119–146.
69. Lopez C, Blanke O, Mast FW (2012) The human vestibular cortex revealed by coordinate-based activation likelihood estimation meta-analysis. Neuroscience 212: 159–179.
70. Dichgans J, Held R, Young LR, Brandt T (1972) Moving visual scenes influence the apparent direction of gravity. Science 178: 1217–1219.
71. Marendaz C (1998) Nature and dynamics of reference frames in visual search for orientation: implications for early visual processing. Psychol Sci 9: 27–32.
72. Bray A, Subanandan A, Isableu B, Ohlmann T, Golding JF, et al. (2004) We are most aware of our place in the world when about to fall. Current biology : CB 14: R609–610.
73. Lacour M, Barthelemy J, Borel L, Magnan J, Xerri C, et al. (1997) Sensory strategies in human postural control before and after unilateral vestibular neurotomy. Experimental brain research Experimentelle Hirnforschung Experimentation cerebrale 115: 300–310.
74. Damasio A, Meyer DE (2009) Consciousness: An overview of the phenomenon and of its possible neural basis. In: Laureys S, Tononi G, editors. The neurology of consciousness. Amsterdam: Elsevier. 3–14.
75. Panksepp J (2005) Affective consciousness: Core emotional feelings in animals and humans. Consciousness and cognition 14: 30–80.

2.2 Study 2: First-person perspective relationship to visuo-spatial viewpoint

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RESEARCH ARTICLE

Visuospatial viewpoint manipulation during full-body illusion modulates subjective first-person perspective

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Abstract Self-consciousness is based on multisensory signals from the body. In full-body illusion (FBI) experiments, multisensory conflict was used to induce changes in three key aspects of bodily self-consciousness (BSC): self-identification (which body 'I' identify with), self-location (where 'I' am located), and first-person perspective (from where 'I' experience the world; 1PP). Here, we adapted a previous FBI protocol in which visuotactile stroking was administered by a robotic device (tactile stroking) and simultaneously rendered on the back of a virtual body (visual stroking) that participants viewed on a head-mounted display as if filmed from a posterior viewpoint of a camera. We compared the effects of two different visuospatial viewpoints on the FBI and thereby on these key aspects of BSC. During control manipulations, participants saw a no-body object instead of a virtual body (first experiment) or received asynchronous versus synchronous visuotactile stroking (second experiment). Results showed that within-subjects visuospatial viewpoint manipulations affected the subjective 1PP ratings if a virtual body was seen but had no effect for viewing a non-body object. However, visuospatial viewpoint had no effect on self-identification, but depended on the viewed object and visuotactile synchrony. Self-location depended on visuospatial viewpoint (first experiment) and visuotactile synchrony (second experiment). Our results show that the visuospatial viewpoint from which the virtual body is seen during FBIs modulates the subjective 1PP and that such viewpoint manipulations contribute to spatial aspects of BSC. We compare the present data with recent data revealing vestibular contributions to the subjective 1PP and discuss the multisensory nature of BSC and the subjective 1PP.

Keywords Bodily self-consciousness · Multisensory integration · First-person perspective · Full-body illusion · Visuospatial viewpoint

Introduction

Everyday we experience that self and body are bound together. In order to explain how our brain generates this embodied experience, research on the neural underpinning of bodily self-consciousness (BSC) proposed that BSC consists of at least three main aspects: i.e., self-identification, that is the feeling that a particular body is mine, self-location, that is the feeling of where 'I' am located in space, and first-person perspective (1PP), that is the feeling from where 'I' experience the world around me (Blanke and Metzinger 2009; Blanke 2012; Serino et al. 2013).

Research in neurological patients with out-of-body experiences (OBE) has shown that these three phenomenal aspects may be dissociated from the location of the physical body. During an OBE, patients typically experience ownership for an illusory body in external space (abnormal

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self-identification), they feel their self as elevated above their physical body (abnormal self-location) from where they experience to perceive the world, including their physical body (abnormal 1PP; Blanke and Mohr 2005; Blanke et al. 2002, 2004; De Ridder et al. 2007). In these studies OBEs were linked to the brain's impaired integration of visual, vestibular, tactile, and proprioceptive sensory signals (Blanke et al. 2002; Ionta et al. 2011), suggesting that under normal conditions BSC might be based on multisensory integration mechanisms (Blanke et al. 2004).

Further evidence for this hypothesis came from behavioral experiments in healthy participants that used the so-called full-body illusion (FBI). During one type of FBI, participants received spatially and temporally conflicting sensory information about the location, shape, or size of their body as seen on a head-mounted display. In these studies, participants saw a virtual body from the viewpoint of a camera that filmed the participant's body from behind (2 m distance) and simultaneously received tactile stroking at their physical body (unseen by them) and viewed stroking applied to the back of the virtual body. When stroking was applied in a synchronous fashion participants typically reported increased self-identification and a concomitant bias in self-location toward the virtual body (Lenggenhager et al. 2007; Ehrsson 2007; Guterstam and Ehrsson 2012). These changes in self-identification and self-location were accompanied by changes in visuotactile and audiovisual integration (Aspell et al. 2009, 2010), mental imagery (Lenggenhager et al. 2009; Pfeiffer et al. 2013; Ionta et al. 2011), physiological responses to threat (Petkova et al. 2011; Petkova and Ehrsson 2008; Ehrsson 2007), body temperature (Salomon et al. 2013), and pain responses (Romano et al. 2014; Hänsel et al. 2011). This shows that self-identification and self-location can be experimentally manipulated and that this manipulation modulates cognitive as well as physiological processes regarding the own body.

However, considerably less is known about the multisensory mechanisms underlying the 1PP. Moreover, most research has defined and investigated the 1PP in terms of visual or visuospatial properties, whereas less attention has been given to the multisensory properties of the subjective 1PP, defined as the subjective experience of being directed at the world (Blanke and Metzinger 2009; Metzinger 2003; Ionta et al. 2011; Blanke 2012; Pfeiffer et al. 2013). The former 'perspective' has been defined and investigated as the visuospatial viewpoint of a given visual scene as seen by the participant and thus as centered on the participant's physical body (egocentric viewpoint). This egocentric viewpoint was contrasted with a third-person viewpoint or 'perspective' defined by a visuospatial viewpoint centered at another spatial position of the same scene, but different from the participant's physical body position (allocentric viewpoint; Vogeley and Fink 2003; Vogeley et al. 2004). Insights gained from such explicit visual manipulations of egocentric versus allocentric viewpoints, by task instruction and visual stimulation, provided important insights into processes underlying human social cognition (Aichhorn et al. 2006; Baron-Cohen et al. 1985; Frith and Frith 2003, 2005, 2006), mental spatial transformation (Arzy et al. 2006), and autobiographical memory (Freton et al. 2013). However, it is not known how such viewpoint changes relate functionally and neurally to the perspectival element of BSC: the subjective 1PP.

Ego- and allocentric visuospatial viewpoint manipulations as described above have also been used to investigate their effect on self-identification in a virtual body transfer illusion and the FBI. In an immersive virtual reality experiment, Slater et al. (2010) presented participants with a virtual body and virtual scene as seen from an egocentric (first-person) viewpoint or from a laterally shifted allocentric (third-person) viewpoint. Participants' head movements congruently updated the virtual scenery as seen from each viewpoint, thus providing visuomotor congruency that enhanced the level of immersion. Furthermore, participants received synchronous or asynchronous visuotactile stimulation. Results showed that self-identification ratings and physiological responses (i.e., heart rate deceleration) were higher in the egocentric than allocentric viewpoint conditions and that in the allocentric viewpoint condition stroking additionally modulated these dependent measures of self-identification. In a different study by Petkova et al. (2011), the FBI was induced by presenting to participants either an egocentric or allocentric viewpoint of the abdomen of a mannequin and through additional application of visuotactile stroking (again in synchronous or asynchronous fashion). The authors found that self-identification ratings and physiological responses (here: skin conductance response to threat) were generally higher for egocentric than allocentric viewpoints and that stroking modulated the responses only in the egocentric viewpoint condition. Both Slater et al. (2010) and Petkova et al. (2011) found that self-identification depended on the congruency between the visuospatial viewpoint and the physical body and on viewpoint-dependent effects of visuotactile stroking synchrony. However, whereas visuotactile stroking affected self-identification in the allocentric but not in the egocentric viewpoint condition in the study by Slater et al. (2010), the opposite pattern of result was found in the study by Petkova et al. (2011). Because viewpoint manipulations differed between the studies (e.g., laterally shifted vs. front-facing allocentric viewpoints), it is still unclear which specific visuospatial parameters enable multisensory conflicts (e.g., visuotactile stroking) to induce changes in BSC (e.g., self-identification).

How does the subjective 1PP differ from a mere visual viewpoint from where a scene is perceived? Can changes of the visual viewpoint as tested in these previous studies modulate not only self-identification, but also spatial aspects of BSC such as the subjective 1PP or self-location? Evidence for a dissociation between visual viewpoint and subjective 1PP comes from neurological patients with OBE who reported spatial dissociations between their visual and auditory viewpoints and their subjectively experienced 1PP (Blanke et al. 2004) and also from patients with heautoscopy who alternatingly experienced their subjective 1PP at two distinct visuospatial viewpoints (Brugger et al. 1994; Heydrich and Blanke 2013). De Ridder et al. (2007) for example reported a patient who experienced to see the world from one viewpoint, while experiencing his subjective 1PP and self-location at a different spatial location. This anecdotal clinical evidence about distinct brain mechanisms of visual viewpoint versus the subjective 1PP was corroborated by empirical data in healthy subjects revealing the multisensory mechanisms (tactile, proprioceptive, vestibular, and visual) of the subjective 1PP. This was addressed in two FBI studies that quantified the subjective 1PP as a dependent variable (Ionta et al. 2011; Pfeiffer et al. 2013). In the study by Ionta et al. (2011), participants were presented with visuotactile and visuovestibular conflicts during the FBI. Visuovestibular conflicts consisted of a difference between participant's body posture and the direction of visual gravitational stimuli. Participants lay supine, thus vestibular signals from the otolith organs signaled that the body was facing upwards relative to earth vertical. At the same time, participants saw a video that showed a virtual body in prone posture that was filmed from an elevated location with the camera facing downwards. Thus, vestibular signals (upward direction) and visual signals (downward direction) were in directional conflict. Under these FBI conditions, it was found that half of the experimental participants experienced an upward direction of their subjective 1PP (congruent with vestibular signals), whereas the other half of the participants experienced a downward direction of their subjective 1PP (congruent with visual signals). It was found that participants' judgments of self-location depended on these individual differences in subjective 1PP. These results were replicated by Pfeiffer et al. (2013) in a different subject sample and it was, moreover, found that individual differences in subjective 1PP were congruent with individual differences in visuovestibular integration (as investigated through subjective verticality judgments). Participants with an upward direction of the subjective 1PP (congruent with vestibular signals) were less affected by a visual distractor during subjective verticality judgments, as compared to participants with a downward direction of the subjective 1PP (congruent with visual signals), who were more biased by the visual distractor. Together these results demonstrate that the subjective 1PP was congruent with changes in self-location during the FBI, could be manipulated as a dependent variable between-subjects, and depended on the weighting of visuovestibular signals.

However, it is not known whether systematic changes in the experienced direction of the subjective 1PP can also be induced experimentally within and not just between subjects and whether visual viewpoint manipulations impact the subjective 1PP. Here, we asked whether additionally manipulating visuospatial viewpoints during the FBI could induce within-subject changes of the subjective 1PP and other aspects of BSC (self-location, self-identification). For this, we here repeatedly induced the FBI by robotically supported visuotactile stroking (similar to Pfeiffer et al. 2013) and measured within-subjects the subjective 1PP as the dependent variable. We manipulated the visuospatial viewpoint from which a virtual body was seen on a head-mounted display by combining spatial elevation (high vs. low) with inclination (downward vs. upward) that resulted in two viewpoint conditions: high-downward and low-upward viewpoints. Importantly, participants' body posture and the virtual body posture were not manipulated but were kept constant throughout the experiment. We hypothesized that viewpoint inclination would induce congruent changes of the subjective 1PP. In order to test whether these changes were specific to seeing a human body or would generalize also to non-body objects, we introduced the experimental manipulation Object (body, object) in the paradigm. We hypothesized that during the FBI only seeing a human body and not a non-body object would modulate the subjective 1PP. In a follow-up experiment, we manipulated the synchrony of visuotactile stroking during these viewpoint manipulations in order to link our results from the first experiment to the classical manipulation of BSC during the FBI.

Methods

Participants

In the first experiment, 25 participants were tested (nine females, mean age of 22 years, range of 18–28 years), and in the second experiment, 19 participants were tested (eight females, mean age of 22 years, range of 18–30 years). Participants were students at the Ecole Polytechnique Fédérale de Lausanne, had normal- or corrected-to-normal eyesight, and had no history of neurologic or psychiatric disorder. Participants verbally indicated that they were strongly right-handed. The experimental protocol was approved by the local ethics committee—La Commission d'Ethique de la Recherche Clinique de la Faculté et de Medicine de

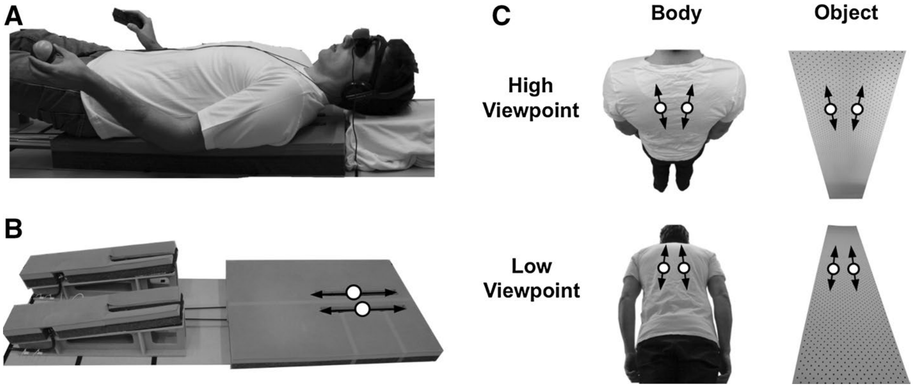

Fig. 1 Experimental setup and stimuli. **a** Participants were lying supine on a robotic device that applied tactile stroking and wore a head-mounted display in which they saw visual stimuli. Responses were given by button press with the *right hand* and participants were holding a ball with the *left hand* to facilitate mental imagery in the mental ball dropping task. **b** Robotic device used for tactile stimulation. Two stroking units (*white circles*) were stroking the back of a participant lying comfortably on soft foam. **c** Visual stimuli showed from a high or low visuospatial viewpoint a virtual human body or a non-body object. Visuotactile stroking consisted of *red dots* (represented here by *white circles*) that moved along the backside of the virtual body or object (*black arrows* represent movement ranges of the dots) and followed the viewpoint-congruent trajectories

l'Université de Lausanne—and was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All participants gave their informed consent prior to their inclusion in the experiment and after the experiment they were fully debriefed about the experimental purpose and received a monetary compensation of 30 Swiss Francs.

Experimental setup

In a darkened room, a custom-made robotic device was mounted on a table at 90 cm above the floor. Figure 1a, b shows the experimental setup and the robotic device which had 200 cm × 90 cm × 10 cm dimensions and two separate stroking units for tactile stimulation at the back of a participant lying supine on the device (Duenas et al. 2011). Stroking units had 20 cm movement range along a linear trajectory, 2–12 cm/s velocity during stroking and were actuated by ultrasonic motors (Shinsei, USR60-E3N, Japan, http://www.shinsei-motor.com). A plastic sphere was mounted on an elastic blade of the stroking unit, which allowed for adaptation of stroking to participant's back curvature. A soft foam cover on the robotic device allowed participants to comfortably lie supine during the experiment. The foam had gaps allowing the plastic spheres to touch the participant's back. Participants wore a white cotton shirt to reduce frictions between the plastic sphere and their back.

Stroking profiles were programmed in MATLAB software (MathWorks, version R13, http://www.mathworks.ch) and saved in text files that were used to determine robotic stroking paths in LabVIEW software (National Instruments Corporation, version 2010b, www.ni.com/labview).

Visual stimuli were presented to participants on a head-mounted display (HMD, Virtual Realities, Virtual Viewer 3D, www.vrealities.com/virtualviewer3d.html) with a resolution of 800 × 600 pixels, representing about 35° of visual angle. Participants wore headphones that presented white noise to cover the acoustic cues from the movements of the robotic device. In-house software (ExpyVR, http://lnco.epfl.ch/expyvr) was used for visual stimulus presentation, real-time synchronization of visual stroking with robotic stroking, and response recording. Responses were recorded with a serial keypad (Targus Numeric Keypad AKP10US, www.targus.com) on which participants responded with their right hand.

Experimental design

A full-factorial 2 × 2 repeated measures experimental design was used in each experiment. In the first experiment, the experimental factors were Viewpoint (levels: high, low) and Object (levels: body, non-body) resulting in four experimental conditions: (1) high Viewpoint and body Object; (2) high Viewpoint and non-body Object; (3) low Viewpoint and body Object; (4) low Viewpoint and non-body Object (Fig. 1c). In the second experiment, the experimental factors were Viewpoint (levels: high, low) and Stroking (levels: synchronous, asynchronous) resulting in four experimental conditions: (1) high Viewpoint and synchronous Stroking; (2) high Viewpoint and asynchronous Stroking; (3) low Viewpoint and synchronous Stroking; (4) low Viewpoint and asynchronous Stroking.

Stimuli

Visual stimuli were photorealistic images showing a human body (body Object; first and second experiment) or a non-body object of rectangular shape and comparable height and width (non-body Object; first experiment). Both objects were standing upright, i.e., their longitudinal axis was aligned with gravitational vertical. Photos for the stimuli were taken from a fixed eye-to-object distance of 2 m, which was centered on the upper part of the object. The photos were taken from different camera-centered visuospatial viewpoints, as relative to eye level of an average sized observer. Specifically, the photos were taken from 1 m above (or below) eye level and were declined (inclined) by 30° downward to the ground (or upward to the ceiling of the experimental room). All visual cues surrounding the object were then masked by black color to not provide participants with cues about the spatial environment. This resulted in two types of stimuli for the high Viewpoint and low Viewpoint experimental conditions.

Differently to previous studies (Petkova et al. 2011; Slater et al. 2010), all visuospatial viewpoints in the present study were camera-centered and distinct from the viewpoint of the virtual body (allocentric viewpoints). However, because the images were presented to the participant on a head-mounted display and thus the camera viewpoint matched participant's viewpoint, participants perceived the virtual body as if located a few meters in front of them (egocentric viewpoint). Moreover, visual context surrounding the virtual body was removed, such that the viewpoint locations with respect to the external environment were unknown to participants. Thus, a clear definition of our viewpoint manipulations as either egocentric or allocentric seems difficult. Instead, in line with many previous FBI studies, we used camera-centered viewpoints of a virtual body from a distance to induce changes in BSC from the camera viewpoint in the direction of the location and viewpoint of the virtual body (Lenggenhager et al. 2007; Aspell et al. 2009; Ionta et al. 2011; Pfeiffer et al. 2013).

The body object had male gender and was presented to all experimental participants, who were males or females. In order to assess whether gender-mismatch (i.e., male virtual body presented to female participants) had confounded our experimental data, we ran a preliminary analysis of our data consisting of including a between-subjects factor Gender in all ANOVAs laid out in the 'Analysis' section. Results showed no gender-related main effects or interactions (all F values <1), suggesting that gender-mismatch did not affect our data, and we therefore decided to include all data from all participants in subsequent statistical analysis.

In addition to visuospatial viewpoint, we manipulated the synchrony of visuotactile stroking (second experiment) in order to be able to compare our results to previous studies on the FBI. Visual stroking consisted of virtually augmenting two red dots on the back of the virtual body/object and moving them along pre-defined stroking sequences (Fig. 1c, black arrows indicate the movement range of the red dots). Visual stroking was applied along a movement range that was centered on the virtual body/object; the motion of the red dot corresponded to the visuospatial viewpoint manipulation. Specifically, a downward stroke along the virtual body/object was visually seen in the high (low) Viewpoint condition as two red dots converging (diverging) and decreasing (increasing) in size and thus followed congruently the anatomy of the virtual body/object (Fig. 1c, see difference in orientation of black arrows in high and low viewpoint condition). Tactile stroking consisted of moving two plastic spheres along the back of the participant lying on the robotic device (Fig. 1a, b).

The sequences of visual stroking (seen on the HMD) and tactile stroking (felt on participant's back) were either synchronous (first and second experiment) or asynchronous (second experiment). Two stroking profiles were created before the experiment. Each profile consisted of a random sequence of positions in 0–20 cm distance range, 2–12 cm/s velocity range, and 40 s duration. The stroking profiles varied randomly in length, speed, direction, and inter-stroke-intervals (0–1.5 s). Thus, when different profiles were simultaneously executed they were spatially incongruent. During the experiment, either twice the same profile or both incongruent profiles were randomly assigned to the red dots (seen on the HMD) and the stroking units (touching the back of the participant), which resulted in synchronous or asynchronous visuotactile stroking.

Measures of bodily self-consciousness

Subjective 1PP was measured by presenting to participants on the HMD the phrase 'Orientation?' in white on black background along with the words 'upward' and 'downward' at the left and right bottom of the screen. Participants were trained to rate by button press their experienced direction of the subjective 1PP according to the question 'Did you have the impression as if you were looking upward/downward at a body/object above/below you?'. Participants responded with two alternative forced choices using either the right index finger for rating 'upward' (coded 0) or the right middle finder for rating 'downward' (coded 1).

Self-location was measured using the mental ball dropping (MBD) task, which has previously been shown to be a sensitive measure of self-location (Lenggenhager et al. 2009; Ionta et al. 2011; Pfeiffer et al. 2013). The MBD task was performed in three sequential steps: First, participants imagined to drop a ball from their hand upon which they pressed a button with their right index finger; secondly, they imagined the ball falling toward the ground during which they held the button depressed; finally, participants imagined the ball hitting the ground upon which they released the button. The duration of button press (response time, RT) was used as a measure of self-location (i.e., height) above the ground. Note that participants were familiarized with the task procedure before the experiment and performed at least 20 repetitions of the MBD task before the experiment.

Self-identification, along with other items on illusory touch and other self-related experiences, were rated in the FBI questionnaire (Lenggenhager et al. 2009; Pfeiffer et al. 2013). Figure 3c lists all items of the questionnaire. The questionnaire inquired about the quality of the FBI experience and each question was presented separately on the screen in white color on black background in the center of the screen along with a visual analogue scale, i.e., a horizontal and continuous visual scale with 11 levels. Questions were presented in random order; participants had no time limits to answer each question and gave their ratings by navigating a mouse curser along the visual analogue scale. Questions had an 11-point scale that ranged from 1 ('weak feeling') to 11 ('strong feeling').

Procedure

Each of the four experimental conditions was repeated 15 times in random order. The total of 60 experimental trials was presented in three separate runs of 20 trials. Between runs participants were allowed pauses in lying posture on the robotic device.

An experimental trial began with presenting visuo-tactile stroking for 40 s. Participants were instructed to attend simultaneously to the visual stimulation (seen on the HMD) and the tactile stimulation (felt on the participant's back). Immediately after that, tactile stroking stopped and all visual stimuli were removed from the HMD and a black screen was shown for 1 s. Then, an auditory beep sound was presented for 200 ms, cueing participants to perform a MBD task within 6 s (adapted from Lenggenhager et al. 2009; Ionta et al. 2011; Pfeiffer et al. 2013), this procedure was repeated three times resulting in three repeated measures of MBD RTs. After that, participants rated their subjective 1PP by button press within 6 s. Then a fixation cross was presented on the screen during a resting phase of 15 s before the next trial began.

After having completed the FBI experiment on the robotic device, participants were comfortably seated in front of a computer screen on which they rated the FBI questionnaire separately for each of four experimental conditions. Between subjects, the order of condition-wise questionnaire administration and the order of question were randomized. There was no time limit to complete the questionnaire ratings.

Analysis

After having recorded raw data from all participants, the data were pre-processed and condition-averages were calculated.

Subjective 1PP ratings were processed by calculating proportion scores by dividing the number of 'downward' ratings by the number of total ratings for each condition. Omitted responses (<5 % per subject) were excluded from this analysis. Proportion scores indicated the proportion of having rated 'downward' in each experimental condition and ranged from 0 (never rated 'downward') to 1 (always rated 'downward').

Response times (RTs) from the MBD task (i.e., measure of self-location) were processed by removal of omissions and RTs shorter than 200 ms (<5 % per subject), which is considered too short for this type of mental imagery (Pfeiffer et al. 2013; Lenggenhager et al. 2009). First, we calculated trial-average RTs across three subsequent repetitions of the MBD task and then calculated condition-average RTs for each participant.

FBI questionnaire ratings were recorded separately for four experimental conditions with each 10 questions. In order to account for response tendencies of participants, e.g., general (dis-)agreement to all questions or generally using extreme ends of the scale, that might have confounded the interpretation of questionnaire data, we transformed the data to ipsative scores (Broughton and Wasel 1990; Cattell 1944). Ipsative normalization was performed within-subjects and consisted of calculating across all questions the average score and the standard deviation of scores. Then, each rating was centered (i.e., subtracting the average score) and normalized (i.e., divided by the standard deviation). Ipsative scores reflect agreement (i.e., positive values) or disagreement (i.e., negative values) relative to the average response of the participant across all questions (i.e., zero value), where each unit reflects a standard deviation agreement (+1) or disagreement (−1) with questionnaire item. This procedure resulted in condition-wise ipsative scores for each question.

Condition-average subjective 1PP ratings and RTs from the MBD task were statistically analyzed using separate 2 × 2 repeated measures ANOVAs. For proportion scores of 1PP and RTs for self-location, we applied an a priori alpha level threshold of .05. Post hoc comparisons were performed for significant interactions from the ANOVA and thus an alpha level threshold of .05 was used—uncorrected for multiple comparisons. Questionnaire data of 10 questions were analyzed using separate 2 × 2 repeated measures ANOVAs for each of the questions. We corrected for multiple comparisons using Bonferroni correction (Bonferroni 1935), which resulted in an alpha level threshold of .005.

Results

Experiment 1

Subjective 1PP

Statistical analysis revealed a main effect of Viewpoint ($F(1, 24) = 10.80$, $p = .003$, $\eta^2 = .31$; Fig. 2a), reflecting more frequent 'downward' 1PP for high Viewpoint ($M = .64$, SE = .06) than for low Viewpoint ($M = .32$, SE = .05), which shows congruency between 1PP ratings and visual viewpoint inclination (see 'Stimuli' section). Critically, we also found a significant Viewpoint × Object interaction ($F(1, 24) = 8.22$, $p = .008$, $\eta^2 = .26$; Fig. 2a), reflecting that when participants were presented with a virtual body they rated to have experienced a 'downward' direction of the 1PP more frequently in the high Viewpoint condition ($M = .75$, SE = .07) compared to low Viewpoint condition ($M = .21$, SE = .05) (post hoc paired-samples *t* test: $t(24) = 5.16$, $p < .001$). Instead, when presented with a non-body object, participants rated the subjective 1PP not differently between high Viewpoint ($M = .53$, SE = .07) and low Viewpoint ($M = .44$, SE = .08; post hoc paired-samples *t* test: *t* value < 1). These results suggest that the effects of the visuospatial viewpoint on the subjective 1PP are body-specific.

Self-location

Statistical analysis of MBD RTs showed a marginally significant main effect of Viewpoint ($F(1, 24) = 4.17$, $p = .052$, $\eta^2 = .15$; Fig. 2b) with slightly higher self-location for high Viewpoint ($M = 926$ ms, SE = 41 ms) than for low Viewpoint ($M = 914$ ms, SE = 41 ms). Thus, self-location showed a difference in height estimation congruent with the viewpoint elevation manipulation. There was no main effect of Object and no Viewpoint × Object interaction (all *F* values <1). Together these results suggest that visuospatial viewpoint tended to affect self-location independently of whether a body or non-body object was shown. Note that all experimental conditions were presented in synchronous visuotactile stroking, which typically induces self-location changes in the direction of the seen virtual body during the FBI (Ionta et al. 2011; Lenggenhager et al. 2009).

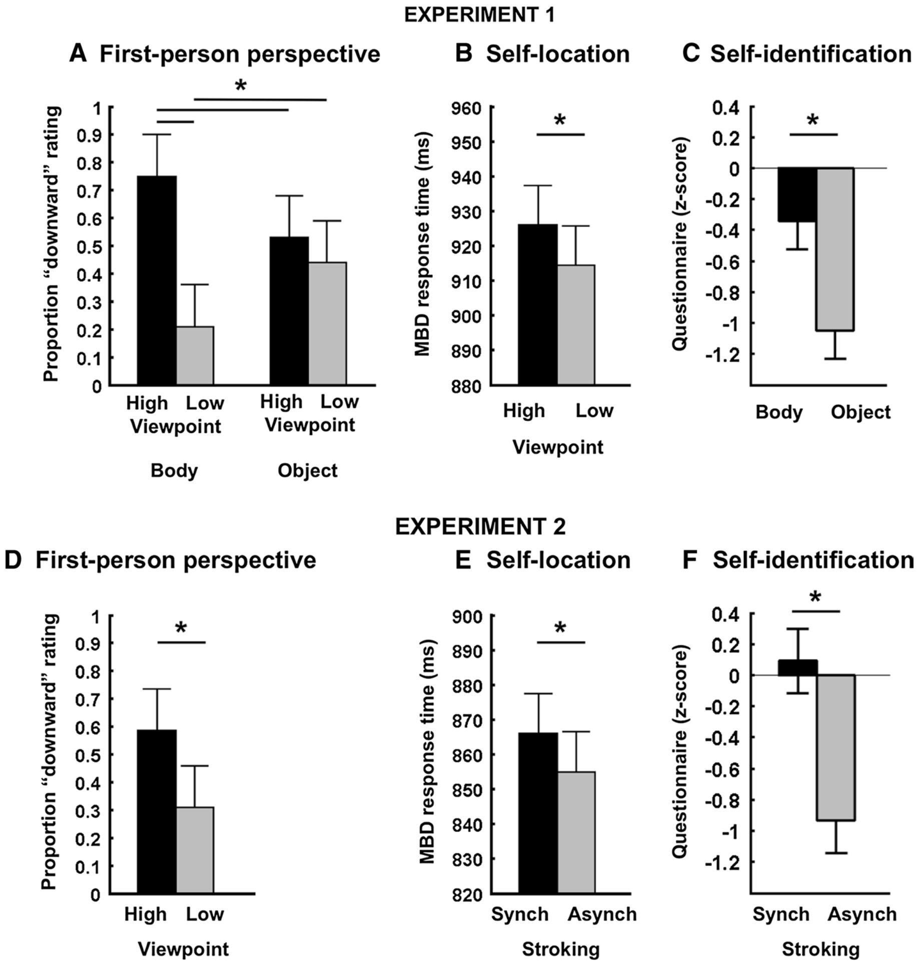

Fig. 2 Results from Experiment 1 (**a–c**) and Experiment 2 (**d–f**) for subjective 1PP ratings (**a, d**), RTs of the MBD task, our measure of self-location, (**b, e**) and questionnaire ratings for self-identification (**c, f**). *Error bars* in all plots show 95 % confidence intervals of within-subjects interaction variance from the repeated measures ANOVA (Loftus and Masson 1994)

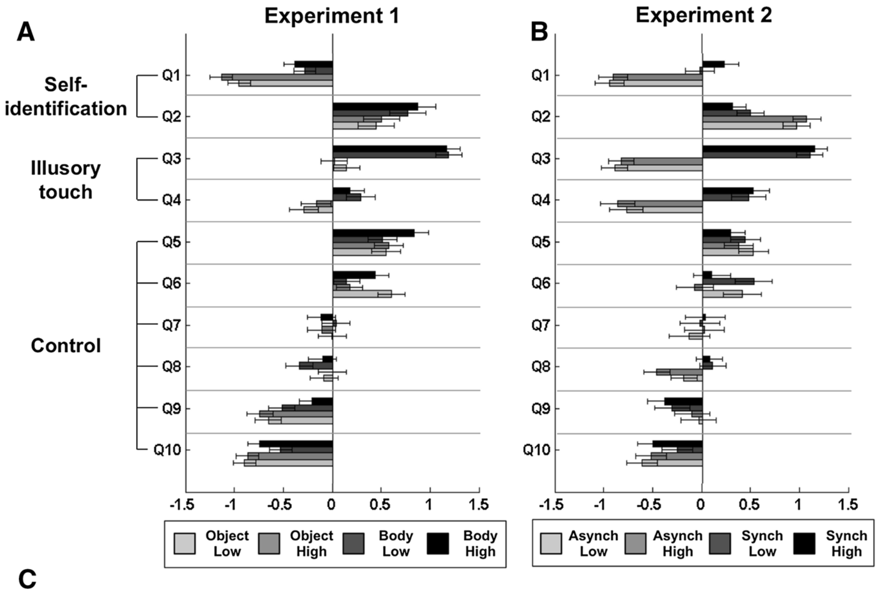

Fig. 3 Questionnaire results summarized. **a–b** Ipsative scores for all questions (*y*-axis) as a function of experimental conditions (*shades of gray*) indicate participants average responses by a value of zero and agreement (+) and disagreement (−) in standard deviation units. *Error bars* show 95 % confidences intervals. **c** Questions of the FBI questionnaire

C

1. How strong was the feeling that the body you saw was you?
2. How strong was the feeling that you were looking at someone else?
3. How strong was the feeling that the touch you felt was located where you saw the stroking?
4. How strong was the feeling that the red dot you saw was directly touching you?
5. How strong was the feeling that you were located at some distance behind the visual image of the body that you saw?
6. How strong was the feeling that you were drifting downwards or upwards?
7. How strong was the feeling that you had more than one body?
8. How strongly did you feel the touch simultaneously at two locations in space?
9. How strong was the feeling to float in the air?
10. How strong was the feeling that you were dissociated from your body (as if your self and your body were in different locations)?

FBI questionnaire

Figure 3a summarizes the questionnaire results. FBI questionnaire score analysis revealed a significant main effect of Object for self-identification (Q1: $F(1, 24) = 19.39$, $p < .001$, $\eta^2 = .45$; Fig. 2c), reflecting higher scores for the body Object condition ($M = -.34$, SE = .14) than the non-body Object condition ($M = -1.05$, SE = .09). We also found a main effect of Object for illusory touch (Q3: $F(1, 24) = 31.90$, $p < .001$, $\eta^2 = .57$) showing higher scores for the body Object condition ($M = 1.17$, SE = .16) than the non-body Object condition ($M = .07$, SE = .17). No further questions showed a significant main effect of Object, and there were no main effects of Viewpoint and no viewpoint × object interaction. Together these results suggest that during synchronous visuotactile stimulation, self-identification and illusory touch increased when stroking was visually presented on a virtual human body as compared to a non-body object. These results likely reflect effects of top-down knowledge about body-identity on self-identification and illusory touch.

Summary of results

Our results showed that manipulating participants' visuospatial viewpoint and the identity of the visual stimulus during the FBI affected three components of BSC. In particular, visuospatial viewpoint had a specific effect on self-location, but not on self-identification as measured through questionnaire scores: Participants localized themselves toward a higher location in the high Viewpoint conditions. Conversely, object identity selectively affected self-identification and, in line with previous studies, self-identification was rated higher when a virtual body was presented as compared to a non-body object (Lenggenhager et al. 2007; Aspell et al. 2009). Finally, only the experienced direction of the 1PP was affected by the combination of the two factors and visuospatial viewpoint effects on subjective 1PP were specific to seeing a virtual body, but absent for the non-body object.

Experiment 2

Subjective 1PP

Statistical analysis revealed a main effect of Viewpoint ($F(1, 18) = 5.91$, $p = .026$, $\eta^2 = .25$; Fig. 2d), reflecting more frequent 'downward' 1PP for high Viewpoint ($M = .59$, SE = .08) than for low Viewpoint ($M = .31$, SE = .06). These results are consistent with results from experiment 1. The analysis showed no main effect of

Stroking and no Viewpoint × Stroking interaction (all F values <1).

Self-location

Statistical analysis of MBD RTs showed a main effect of Stroking ($F(1, 18) = 6.44$, $p = .021$, $\eta^2 = .26$; Fig. 2e) with higher self-location for the synchronous Stroking ($M = 866$ ms, SE = 51 ms) than for the asynchronous Stroking conditions ($M = 855$ ms, SE = 50 ms). These results show that the self-location drifted upwards toward the image of the virtual body (shown in the HMD) and was thus corresponding to the direction of participants' body posture lying on the back. However, there was no main effect of Viewpoint and no viewpoint × stroking interaction (all F values <1). These results suggest that visuospatial viewpoint had no effect on self-location, but that self-location drifted independently of viewpoint in an upward direction congruently with participants' body orientation on the robotic device.

FBI questionnaire

Figure 3b summarizes the questionnaire results. Questionnaire score analysis revealed a significant main effects of Stroking for questions inquiring about self-identification (Q1: $F(1, 18) = 32.61$, $p < .001$, $\eta^2 = .64$; Q2: $F(1, 18) = 12.87$, $p = .002$, $\eta^2 = .42$; Fig. 2f) and illusory touch (Q3: $F(1, 18) = 112.10$, $p < .001$, $\eta^2 = .86$; Q4: $F(1, 18) = 29.21$, $p < .001$, $\eta^2 = .62$). The two questions concerning self-identification showed a consistent result: Self-identification with the virtual body (Q1) was rated higher for synchronous ($M = .09$, SE = .18) than asynchronous Stroking ($M = -.94$, SE = .14), and identifying the virtual body as being somebody else (Q2) was rated higher for asynchronous ($M = 1.00$, SE = .22) than synchronous stroking ($M = .39$, SE = .23). Both questions on illusory touch were rated higher for synchronous (Q3: $M = 1.11$, SE = .11; Q4: $M = .49$, SE = .23) than asynchronous Stroking (Q3: $M = -.87$, SE = .17; Q4: $M = -.83$, SE = .15). These results are consistent with previous FBI studies using a variety of different stimulation and virtual reality protocols (Ehrsson 2007; Lenggenhager et al. 2007, 2009; Petkova et al. 2011). None of the questions that are generally given as control questions in the FBI (Q5–Q10) showed significant main effects or interactions. Subjective 1PP, in addition to trial-wise ratings, was also rated in the FBI questionnaire. Notably, no question showed a main effect or interaction with Viewpoint, thus neither self-identification ratings (Q1, Q2), nor illusory touch ratings (Q3, Q4) were affected by visuospatial viewpoint (all p values >.5).

Discussion

Within-subject manipulation of subjective 1PP

We found that within-subjects subjective 1PP changed congruently with our visuospatial viewpoint manipulations, although the physical body of our participants was upward-directed in supine posture throughout all experiments. Participants experienced a downward-directed 1PP more often when they saw a virtual body from a downward-directed viewpoint than from an upward-directed viewpoint. Notably, these changes were obtained by repeated measurements within-subjects and agree with the phenomenology of OBEs of neurological origin. Patients often experience disembodied downward-directed 1PP while their physical body is upward-directed in supine posture (Blanke et al. 2002, 2004; De Ridder et al. 2007). Our results also extend previous FBI studies in healthy individuals (Pfeiffer et al. 2013; Ionta et al. 2011) where downward-directed viewpoints were used to induce visuovestibular conflict about the direction of constant gravitational acceleration. These manipulations induced between-subjects changes of the subjective 1PP (i.e., in terms of the experienced direction of the 1PP). In the present study, downward- and upward-directed visuospatial viewpoint manipulation induced congruent changes of the subjective 1PP within-subjects. Our data indicate that visuospatial viewpoint manipulations are more powerful in altering the subjective 1PP across subjects when compared to visuovestibular conflicts used in previous studies (Pfeiffer et al. 2013; Ionta et al. 2011).

Body-specific manipulation of subjective 1PP

In the present study, subjective 1PP was modulated by viewpoint only when a virtual human body was presented, but not for a non-body object. This body-specific effect was found during ongoing synchronous stroking that is known to induce self-identification with the virtual body, but not a non-body object as in previous FBI studies (Lenggenhager et al. 2007; Aspell et al. 2010; Petkova and Ehrsson 2008).

Similar body-specific effects have previously been described in related studies on BSC. For example, the rubber hand illusion is abolished when a non-body object instead of a fake hand is shown (Tsakiris and Haggard 2005). Similarly, a body-shaped object, such as a mannequin, but not a non-body object, allows inducing the FBI (Aspell et al. 2009; Lenggenhager et al. 2007). Brain imaging work has shown that a network of posterior brain regions is highly tuned to extract the visual shape of body parts or whole bodies, for example in the extrastriate body area in the lateral occipital cortex (Kanwisher et al. 1997; Astafiev et al. 2004; Gentile et al. 2013). This literature also provides evidence that visual processing of the body (or face) depends on the spatial orientation of the image (de Gelder et al. 2010; Minnebusch and Daum 2009 for reviews). This has been tested by the body/face inversion effect, consisting in RT or neural activation differences for visual processing upright versus inverted body or face (but not object) stimuli. The body inversion effect gradually depends on the angular deviation magnitude between upright and rotated image (Minnebusch et al. 2010). Accordingly, our visual body stimuli differed in the rotational tilt of the body stimulus with respect to the camera viewpoint (Fig. 1c). Based on the previous literature, it seems plausible that the body processing brain network encoded orientation differences of the virtual body (but not the non-body object) and that therefore subjective 1PP ratings depended on information encoded in the body processing network.

Other studies have shown that vision of bodily shapes is relevant to multisensory integration and seeing one's own body enhances touch processing (Kennett et al. 2001) and reduces tactile pain (Longo et al. 2012) as compared to seeing a non-body object. In addition to that, these body-specific effects on the subjective 1PP show that global visual features alone cannot induce these changes, but that more detailed visuospatial information is required. Specifically, in both body and object conditions, global visual features were identical. Thus, the location where the visual perspectival lines converged on the display was identical, i.e., for high viewpoint the lines converged in the lower part of the screen, whereas for low viewpoints the lines converged in the upper part of the screen. Yet subjective 1PP was modulated differently by the visual viewpoint only in the body condition.

Subjective 1PP and visuospatial viewpoint

Our results showed that subjective 1PP ratings (i.e., upward, downward) depended on the visuospatial viewpoint inclination angle (i.e., upward for low viewpoint, downward for high viewpoint) when a virtual body was seen. This suggests that visuospatial viewpoint information is highly relevant to subjective 1PP experience.

Are subjective 1PP ratings more than judgments of visual features of the experimental stimuli? This is indeed suggested by the absence of viewpoint effects on subjective 1PP ratings when a non-body object was seen, i.e., subjective 1PP ratings were at chance level for both viewpoint conditions when a non-body object was shown (see Fig. 2a). Furthermore, visual judgments would have led to extreme values for subjective 1PP ratings (i.e., 0 or 1 proportion of downward 1PP rating). This was not observed, rather, for each participant subjective 1PP ratings ranged between .2 and .9 proportion per experimental condition, which is also reflected in the group average proportions ranging in Experiment 1 from .2 to .75 proportion downward rating (Fig. 2a) and in Experiment 2 from .3 to .6 proportion downward rating (Fig. 2d). Furthermore, in a previous FBI study, we presented the same downward-directed visuospatial viewpoint to all participants but observed individual differences in subjective 1PP ratings depending on visuovestibular integration and furthermore found within-subjects modulation of subjective 1PP ratings by visuotactile stroking (Pfeiffer et al. 2013). We note that two perceptual interpretations of our visual stimuli were possible. Participants may have either experienced viewing the scene from a fixed camera viewpoint and a virtual body in front of them at different rotational tilt angles or they may have experienced viewing a virtual body at a fixed spatial orientation from differently tilted camera viewpoints. Whereas the former experience (i.e., fixed viewpoint) should have decreased variance in 1PP ratings across conditions, the latter experience (i.e., fixed virtual body) could have been associated in viewpoint-dependent changes of 1PP ratings as observed in our experiments. However, our study did not directly address this issue and further studies should directly address this issue. Together, the present and the previous results show that in healthy subjects during the FBI subjective 1PP ratings depend on visual, vestibular, and tactile signals. Furthermore, visuospatial viewpoint information is highly relevant to subjective 1PP ratings, but only if a virtual body is seen.

Subjective 1PP: no modulation by visuotactile stroking

Results from the second experiment showed no effects of visuotactile stimulation on the subjective 1PP. This observation differs from previous data showing that asynchronous stroking induced more frequent 'downward' 1PP ratings than synchronous stroking (Pfeiffer et al. 2013). However, different degrees of visuovestibular conflict were used in these studies, i.e., 180° directional conflicts were used in the study by Pfeiffer et al. (2013) and 90° directional conflicts were used in the present study. Thus, multisensory—visual, tactile, and vestibular—signals seem to determine the subjective 1PP. Moreover, we note that visuotactile stimuli related to the stroking manipulation were uninformative about the spatial configuration of the virtual body and the participant's body with respect to the external environment. That is, in all experimental conditions, visual stroking (i.e., red dots) and tactile stroking (i.e., touch at the back) were applied to the back of the virtual body and participant's body and were seen from 2-m distance. The observation that visuotactile stroking in the present conditions does not modulate the subjective 1PP raises the question which combinations of multisensory visual-tactile-vestibular stimulus combinations most strongly affect the subjective 1PP. Previous behavioral and psychophysics studies have provided evidence that the perception of the spatial orientation of the own body in space is affected, for instance, by footsole pressure (Lackner 1992; Lackner and DiZio 2000), neck-muscle vibration (Lackner and DiZio 2005), large-field optokinetic stimulation (De Saedeleer et al. 2013), or static tilts of the visual environments (Tiliket et al. 1996). These multisensory effects on spatial perception suggest that similar stimulations may also impact spatial aspects of BSC, in particular the subjective 1PP.

Subjective 1PP relationship to self-location

In addition to the effects on 1PP, our results showed that self-location was affected by viewpoint. In the first experiment in the elevated viewpoint condition, subjects judged themselves to be higher above the ground, whereas the lowered viewpoint was associated with self-location that was closer to the ground. Thus, self-location and 1PP were similarly affected by viewpoint. Associations between 1PP and self-location were also found previously between-subjects during visuovestibular conflict (Ionta et al. 2011; Pfeiffer et al. 2013). The present study shows congruency between subjective 1PP and self-location only in these conditions and not related to stroking or for the non-body object.

We argue that the absence of an association between 1PP and self-location in the present study may be explained by the fact that weak and constant visuovestibular conflicts were employed and thus the present study differed from the results of previous studies where strong visuovestibular conflicts were presented (Pfeiffer et al. 2013; Ionta et al. 2011). More precisely, in the present experiment the visuovestibular conflict (between the visual gravity cues of the virtual body and the vestibular cues of the participant's body) were less strong. There was only a 90° visuovestibular angle difference in the present study, whereas (Ionta et al. 2011) employed a conflict of 180°. Here, we manipulated the visual viewpoint, thus the visuospatial representation showed less consistent effects on self-location, but more consistent effects on 1PP.

Self-identification: no modulation by visuospatial viewpoint

Self-identification with a virtual body depended on the synchrony between stroking felt on one's own body and seen on the avatar's body, self-identification was stronger when seeing a virtual body, and independent of the participant's visuospatial viewpoint manipulation. We found in the first experiment higher self-identification with a virtual body than a non-body object when stroked synchronously, and in the second experiment, higher self-identification ratings for synchronous than asynchronous stroking. Our results confirm previous bodily illusion studies that manipulated the synchrony of visuotactile stroking or tapping on virtual or fake hands (Botvinick and Cohen 1998), faces (Sforza et al. 2010; Tsakiris 2008), or whole bodies (Ehrsson 2007; Lenggenhager et al. 2007). Our results also agree with the previous studies showing body-specific effects of stroking for fake hands (Tsakiris and Haggard 2005) and whole bodies (Lenggenhager et al. 2007; Aspell et al. 2009). Together, the present results confirm that low-level cues in multisensory stimuli, such as temporal synchrony, as well as high-level body shape information, are processed by the central nervous system to generate self-identification with the whole body. Furthermore, our results show that our manipulations of viewpoint did not prevent or modulate the induction of the FBI and that using well-controlled robotic stroking and virtual reality can be used to manipulate self-identification with a virtual body.

However, viewpoint manipulation did not affect self-identification in both our experiments and this seems to contradict viewpoint effects reported in the study by Slater et al. (2010) for virtual body transfer and by Petkova et al. (2011) for the FBI. These studies did find that different visuospatial viewpoints affected subjective ratings of self-identification and objective measures, such as heart beat and skin conductance response. However, these authors manipulated egocentric versus allocentric visuospatial viewpoints and thus compared the effects of extracorporal (third-person) and body-centered (first-person) viewpoints. On the contrary, in the present study, we compared two allocentric, i.e., two extracorporeal, viewpoints, and then we measured their effects on different aspects of BSC.

In other words, the studies by Slater et al. (2010) and Petkova et al. (2011) compared a visuospatial viewpoint that was embodied within a virtual body with a disembodied viewpoint (as seen from a distance) from a virtual body, reporting stronger self-identification for embodied versus disembodied viewpoints. In our study, we compared two disembodied viewpoints that differed in terms of the elevation along the vertical axis. Using the same distance between both disembodied viewpoints from the virtual body, our viewpoints were either elevated-downward directed or lowered-upward directed. Therefore, our results do not contradict, but rather extend the results by Slater et al. (2010) and Petkova et al. (2011) by showing that self-identification with a virtual body from a distance does not depend on elevation or direction of viewpoint, but can be achieved under different visuospatial conditions.

Conclusion

Manipulating the visuospatial viewpoint elevation level above the ground from which healthy participants observed a humanoid virtual body induced congruent changes of the experienced direction of the subjective 1PP. Similar manipulation of visuospatial viewpoints for observing a non-body object did not modulate subjective 1PP experience, indicating that visuospatial viewpoints affected the subjective experience at what 'I' am directed (i.e., subjective 1PP) only if a humanoid body shape was seen. Visuospatial viewpoint manipulations had no effects on self-identification with a virtual body, which rather depended on visuotactile stroking synchrony. Thus, subjective 1PP and self-identification depended on different sensory stimulation parameters, suggesting potentially distinct underlying neural representation. Together, our results provide evidence for a close relationship between visual processing of body shape and visuospatial viewpoints contributing to spatial aspects of BSC. Furthermore, our results extend previous studies by demonstrating for the first time that within-subjects manipulation of subjective 1PP is malleable. More generally, our study showed that combining virtual reality, robotics technology, and cognitive neuroscience experimental approaches can further our understanding of the neurobiological basis of self-consciousness.

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References

Aichhorn M, Perner J, Kronbichler M, Staffen W, Ladurner G (2006) Do visual perspective tasks need theory of mind? Neuroimage 30(3):1059–1068. doi:10.1016/j.neuroimage.2005.10.026

Arzy S, Thut G, Mohr C, Michel CM, Blanke O (2006) Neural basis of embodiment: distinct contributions of temporoparietal junction and extrastriate body area. J Neurosci 26(31):8074–8081. doi:10.1523/JNEUROSCI.0745-06.2006

Aspell JE, Lenggenhager B, Blanke O (2009) Keeping in touch with one's self: multisensory mechanisms of self-consciousness. PLoS ONE 4(8):e6488. doi:10.1371/journal.pone.0006488

Aspell JE, Lavanchy T, Lenggenhager B, Blanke O (2010) Seeing the body modulates audiotactile integration. Eur J Neurosci 31(10):1868–1873. doi:10.1111/j.1460-9568.2010.07210.x

Astafiev SV, Stanley CM, Shulman GL, Corbetta M (2004) Extrastriate body area in human occipital cortex responds to the performance of motor actions. Nat Neurosci 7(5):542–548. doi:10.1038/nn1241

Baron-Cohen S, Leslie AM, Frith U (1985) Does the autistic child have a "theory of mind"? Cognition 21(1):37–46

Blanke O (2012) Multisensory brain mechanisms of bodily self-consciousness. Nat Rev Neurosci 13(8):556–571. doi:10.1038/nrn3292

Blanke O, Metzinger T (2009) Full-body illusions and minimal phenomenal selfhood. Trends Cogn Sci 13(1):7–13. doi:10.1016/j.tics.2008.10.003

Blanke O, Mohr C (2005) Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin implications for neurocognitive mechanisms of corporeal awareness and self-consciousness. Brain Res Brain Res Rev 50(1):184–199. doi:10.1016/j.brainresrev.2005.05.008

Blanke O, Ortigue S, Landis T, Seeck M (2002) Stimulating illusory own-body perceptions. Nature 419(6904):269–270. doi:10.1038/419269a

Blanke O, Landis T, Spinelli L, Seeck M (2004) Out-of-body experience and autoscopy of neurological origin. Brain 127(Pt 2):243–258. doi:10.1093/brain/awh040

Bonferroni CE (1935) l calcolo delle assicurazioni su gruppi di teste. In: Studi in Onore del Professore Salvatore Ortu Carboni. Rome, pp 13–60

Botvinick M, Cohen J (1998) Rubber hands 'feel' touch that eyes see. Nature 391(6669):756. doi:10.1038/35784

Broughton R, Wasel N (1990) A text-stimuli presentation manager for the IBM PC with ipsatization correction for response sets and reaction times. Behav Res Methods Instrum Comput 22(4):421–423

Brugger P, Agosti R, Regard M, Wieser HG, Landis T (1994) Heautoscopy, epilepsy, and suicide. J Neurol Neurosurg Psychiatry 57(7):838–839

Cattell RB (1944) Psychological measurement: normative, ipsative and interactive. Psychol Rev 51:292–303

de Gelder B, Van den Stock J, Meeren HK, Sinke CB, Kret ME, Tamietto M (2010) Standing up for the body. Recent progress in uncovering the networks involved in the perception of bodies and bodily expressions. Neurosci Biobehav Rev 34(4):513–527. doi:10.1016/j.neubiorev.2009.10.008

De Ridder D, Van Laere K, Dupont P, Menovsky T, Van de Heyning P (2007) Visualizing out-of-body experience in the brain. N Engl J Med 357(18):1829–1833. doi:10.1056/NEJMoa070010

De Saedeleer C, Vidal M, Lipshits M, Bengoetxea A, Cebolla AM, Berthoz A, Cheron G, McIntyre J (2013) Weightlessness alters up/down asymmetries in the perception of self-motion. Exp Brain Res 226(1):95–106. doi:10.1007/s00221-013-3414-7

Duenas J, Chapuis D, Pfeiffer C, Martuzzi R, Ionta S, Blanke O, Gassert R (2011) Neuroscience robotics to investigate multisensory integration and bodily awareness. Conf Proc IEEE Eng Med Biol Soc 8348–8352. doi:10.1109/IEMBS.2011.6092059

Ehrsson HH (2007) The experimental induction of out-of-body experiences. Science 317(5841):1048. doi:10.1126/science.1142175

Freton M, Lemogne C, Bergouignan L, Delaveau P, Lehericy S, Fossati P (2013) The eye of the self: precuneus volume and visual perspective during autobiographical memory retrieval. Brain Struct Funct. doi:10.1007/s00429-013-0546-2

Frith U, Frith CD (2003) Development and neurophysiology of mentalizing. Philos Trans R Soc Lond B Biol Sci 358(1431):459–473. doi:10.1098/rstb.2002.1218

Frith C, Frith U (2005) Theory of mind. Curr Biol 15(17):R644–R646. doi:10.1016/j.cub.2005.08.041

Frith CD, Frith U (2006) The neural basis of mentalizing. Neuron 50(4):531–534. doi:10.1016/j.neuron.2006.05.001

Gentile G, Guterstam A, Brozzoli C, Ehrsson HH (2013) Disintegration of multisensory signals from the real hand reduces default limb self-attribution: an fMRI study. J Neurosci 33(33):13350–13366. doi:10.1523/JNEUROSCI.1363-13.2013

Guterstam A, Ehrsson HH (2012) Disowning one's seen real body during an out-of-body illusion. Conscious Cogn 21(2):1037–1042. doi:10.1016/j.concog.2012.01.018

Hänsel A, Lenggenhager B, von Kanel R, Curatolo M, Blanke O (2011) Seeing and identifying with a virtual body decreases pain perception. Eur J Pain 15(8):874–879. doi:10.1016/j.ejpain.2011.03.013

Heydrich L, Blanke O (2013) Distinct illusory own-body perceptions caused by damage to posterior insula and extrastriate cortex. Brain 136:790–803. doi:10.1093/brain/aws364

Ionta S, Heydrich L, Lenggenhager B, Mouthon M, Fornari E, Chapuis D, Gassert R, Blanke O (2011) Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. Neuron 70(2):363–374. doi:10.1016/j.neuron.2011.03.009

Kanwisher N, McDermott J, Chun MM (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 17(11):4302–4311

Kennett S, Taylor-Clarke M, Haggard P (2001) Noninformative vision improves the spatial resolution of touch in humans. Curr Biol 11(15):1188–1191

Lackner JR (1992) Spatial orientation in weightless environments. Perception 21(6):803–812

Lackner JR, DiZio PA (2000) Aspects of body self-calibration. Trends Cogn Sci 4(7):279–288

Lackner JR, DiZio P (2005) Vestibular, proprioceptive, and haptic contributions to spatial orientation. Annu Rev Psychol 56:115–147. doi:10.1146/annurev.psych.55.090902.142023

Lenggenhager B, Tadi T, Metzinger T, Blanke O (2007) Video ergo sum: manipulating bodily self-consciousness. Science 317(5841):1096–1099. doi:10.1126/science.1143439

Lenggenhager B, Mouthon M, Blanke O (2009) Spatial aspects of bodily self-consciousness. Conscious Cogn 18(1):110–117. doi:10.1016/j.concog.2008.11.003

Loftus GR, Masson M (1994) Using confidence intervals in within-subjects designs. Psychon Bull Rev 1(4):476–490

Longo MR, Iannetti GD, Mancini F, Driver J, Haggard P (2012) Linking pain and the body: neural correlates of visually induced analgesia. J Neurosci 32(8):2601–2607. doi:10.1523/JNEUROSCI.4031-11.2012

Metzinger T (2003) Being no one. MIT Press, Boston

Minnebusch DA, Daum I (2009) Neuropsychological mechanisms of visual face and body perception. Neurosci Biobehav Rev 33(7):1133–1144. doi:10.1016/j.neubiorev.2009.05.008

Minnebusch DA, Keune PM, Suchan B, Daum I (2010) Gradual inversion affects the processing of human body shapes. Neuroimage 49(3):2746–2755. doi:10.1016/j.neuroimage.2009.10.046

Petkova VI, Ehrsson HH (2008) If I were you: perceptual illusion of body swapping. PLoS ONE 3(12):e3832. doi:10.1371/journal.pone.0003832

Petkova VI, Khoshnevis M, Ehrsson HH (2011) The perspective matters! Multisensory integration in ego-centric reference frames determines full-body ownership. Front Psychol 2:35. doi:10.3389/fpsyg.2011.00035

Pfeiffer C, Lopez C, Schmutz V, Duenas JA, Martuzzi R, Blanke O (2013) Multisensory origin of the subjective first-person perspective: visual, tactile, and vestibular mechanisms. PLoS ONE 8(4):e61751. doi:10.1371/journal.pone.0061751

Romano D, Pfeiffer C, Maravita A, Blanke O (2014) Illusory self-identification with an avatar reduces arousal responses to painful stimuli. Behav Brain Res 261:275–281. doi:10.1016/j.bbr.2013.12.049

Salomon R, Lim M, Pfeiffer C, Gassert R, Blanke O (2013) Full body illusion is associated with widespread skin temperature reduction. Front Behav Neurosci 7:65. doi:10.3389/fnbeh.2013.00065

Serino A, Alsmith A, Costantini M, Mandrigin A, Tajadura-Jimenez A, Lopez C (2013) Bodily ownership and self-location: components of bodily self-consciousness. Conscious Cogn 22(4):1239–1252. doi:10.1016/j.concog.2013.08.013

Sforza A, Bufalari I, Haggard P, Aglioti SM (2010) My face in yours: visuo-tactile facial stimulation influences sense of identity. Soc Neurosci 5(2):148–162. doi:10.1080/17470910903205503

Slater M, Spanlang B, Sanchez-Vives MV, Blanke O (2010) First person experience of body transfer in virtual reality. PLoS ONE 5(5):e10564. doi:10.1371/journal.pone.0010564

Tiliket C, Ventre-Dominey J, Vighetto A, Grochowicki M (1996) Room tilt illusion. A central otolith dysfunction. Arch Neurol 53(12):1259–1264

Tsakiris M (2008) Looking for myself: current multisensory input alters self-face recognition. PLoS ONE 3(12):e4040. doi:10.1371/journal.pone.0004040

Tsakiris M, Haggard P (2005) The rubber hand illusion revisited: visuotactile integration and self-attribution. J Exp Psychol Hum Percept Perform 31(1):80–91. doi:10.1037/0096-1523.31.1.80

Vogeley K, Fink GR (2003) Neural correlates of the first-person-perspective. Trends Cogn Sci 7(1):38–42

Vogeley K, May M, Ritzl A, Falkai P, Zilles K, Fink GR (2004) Neural correlates of first-person perspective as one constituent of human self-consciousness. J Cogn Neurosci 16(5):817–827. doi:10.1162/089892904970799

2.3 Study 3: First-person perspective dependence on visual gravity cues

First-person perspective dependence on visual gravity cues

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Abstract

Bodily self-consciousness, the sense of being a subject in a body, involves a first-person perspective (1PP), i.e. the experience that 'I' am directed at the world. Here we asked whether 1PP depends on multisensory conflicts about the direction of gravity. Sixteen healthy subjects received visuo-tactile synchronous or asynchronous stroking to induce a full-body illusion. The critical manipulation was presenting gravitational virtual object motion directed toward (congruent with veridical gravity) or away from the participant (incongruent with veridical gravity). Analysis showed that these visual gravitational cues induced direction-congruent changes of 1PP, reflected in more frequent downward 1PP ratings for away than toward virtual object motion. Also, a clear association between downward 1PP experience and elevated self-location measures was found. Together, these results suggest a major contribution of visual motion cues to a gravitational reference frame for 1PP experience. We discuss these subjective and behavioral results regarding current knowledge on multisensory and neural mechanisms of bodily self-consciousness.

Keywords

Full-body illusion; multisensory integration; first-person perspective; gravity; virtual reality; self-consciousness;

Introduction

Bodily self-consciousness (BSC) is the sense of being a subject in a body and is thought to involve self-identification (the experience of owning a body), self-location (the experience of where 'I' am in space), and first-person perspective (1PP; the experience that 'I' am directed at the world; (Blanke & Metzinger, 2009)). A prominent model proposes that BSC is based on brain mechanisms integrating multisensory bodily signals (Blanke, 2012; Ehrsson, 2012; Haggard, Taylor-Clarke, & Kennett, 2003; Jeannerod, 2003). Experimental studies support this proposal, showing that multisensory conflict about the appearance or location of one's own body can induce systematic changes of self-identification and self-location (Adler, Herbelin, Similowski, & Blanke, 2014; Aspell et al., 2013; Lenggenhager, Tadi, Metzinger, & Blanke, 2007; Macauda et al., 2014; Palluel, Aspell, & Blanke, 2011; Petkova & Ehrsson, 2008; Salomon, Lim, Pfeiffer, Gassert, & Blanke, 2013). Consistently, visual information often dominates concurrent somatosensory, vestibular, or interoceptive signals—referred to as visual capture (Aspell et al., 2013; Botvinick & Cohen, 1998; Ehrsson, 2007; Lenggenhager et al., 2007; Suzuki, Garfinkel, Critchley, & Seth, 2013). For instance, during the rubber hand illusion (RHI) a seen fake/virtual hand, within peripersonal space, is touched in synchrony with the participant's own hidden hand, which induces increased hand ownership and proprioceptive drift toward the seen fake/virtual hand (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). During the full body illusion (FBI) similar visuo-tactile synchronous stroking of the trunk of a virtual body, in peripersonal or extrapersonal space, and the participant's body leads to increased self-identification and self-location changes toward the seen virtual body (Ehrsson, 2007; Lenggenhager et al., 2007; Petkova & Ehrsson, 2008). Collectively, these data suggest that the brain strongly relies on visual cues for assign assigning self-identification and self-location to a physical object, the body.

However, much less is known about the multisensory mechanisms of 1PP. This is surprising because, at the phenomenal level, the 1PP relates the self as the experiencing subject to the object or content of experience (Blanke & Metzinger, 2009; Heidegger, 1962; Metzinger, 2003, 2013). Arguably, conscious experience of the world involves the spatial dimension (i.e. weak 1PP; Blanke & Metzinger, 2009; Metzinger, 2013; see also Discussion), reflected in a spatially directed 1PP anchored to a point of reference in the head or trunk—also referred to as self- or ego-center (Alsmith & Longo, 2014; Limanowski & Hecht, 2011)—and directed at events or objects, including one's own body, in the external world (Metzinger, 2013). Of note, 1PP is not necessarily limited to visuo-spatial representations of the brain, but also includes auditory, somatosensory, and vestibular frames of reference (Blanke, 2012; Pfeiffer, Schmutz, & Blanke, 2014; Schwabe & Blanke, 2008). Indeed, it has been argued that 1PP is more than a mere visual stimulus, because it is an integrated multisensory experience by subject (i.e. the self; Metzinger, 2013; Pfeiffer, Schmutz, et al., 2014). Given the evidence for a primacy of visual capture during multisensory spatial conflict related to self-identification and self-location (Botvinick & Cohen, 1998; Ehrsson, 2007; Lenggenhager et al., 2007), the question arises whether a similar mechanism applies for 1PP? In this study, we particularly focus on the role of visual cues during multisensory conflict about gravity.

Gravity, i.e. the constant linear attraction force by the earth's mass, is an absolute reference of the earth-vertical direction and has framed the evolution of the primate species, including the emergence of consciousness (Deroualle & Lopez, 2014; Lenggenhager & Lopez, 2015). Neuroimaging and experimental results suggest that the brain stores internal models of gravity for accounting for the effects of gravity in perception and motor control (McIntyre, Zago, Berthoz, & Lacquaniti, 2001; Sciutti et al., 2012). These representations depend on gravitational cues from vestibular, somatosensory, and visual signals, optimizing inherent sensory ambiguities with a single sense modality, e.g. equivalence of linear head motion and gravitational acceleration for the vestibular otolith organs (Angelaki & Cullen, 2008). Recent works emphasize the relevance of visual cues in perception of spatial orientation and motion of the body or of objects under the influence of gravity (Berthoz, 1991; De Saedeleer et al., 2013; Indovina et al., 2005; Indovina et al., 2013). Interestingly, in microgravity (i.e. absence of gravity during spaceflight) complex bodily illusions are very frequent

(Lopez, Halje, & Blanke, 2008). Although functionally meaningless, astronauts in microgravity persist in seeing a single upright direction as being aligned with the visual layout of the spacecraft. This latter perception, however, may frequently and instantly flip in steps of 90 or 180 degree angles (i.e. room-tilt illusion; Tiliket, Ventre-Dominey, Vighetto, & Grochowicki, 1996), resembling thus altered 1PP experiences in out-of-body experiences (OBEs) of neurological origin (for discussion see Lopez et al., 2008) and those induced experimentally in healthy subjects (Ionta et al., 2011; Pfeiffer et al., 2013; Pfeiffer, Schmutz, et al., 2014).

In order to reveal the role of multisensory gravitational cues for 1PP in healthy subjects, in a series of previous FBI studies we studied the effect of directional conflict between visual, vestibular and somatosensory gravitational cues on repeated inquiries about participant's experienced direction of 1PP (Ionta et al., 2011; Pfeiffer et al., 2013; Pfeiffer, Schmutz, et al., 2014). Specifically, supine participants (gravity directed toward them) concurrently viewed a prone virtual body as if seen from an elevated downward-directed visual viewpoint (visual gravity directed away from participants). Inducing the FBI under these conditions, about half of the tested participants experienced mostly an upward direction of 1PP (up-group) whereas the remainder experienced mostly a downward direction of 1PP (down-group). These individual differences of 1PP were further associated to different patterns of self-location change, related to visuo-tactile stroking during FBI, and to individual differences in subjective visual vertical ratings (Ionta et al., 2011; Pfeiffer et al., 2013). In a different FBI study (gravity-unrelated) visuo-spatial viewpoint manipulations related to a human-shaped virtual body induced within-subject changes of 1PP (Pfeiffer, Schmutz, et al., 2014). However, day-to-day conscious experience is not always related to human bodies, and it remains unclear whether visual gravitational cues induce more pronounced and reliable changes of 1PP than previously observed (Ionta et al., 2011; Pfeiffer et al., 2013).

In order to address these issues, we adapted a previous FBI protocol (Pfeiffer et al., 2013) to the concurrent presentation of dynamic visual gravitational motion of a virtual object (adapted from Senot, Zago, Lacquaniti, & McIntyre, 2005). Similar visual stimuli were previously used to study the role of gravity in visual perception, showing that gravitational dynamic motion engages processing by the brain's internal models of gravity (Indovina et al., 2005; Indovina et al., 2013; McIntyre et al., 2001). Here we tested whether the direction of gravitational visual object motion would affect subjective 1PP during FBI, reflected in within-subject changes of 1PP ratings on a trial-by-trial basis. We induced the FBI in supine participants (gravity directed towards them) who viewed on a HMD a virtual spherical object accelerating with gravity constant (9.81 ms/s^2) which moved either toward the participant (congruent with veridical gravity) or away from the participant (incongruent with veridical gravity), independent of the applied visuo-tactile stroking manipulations. We hypothesized that these salient dynamic visual gravitational cues surrounding the virtual body might interfere with changes in 1PP induced by concurrent static visuo-vestibular conflicts and visuo-tactile stimulation (Ionta et al., 2011; Pfeiffer et al., 2013; Pfeiffer, Schmutz, et al., 2014) inducing changes of the subjective 1PP in the direction of the visual gravitational motion. We also recorded self-location measures and questionnaires ratings to quantify the FBI experience.

Materials and methods

Participants

Sixteen undergraduate students (6 females, mean age ± SD: 22.3 ± 2.5 years) of the Ecole Polytechnique Fédérale de Lausanne participated. All were right-handed, had normal or corrected-to-normal vision, and no history of neurological or psychiatric disease. The study was conducted in accord with the Declaration of Helsinki and experimental protocol was approved by the local ethical committee—La Commission d'Ethique de la Recherche Clinique de la Faculté et de Medicine de l'Université de Lausanne. Participants gave their informed consent before inclusion to the study and received 30 Swiss Francs for compensation after having participated.

Experimental Setup

Figure 1a-b schematically shows the experimental setup, which was identical to previous experimental setups (Pfeiffer et al., 2013; Pfeiffer, Schmutz, et al., 2014; Romano, Pfeiffer, Maravita, & Blanke, 2014; Salomon et al., 2013). In a darkened room, a custom-made robotic device (stroking robot) was horizontally placed on a table with 90 cm distance to the floor. Participants lay in supine posture on the stroking robot, which consisted of a soft-foam mattress and of two independent stroking units touching the participant at the upper back through holes in the mattress (Duenas et al., 2011; Pfeiffer et al., 2013). The participant was equipped with a head-mounted display (HMD, Virtual Realities, Virtual Viewer 3D, http://www.vrealities.com, field-of-view 35°, resolution 800 x 600, refresh rate 60 Hz) for visual stimulus presentation and in-ear headphones for acoustic pink noise presentation masking mechanical noise of the stroking robot. A serial keypad (Targus Numeric Keypad AKP10US, http://www.targus.com) was placed under the participant's right hand for button press responses with the right hand index and middle fingers. A regular juggling ball (Astrix Flames-N-Games, http://flamesngames.co.uk) with 100 g weight was held by the participant in the left hand to facilitate the Mental Ball Dropping task (see below). Labview software (National Instruments, Austin Texas, http://www.ni.com/) was used to control of the stroking robot and ExpyVR software (http://lnco.epfl.ch/expyvr) was used for visual and acoustic stimuli presentation and timing.

Stimuli

The experimental stimuli were adapted from Pfeiffer et al. (Pfeiffer et al., 2013). The participant lay supine (gravity directed toward the participant) and viewed in the HMD a photorealistic back-view image of a male human body (virtual body) at approximately 2 meters in front of the participant. The clothing (i.e. white shirt) and the limb posture of the virtual body matched to clothing and posture of the participant

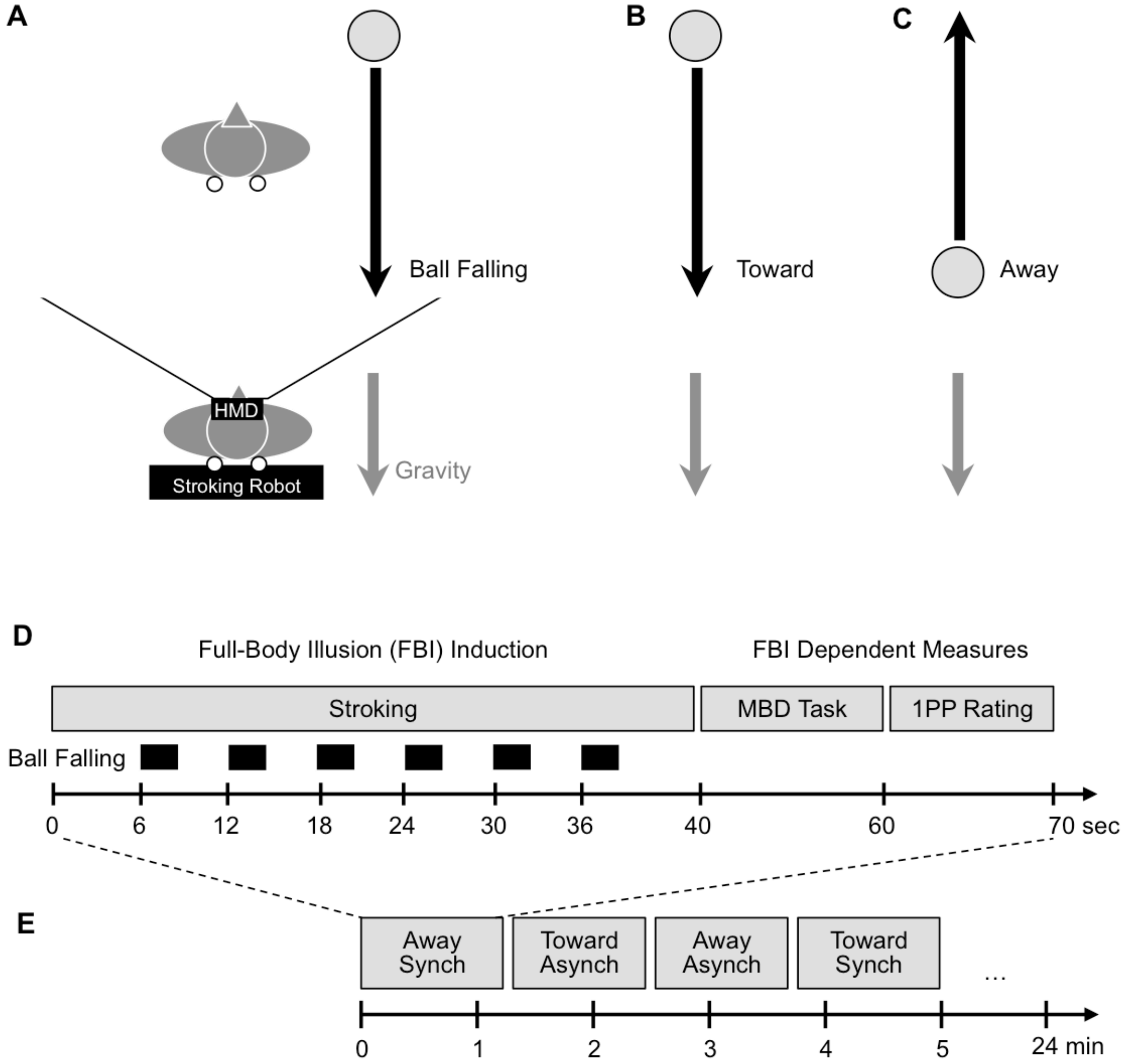

Figure 1 Full-body illusion (FBI) experimental setup and procedure. (a) Schematic side-view of the experimental setup showing a participant lying supine on a robotic device (*stroking robot*), used for tactile stroking, and wearing a head-mounted display (*HMD*) in which the participant saw visual stroking of a virtual body (*white circles;* illustrating both visual and tactile stroking). Visual gravitational cues consisted of a virtual ball falling (*gray circle and black arrow*) that was congruent or incongruent with the direction of gravity (*gray arrow*). An exemplar toward ball falling trial is shown. Note that during each experimental trial virtual balls repeatedly fell at random at the right side (shown here) or left side of the display. (b-c) Toward (congruent with gravitational direction) and away (incongruent with gravitational direction) visual ball falling stimuli are shown (black arrows) and gravitational direction is shown in gray. (d**)** Sequence of events for a single trial showing an initial full-body illusion (FBI) induction phase with continuous visuo-tactile (synchronous or asynchronous) stroking and occasional (toward or away) virtual ball falling stimuli. This was followed by the dependent measures of self-location (*MBD task*) and subjective first-person perspective (*1PP judgment*). (e) Randomized trial order during exemplar experimental run of 24 min duration.

during the experiment. A black colored background surrounded the virtual body such that no information about the surrounding space was visible to the participant.

Based on previous observations that static directional conflict of visual (away direction) and veridical gravity induced changes of subjective 1PP in some participants (Ionta et al., 2011; Pfeiffer et al., 2013), we here presented the similar static visual gravitational cues. They consisted of showing the virtual body in prone posture seen from an elevated downward-directed viewpoint directly above the virtual body (visual gravity directed away from the observer), showing gravitational pull on the virtual body's shoulders and clothing and of daylight directed to the virtual body's back (see Pfeiffer et al., 2013).

However, the main manipulation of the present study was presenting different dynamic visual gravitational cues, based on previous works showing gravitational effects on visual motion perception (Indovina et al., 2005; McIntyre et al., 2001; Senot et al., 2005; Zago, McIntyre, Senot, & Lacquaniti, 2008). In the HMD a three-dimensional white spherical object (virtual ball) was shown. The virtual ball initially appeared at a dedicated position in virtual space (see below) where it remained static for 1 sec and subsequently accelerated for 2 sec with a gravity-matching acceleration (9.81 cm/s^2) along a linear trajectory in parallel to the line of sight of the participant, without colliding with the virtual object or the participant's point of view. This procedure gave the impression that the virtual ball was falling under the influence of gravity (i.e. for similar stimulus see Senot et al., 2005). Critically, we manipulated the direction of virtual ball falling (Figure 1a-c). In one condition, the virtual ball appeared at a location far behind the virtual body and then accelerated towards the participant until it disappeared outside the field of view (*toward* Visual Gravity condition). In another condition, the virtual ball appeared at a location close to the participant and then accelerated away into depth until occluded by the virtual body (*away* Visual Gravity condition). Note that, whereas *toward* ball falling was congruent with the effects of veridical gravity on physical objects viewed by the participant in supine posture, *away* ball falling was incongruent with veridical gravity. The virtual ball falling stimuli thus served as dynamic visual cues simulating different visual gravity directions. We hypothesized that these dynamic visual gravitational cues might induce stronger changes of 1PP than previously observed for static visual gravitational cues only (Ionta et al., 2011; Pfeiffer et al., 2013).

In the context of these multisensory gravitational conflicts we induced the FBI with a classic visuo-tactile stroking manipulation (see Lenggenhager et al., 2007). Visual stroking was shown in the HMD as two red dots on the upper back of the virtual body with a diameter, position and movement range corresponding to the tactile stroking of the participant's back (Figure 1a). Tactile stroking consisted of random linear strokes by two independent stroking units along the upper back, i.e. on the left and right side of the back moving in parallel to the spinal cord. On each trial and for each of the stroking units, a different pseudo-random stroking sequence was used (strokes in a 0-20 cm distance range, 2-12 cm/s velocity range, variable 0-1.5 s inter-stroke intervals). During the experiment, visual and tactile stroking was simultaneously presented either in perfect synchrony (synchronous Stroking condition) or asynchronously in terms of moment-by-moment stroking position, movement direction, and velocity. The overall amount of stroking was matched between the asynchronous sequences (asynchronous Stroking condition). As shown by many previous studies, such synchronous stroking induces increased self-identification and self-location changes towards the virtual body when compared to the asynchronous stroking control condition (Ehrsson, 2007; Lenggenhager et al., 2007).

Experimental design and procedure

A 2 (Visual Gravity: towards, away) by 2 (Stroking: synchronous, asynchronous) within-subjects full-factorial experimental design was used. The four experimental conditions were presented 15 times in random order. The 60 experimental trials were presented in three runs of 20 trials. Figure 1c-d show the sequence of events of an experimental trial and an experimental run. First, the FBI was induced by presenting in the HMD the virtual body and by (synchronous or asynchronous) visuo-tactile stroking during 40 sec. During this period, repeated virtual ball falling stimuli were presented at 6, 12, 18, 24, 30, and 36 sec post-stimulus onset. All stimuli presented during this showed virtual ball falling in the same direction (away or towards) but were randomly presented at the left side (three times) or the right side (three times) of the screen in order to avoid anticipation. Immediately after that, the robotic stroking was stopped and all visual stimuli were removed from the screen upon which two dependent measures of the FBI were recorded during 30 sec (see below). This was followed by a fixed inter-trial-interval of 5 sec.

Dependent measures of the Full-Body Illusion

The 1PP judgment served as a repeated measure of the experienced direction of participant's 1PP (as initially introduced by Ionta et al., 2011). Participants viewed at the center of the display the word *'Orientation?'*, at the bottom left side the word *'Upwards'* and at the bottom right side the word *'downward'*. Participants were instructed that, upon viewing this display, they should answer the question *'Did you have the impression as if you were looking upwards at a body above you or as if you were looking downward at a body below you?'* using a two-alternative forced-choice response format, i.e. rating *'Upwards'* by pressing the right index finger button or by rating *'downward'* by pressing the right middle finger button. They were asked to rate their 1PP experience they had most of the time during the previous 40-sec stroking period. The judgment was given unspeeded within 10 sec after onset of the display.

The Mental Ball Dropping task (MBD; adapted from Lenggenhager et al., 2009) served as our measure of self-location. The MBD task began with the presentation of a white fixation cross on black background in the HMD for 1 sec. This was followed by a brief acoustic beep for 500 ms, which served as a go signal for initiating mental imagery. Participants imagined releasing the juggling ball (held in the left hand) and estimated the duration of ball falling to the ground. With the right index finger, the participant pressed a button at the moment of imagined ball release from the hand, held it pressed during imagined ball falling, and released the button at the moment of imagined ball impact on the ground. Thus, the duration of button press served as response time (RT) measure, i.e. a proxy of estimated self-location above the floor.

Before the experiment, the participant performed 20 practice trials including actual juggling ball drops from different heights. During an experimental trial, participants performed three subsequent repetitions of the MBD task and they had 6 sec to complete each repetition of the task.

The FBI Questionnaire (adapted from Lenggenhager et al., 2009) was administered after completion of the experiment on the robotic device. A total of ten questions (Figure 3b) inquired about different aspects of the illusion experience. Of those ten items, three were sensitive to the FBI experience (Experimental questions: Q1-Q3) and seven items served as control (Control questions: Q4-Q10). The questions were presented in random order at the center of a computer screen where seated participants gave their ratings along an 11-point horizontal visual analogue scaled labeled at the left side *'weak feeling'* and at the right side *'strong feeling'*. Ratings were given in an unspeeded fashion by button presses. Because this study primarily focused on the effects of visual gravitational cues on repeated measures of the subjective 1PP and for time-keeping reasons, we administered the FBI questionnaire twice in random order between participants: once regarding the overall synchronous Stroking trials and once regarding the asynchronous Stroking trials. The FBI questionnaire served mainly to assess that a basic FBI was induced during the experiment.

Analysis

Inspection of raw data showed for two participants a large number of MBD RT outliers (> 20 percent) and missing 1PP judgments, suggesting low task compliance. We excluded the data of these participants from further statistical analysis.

Subjective 1PP ratings were quantified as proportion scores by dividing the number of *'downward'* ratings by the total number of 1PP judgments per condition. The 1PP proportion score ranged from 0 (i.e. never rated *'downward'*) to 1 (i.e. always rated *'downward'*). Condition-wise scores from all participants were submitted to statistical analysis using a 2 (Visual Gravity: toward, away) x 2 (Stroking: synchronous, asynchronous) repeated measures ANOVA. We used Matlab (version R13, The MathWorks, Massachusetts, http://www.mathworks.ch/) and SPSS (version 17.0, IBM, http://www.ibm.com/software/analytics/spss*)* software for data analysis.

MBD RTs (self-location) were processed by removing outlier values exceeding 3.5 standard deviations about the individual average (i.e. on average 4.5% of the RTs were removed). Condition-averages were then calculated and subjected to statistical analysis using a 2 (Visual Gravity: toward, away) x 2 (Stroking: synchronous, asynchronous) repeated measures ANOVA.

Correlation analysis between the repeated measures for the subjective 1PP ratings and MBD RTs was conducted to investigate whether associations between these spatial aspects of bodily self-consciousness were present during our experimental manipulations. This required z-standardization of MBD RTs (average = 0, SD = 1) immediately after outlier removal and before calculating condition-averages. Thereby the variance ranges of the resulting condition-average RTs and the 1PP proportion scores where homogenized. We then subjected the paired condition-wise RTs and 1PP scores from all participants to linear regression analysis to investigate systematic relationships between self-location and subjective 1PP irrespective of the specific experimental condition.

The FBI questionnaire scores were analyzed by calculating for each participant the average scores across Experimental questions (Q1-Q3) and the average scores across Control questions (Q1-Q7) separately for the synchronous and asynchronous Stroking condition. The resulting scores were then subjected to statistical analysis using a 2 (Question: experimental, control) x 2 (Stroking: synchronous, asynchronous) repeated measures ANOVA. For all statistical analyses, an alpha threshold of .05 was used. Because paired t-tests for post-hoc comparisons were calculated only based on significant interactions, no correction for multiple comparisons was applied.

Predicted outcomes

Based on the idea that subjective 1PP depends on integrated spatial information from the body and the external world (Blanke, 2012; Blanke, Landis, Spinelli, & Seeck, 2004; Pfeiffer et al., 2013), we hypothesized that salient dynamic visual gravitational cues will induce changes of subjective 1PP and dominate over static visual, vestibular, and somatosensory gravitational cues. Thus, more upward 1PP ratings should be observed for virtual balls falling toward the participant (congruent with veridical gravity) and more *'downward'* 1PP ratings for virtual balls falling away from the participant (incongruent with veridical gravity).

Given the open question whether or not 1PP and self-location depend on similar or distinct functional mechanisms (Pfeiffer, 2015; Pfeiffer, Serino, & Blanke, 2014; Serino et al., 2013), we hypothesized that the relationship between 1PP and self-location should be positive. Specifically, we hypothesized an association between away visual gravity, *'downward'* 1PP ratings, and long MBD RTs (i.e. higher self-location) as found previously individual differences of subjective 1PP during static multisensory gravitational conflict (Ionta et al., 2011; Pfeiffer et al., 2013).

Regarding the overall experience of the FBI, we hypothesized in line with numerous previous studies that visuo-tactile stroking will induce a basic FBI experience, as reflected in higher questionnaire ratings for synchronous than asynchronous stroking for critical questionnaire items (Q1-Q3).

Results

Statistical analysis of 1PP proportion scores revealed a main effect of Visual Gravity (F(1, 13) = 15.20, p = .002, η^2 = .54; Figure 2a), reflecting more frequent '*downward'* 1PP ratings for away Visual Gravity (M = .60, SE = .07) than for toward Visual Gravity (M = .26, SE = .04), which suggests that 1PP experience during the FBI

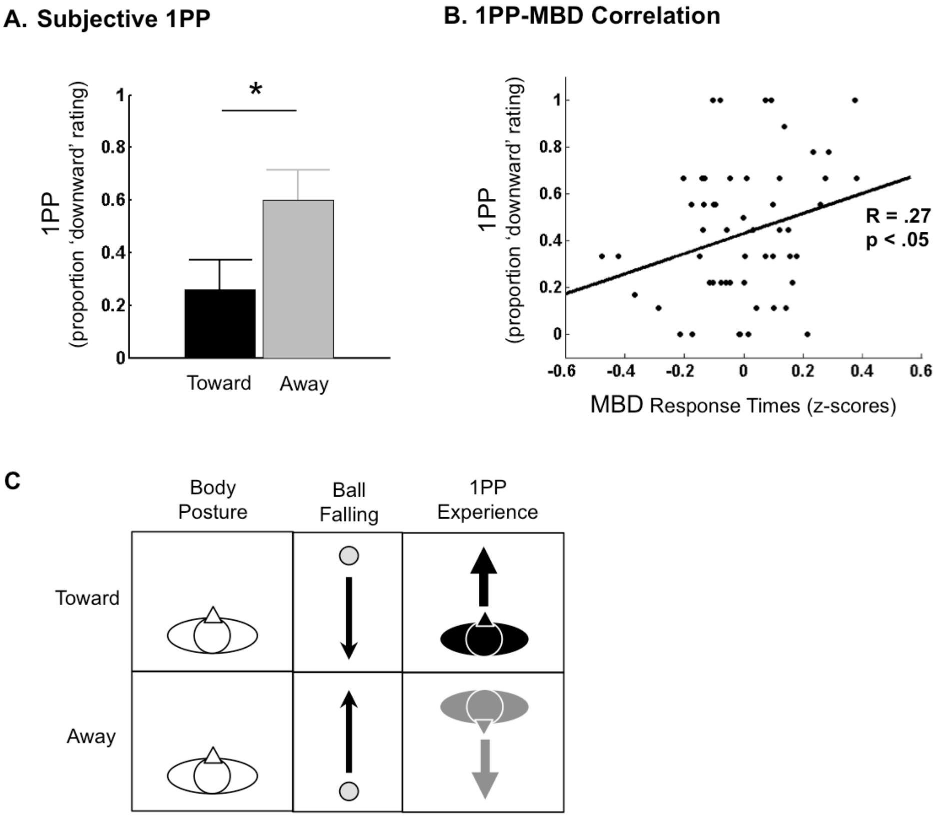

Figure 2 Results from the FBI. (a) Results for subjective 1PP showed a higher proportion *'downward'* ratings for away than for toward Visual Gravity. Error bars show 95 % confidence intervals of within-subjects interaction variance from the repeated measures ANOVA (Loftus & Masson, 1994) (b) Correlation between 1PP *'downward'* ratings and response times of the MBD task (self-location). (c) Results for subjective 1PP and self-location summarized, showing that for toward and away Visual Gravity conditions the participant's body posture, the ball falling direction and the experienced direction of 1PP.

depends on the direction of dynamic visual gravitational motion. No main effect of Stroking (F(1, 13) = .13, p = .72, η^2 = .01) and no Visual Gravity x Stroking interaction were observed (F(1, 13) = 3.80, p = .07, η^2 = .23).

Analysis of MBD RTs showed no significant main effects nor interaction (Visual Gravity main effect: F(1, 13) = 2.19, p = .16, η^2 = .14; Stroking main effect: F(1, 13) = 3.19, p = .10, η^2 = .20; Visual Gravity x Stroking interaction: F(1, 13) = .52, p = .46, η^2 = .04;), suggesting that overall self-location as measured by the MBD task was not modulated under the present experimental conditions.

Correlation analysis between 1PP proportion scores and MBD RTs across experimental conditions showed a significant positive correlation ($R = .27$, $p = .047$; Figure 2b), reflecting that more frequent *'downward'* 1PP ratings were associated with prolonged MBD RTs, i.e. higher self-location.

Statistical analysis of combined FBI questionnaire scores revealed a main effect of Question ($F(1, 13) = 6.34$, $p = .03$, $\eta^2 = .33$), a main effect of Stroking ($F(1, 13) = 46.82$, $p < .001$, $\eta^2 = .78$) and a critical Question x Stroking interaction ($F(1, 13) = 32.59$, $p < .001$, $\eta^2 = .71$; Figure 3a).

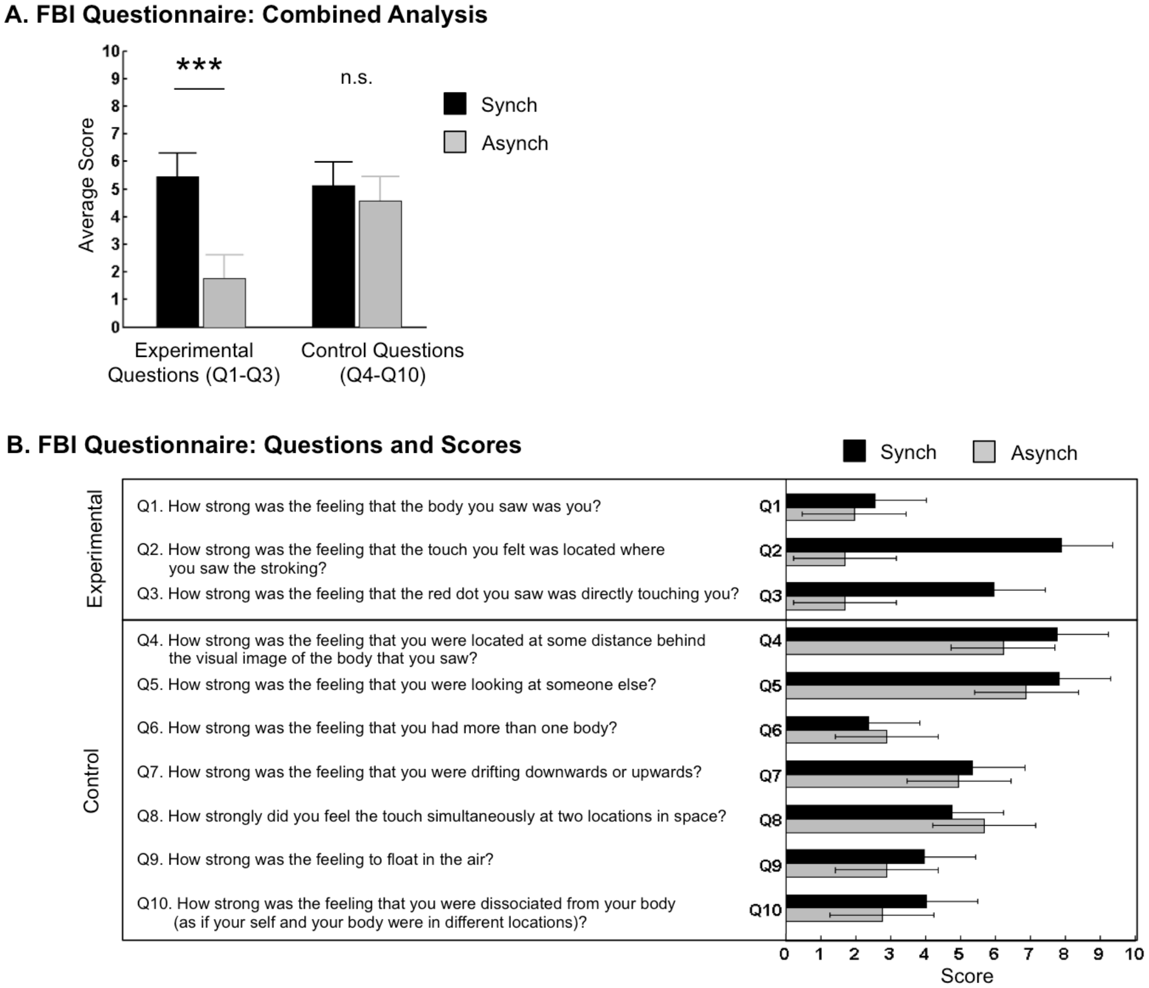

Figure 3 Questionnaire results. (a) Combined analysis comparing critical (Q1-Q3) and control (Q4-Q10) question average scores. Results show visuo-tactile stroking dependent modulation of questionnaire scores for critical questions and no modulation for control questions. (b) Questions of the FBI questionnaire and group-average scores for each questionnaire item for the synchronous and asynchronous Stroking conditions. Error bars represent 95 % confidence intervals.

In order to uncover the meaning of the interaction, post-hoc comparisons using paired-samples *t*-tests were conducted between the synchronous and asynchronous Stroking conditions separately for the experimental (average score of Q1-Q3) and control questions (average score of Q4-Q10). Post-hoc comparisons revealed a significant difference for experimental questions ($t(13) = 8.32$, $p < .001$), reflected an overall higher score for synchronous Stroking (M = 6.45, SE = .50) than for asynchronous Stroking (M = 2.64, SE = .40). By contrast, no difference between synchronous and asynchronous Stroking conditions was found for control questions ($t(13) = 1.55$, $p = .15$). Figure 3b shows question-wise average ratings to the FBI questionnaire. Thus, despite the presentation of different visual gravitational cues, the manipulation of visuo-tactile stroking synchrony reproduced the FBI of previous studies (e.g. Lenggenhager et al., 2007).

Discussion

We initially asked whether dynamic visual gravitational cues could induce changes of subjective 1PP in a more reliable fashion than previously observed in FBI studies. This was confirmed by our results, showing a strong modulation of 1PP ratings by visual gravitational object motion. Furthermore, a positive correlation between *'downward'* 1PP experience and elevated self-location was found. Finally, our manipulation of the synchronicity of visuo-tactile stroking induced the FBI but not further modulated subjective 1PP and self-location. In the following we discuss these results in separate sections for subjective 1PP, self-location, and self-identification.

Subjective 1PP: Dependence on visual gravitational motion

Supine participants (gravity directed toward the participant) more frequently experienced a downward direction of 1PP for away (incongruent with veridical gravity) than for toward (congruent with veridical gravity) virtual ball falling (see

Figure 2c). Thus, subjective 1PP changed trial-by-trial according to the direction of dynamic visual gravitational cues and was not limited to static gravitational cues constantly present during the experiment, i.e. the prone virtual body (visual gravity directed away from the participant) or the vestibular/somatosensory cues signaled by the participant's supine posture (gravity directed toward the participant).

These results are in line with previous FBI studies about visual contributions to subjective 1PP. For instance, static directional conflict between visual (i.e. visual gravity directed away from the participant) and vestibular/somatosensory cues (i.e. veridical gravity directed toward the participant) induced in 30-50 percent of the experimental subjects an experienced downward direction of the 1PP (i.e. congruent with the visual stimulus; Ionta et al., 2011; Pfeiffer et al., 2013). These individual differences were systematically related to visual biases during visual verticality judgments, i.e. down-group participants (i.e. 1PP congruent with the visual stimulus during FBI) showed larger deviations from vertical than up-group participants (i.e. 1PP congruent with vestibular/somatosensory signals) when a visual distractor was presented during subjective visual vertical ratings (Pfeiffer et al., 2013). Another study found that visuo-spatial viewpoint manipulations modulated subjective 1PP (Pfeiffer, Schmutz, et al., 2014). Thus, during constant directional conflict of multisensory gravitational cues, visual signals often determined the experienced direction of 1PP.

Our results extended these observations by showing that dynamic visual gravitational cues induced more pronounced within-subject changes of subjective 1PP (i.e. ~ .4 proportion score difference between away versus toward Visual Gravity) than previously observed (i.e. ~.15 proportion score difference between up-group versus down-group participants; experiment 2 in Pfeiffer et al., 2013). Analogous to visual capture observed in many RHI and FBI studies (Botvinick & Cohen, 1998; Ehrsson, 2007; Lenggenhager et al., 2007), our results provide further evidence for visual capture underlying 1PP experience, reflected in dynamic visual gravitational cues dominating over concurrent static visual, vestibular, and somatosensory gravitational cues. This might seem surprising at first sight, because static multisensory gravitational cues were constantly present throughout the experiment, whereas visual gravitational object motion was presented occasionally during single trials. Likewise, the participants received no specific instructions about the significance of contextual virtual object motion or the relationship to 1PP ratings. Thus, cognitive biases unlikely explain the results observed.

There is solid evidence that gravity contributes to visual perception. For instance, manipulation of gravitational virtual object motion (similar to our study) affected ball-catching task performance and further modulated neural activations in accord with the idea that internal models of gravity automatically and routinely engage in visual motion perception (Indovina et al., 2005; McIntyre et al., 2001; Senot et al., 2005). Similar results were found for visual stimulation-induced self-motion perception (De Saedeleer et al., 2013; Indovina et al., 2013) and the processing of emotional faces (Thompson, 1980). Our results extend these observations to BSC, showing that the visual experience of what 'I' am directed at depends on visual information about gravity, resembling altered own-body and verticality perception during room-tilt illusions in microgravity (Lopez et al., 2008; Tiliket et al., 1996).

What functional mechanisms might explain the visual dominance observed in the present and in previous FBI studies? We speculate that sensory weighting might underlie the perceptual effects observed (for a related idea on vestibular contributions to hand ownership see Ferre, Berlot, & Haggard, 2015). Specifically, in supine posture visual cues might be more relevant than vestibular and somatosensory cues, because vision signals desired or harmful objects in the surrounding environment that might be relevant for survival. In line with this proposal is the fact that OBEs, which are marked by changes of the visual 1PP, most often occur in supine posture (Green, 1968; Kovacs, Raabe, & Greenlee, 2008), where the body does not engaged in postural stabilization. Also, somatosensory and vestibular signals might receive less novel information as compared to upright body position or in motion, thus during multisensory integration visual signals might receive more weight for determining the current spatial model of conscious experience.

More generally, our study focused on visuo-spatial aspects of 1PP. The philosopher Metzinger distinguishes between a ‘weak 1PP’, i.e. a visuo-spatial, geometric, perceptual model, which is necessary but insufficient to explain a minimal sense of selfhood. Further, he defines a ‘strong 1PP’ as the experience of being directed at a goal state via agency, being directed at a perceptual object via attention and being directed at cognitive content, which is both necessary and sufficient for minimal phenomenal selfhood (Blanke & Metzinger, 2009; Metzinger, 2003, 2009, 2013). Clearly, this conceptual distinction is useful and can guide future empirical research on 1PP in the context of motor and cognitive control. Our results however, suggest that a basic sense of self, of being located in and directed at the world is shaped by multisensory input from the body, and more precisely by visual gravitational cues. This, we observed in the absence of goal-directed action, without explicit attention manipulation, during passive observations. Thus, our data more generally support the idea of multisensory contributions of bodily signals to BSC.

Self-location: Association with subjective 1PP

Analysis of self-location data (MBD RTs) revealed no effect of our experimental manipulations as reported previously for comparable conditions. This seems surprising at first, considering that both the OBE of neurological origin and previous FBI studies are marked by changes in self-location (Blanke, Ortigue, Landis, & Seeck, 2002; De Ridder, Van Laere, Dupont, Menovsky, & Van de Heyning, 2007; Lenggenhager et al., 2007). Considering however that the specific measure of self-location used here, i.e. the MBD task, requires a representation of distance to the ground floor, but that the visual stimuli that we used suggested a virtual space reaching far into depth, it is possible that the mental representation of ground floor was affected. In previous studies, which observed a modulation of MBD RTs (Ionta et al., 2011; Lenggenhager et al., 2009), a surface supporting the virtual body was shown and their absence in the present study may have affected the present self-location data. Alternatively, the dynamic visual stimuli may have affected self-location judgments based on the MBD task. More work is required to develop measures of self-location with direct reference to the virtual body and allowing quantifying the effects of gravity on self-location.

However, correlation analysis between self-location and 1PP revealed a positive association between both measures with higher levels of self-location being associated with more frequent *'downward'* 1PP experience. This pattern is very similar to the phenomenology of OBEs, during which subjects typically experience a downward-directed 1PP anchored to an elevated location. This has also been observed during related experimentally-induced states by the FBI in healthy subjects; thus, the experience of *'downward'* 1PP included self-location changes from an elevated location in downward direction, whereas an experienced *'upward'* direction of 1PP showed self-location changes from lowered location in upward direction (Ionta et al., 2011; Pfeiffer et al., 2013). These changes of self-location depended on visuo-tactile stroking synchrony, which induced self-location change toward the seen virtual body location as compared to asynchronous stroking (Lenggenhager et al., 2009; Lenggenhager et al., 2007). Thus self-location depends on multisensory signals and can be experimentally manipulated by visual signals presented in synchrony, but at a spatial distinct location. Thus, also self-location generally depended on visual capture during multisensory conflict, similar to subjective 1PP changes in this study. The association observed between self-location and 1PP in previous studies has stimulated discussion on whether these spatial aspects of BSC might be functionally and neutrally dissociable, or whether they rely on common mechanisms (Serino et al., 2013). Whereas in experimental studies self-location and 1PP often coincide, in neurological patients with OBE, there are instances where auditory self-location and visual 1PP were experienced at distinct spatial locations (De Ridder et al., 2007). Our study design did not directly address the question of whether self-location and 1PP can be separated, however the fact that dynamic visual gravity manipulations strongly affected 1PP and that *'downward'* 1PP ratings correlated with elevated self-location suggest that self-location and 1PP share functional mechanisms.

Self-identification: Dependence on visuo-tactile stroking

Questionnaire results showed that the FBI was overall induced, as reflected in higher average scores for critical questionnaire items (Q1-Q3) for synchronous than for asynchronous visuo-tactile stroking, while control questions (Q4-Q10) were not modulated. These results are in line with numerous previous studies using different variants of the FBI or the RHI (Blanke, 2012; Lenggenhager & Lopez, 2015). Our study extends these results by showing that the presentation of dynamic visual gravitational motion did not abolish the induction of the FBI, suggesting robustness of the stimulation protocol across studies. This further is in line with the observation that the manipulations affecting 1PP, such as visuo-vestibular gravitational conflict or visuo-spatial viewpoint manipulations, did not modulate self-identification, suggesting thus distinct functional mechanisms (for discussion of different functional and neural mechanisms of self-identification and self-location see Blanke, 2012; Serino et al., 2013).

Indeed, one might have anticipated that virtual object motion captures attention away from the virtual body, and when approaching the body represents a potential threat (see e.g. Ehrsson, 2007; Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007) that might have affected the induction of the FBI. Our experimental procedure might have avoided this by having the virtual objects not colliding with the observer's viewpoint or the virtual body, and by presenting the virtual ball falling during relatively short periods relative to the ongoing visuo-tactile stimulation.

By our experimental design, that involved administering the FBI questionnaire after the experiment, we choose to inquire about synchronous and asynchronous stroking conditions irrespectively of the visual gravity condition. This was done both for time-keeping reasons, and because this study aimed at investigating visual gravitational effects on 1PP and self-location. This was based on behavioral and neuroimaging data suggesting functional dissociations of self-identification. Arguably, self-identification is a global feeling of *'mineness'* or ownership for a whole body independent of the specific size and spatial dimensions, whereas self-location and 1PP specifically depend on spatial representations of the self an the external world (see also Blanke & Metzinger, 2009; Metzinger, 2013; Pfeiffer, Serino, et al., 2014).

Outlook

Our study showed that that multisensory gravitational cues contribute to 1PP experience. The direction of visual gravitational motion determined the experienced direction of 1PP, despite conflicting vestibular and somatosensory gravitational signals. One limitation of the present study was that only visual cues, but no vestibular cues, were manipulated. Indeed, a recent study by Macauda et al. (Macauda et al., 2014) found that manipulating visual and vestibular signals about yaw self-motion on a whole-body motion platform affected self-identification with a virtual body (measured by body temperature cooling). With respect to our study on multisensory gravitational contributions of 1PP it would be interesting to simultaneously manipulate the visual and vestibular direction cues to study their relative contributions to 1PP experience. Future studies should also combine the measurement of subjective 1PP ratings, behavioral measures during neuromodulation (e.g. by transcranial magnetic stimulation) in order to establish causal relationships between neural activity and phenomenological aspects of BSC.

Conclusion

Dynamic visual gravitational cues induced congruent changes of the direction of the experienced 1PP during the FBI. Mimicking OBEs of neurological origin, elevated self-location experience was associated to an illusory downward direction of the 1PP. These results suggest that the experience from where 'I' perceive the world depends on visual information about the effect of gravity on environmental objects, which are known to rely on processing of the multisensory vestibular cortex. These results contribute to building an evidence-based theory of how the sense of self relates to neural representations of the body and space.

References

Adler, D., Herbelin, B., Similowski, T., & Blanke, O. (2014). Breathing and sense of self: visuo-respiratory conflicts alter body self-consciousness. *Respiratory Physiology and Neurobiology, 203*, 68-74. doi: 10.1016/j.resp.2014.08.003

Alsmith, A. J., & Longo, M. R. (2014). Where exactly am I? Self-location judgements distribute between head and torso. *Consciousness and Cognition, 24*, 70-74. doi: 10.1016/j.concog.2013.12.005

Angelaki, D. E., & Cullen, K. E. (2008). Vestibular system: the many facets of a multimodal sense. *Annual Review of Neuroscience, 31*, 125-150. doi: 10.1146/annurev.neuro.31.060407.125555

Aspell, J. E., Heydrich, L., Marillier, G., Lavanchy, T., Herbelin, B., & Blanke, O. (2013). Turning Body and Self Inside Out: Visualized Heartbeats Alter Bodily Self-Consciousness and Tactile Perception. *Psychological Science*. doi: 10.1177/0956797613498395

Berthoz, A. (1991). Reference frames for the perception and control of movement. In J. Paillard (Ed.), *Brain and Space* (pp. 81-111). New York: Oxford University Press.

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience, 13*(8), 556-571. doi: 10.1038/nrn3292

Blanke, O., Landis, T., Spinelli, L., & Seeck, M. (2004). Out-of-body experience and autoscopy of neurological origin. *Brain, 127*, 243-258. doi: 10.1093/brain/awh040

Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences, 13*(1), 7-13. doi: 10.1016/j.tics.2008.10.003

Blanke, O., Ortigue, S., Landis, T., & Seeck, M. (2002). Stimulating illusory own-body perceptions. *Nature, 419*(6904), 269-270. doi: 10.1038/419269a

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature, 391*(6669), 756. doi: 10.1038/35784

De Ridder, D., Van Laere, K., Dupont, P., Menovsky, T., & Van de Heyning, P. (2007). Visualizing out-of-body experience in the brain. *The New England Journal of Medicine, 357*(18), 1829-1833. doi: 10.1056/NEJMoa070010

De Saedeleer, C., Vidal, M., Lipshits, M., Bengoetxea, A., Cebolla, A. M., Berthoz, A., . . . McIntyre, J. (2013). Weightlessness alters up/down asymmetries in the perception of self-motion. *Experimental Brain Research, 226*(1), 95-106. doi: 10.1007/s00221-013-3414-7

Deroualle, D., & Lopez, C. (2014). Toward a vestibular contribution to social cognition. *Frontiers in Integrative Neuroscience, 8*, 16. doi: 10.3389/fnint.2014.00016

Duenas, J., Chapuis, D., Pfeiffer, C., Martuzzi, R., Ionta, S., Blanke, O., & Gassert, R. (2011). Neuroscience robotics to investigate multisensory integration and bodily awareness. *Conference Proceedings: IEEE Engineering in Medicine and Biology Society, 2011*, 8348-8352. doi: 10.1109/IEMBS.2011.6092059

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science, 317*(5841), 1048. doi: 10.1126/science.1142175

Ehrsson, H. H. (2012). The concept of body ownership and it's relationship to multisensory integration. In Barry Stein (Ed.), *The New Handbook of Multisensory Processes*. Cambridge MA: MIT Press.

Ehrsson, H. H., Wiech, K., Weiskopf, N., Dolan, R. J., & Passingham, R. E. (2007). Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proceedings of the National Academy of Sciences, 104*(23), 9828-9833. doi: 10.1073/pnas.0610011104

Ferre, E. R., Berlot, E., & Haggard, P. (2015). Vestibular contributions to a right-hemisphere network for bodily awareness: Combining galvanic vestibular stimulation and the "Rubber Hand Illusion". *Neuropsychologia*. doi: 10.1016/j.neuropsychologia.2015.01.032

Green, C. E. (1968). *Out-of-body experiences*. London: Hamish Hamilton.

Haggard, P., Taylor-Clarke, M., & Kennett, S. (2003). Tactile perception, cortical representation and the bodily self. *Current Biology, 13*(5), R170-173.

Heidegger, M. (1962). *Being and time*. New York: Harper and Row.

Indovina, I., Maffei, V., Bosco, G., Zago, M., Macaluso, E., & Lacquaniti, F. (2005). Representation of visual gravitational motion in the human vestibular cortex. *Science, 308*(5720), 416-419. doi: 10.1126/science.1107961

Indovina, I., Maffei, V., Pauwels, K., Macaluso, E., Orban, G. A., & Lacquaniti, F. (2013). Simulated self-motion in a visual gravity field: sensitivity to vertical and horizontal heading in the human brain. *Neuroimage, 71*, 114-124. doi: 10.1016/j.neuroimage.2013.01.005

Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., . . . Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron, 70*(2), 363-374. doi: 10.1016/j.neuron.2011.03.009

Jeannerod, M. (2003). The mechanism of self-recognition in humans. *Behavioural Brain Research, 142*(1-2), 1-15.

Kovacs, G., Raabe, M., & Greenlee, M. W. (2008). Neural correlates of visually induced self-motion illusion in depth. *Cerebral Cortex, 18*(8), 1779-1787. doi: 10.1093/cercor/bhm203

Lenggenhager, B., & Lopez, C. (2015). Vestibular contributions to the sense of body, self, and others. In T. Metzinger & J. M. Windt (Eds.), *Open MIND*. Frankfurt: MIND-Group.

Lenggenhager, B., Mouthon, M., & Blanke, O. (2009). Spatial aspects of bodily self-consciousness. *Consciousness and Cognition, 18*(1), 110-117. doi: 10.1016/j.concog.2008.11.003

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: manipulating bodily self-consciousness. *Science, 317*(5841), 1096-1099. doi: 10.1126/science.1143439

Limanowski, J., & Hecht, H. (2011). Where do we stand on locating the self? *Psychology, 2*(4), 312-317.

Lopez, C., Halje, P., & Blanke, O. (2008). Body ownership and embodiment: vestibular and multisensory mechanisms. *Clinical Neurophysiology, 38*(3), 149-161. doi: 10.1016/j.neucli.2007.12.006

Macauda, G., Bertolini, G., Palla, A., Straumann, D., Brugger, P., & Lenggenhager, B. (2014). Binding body and self in visuo-vestibular conflicts. *The European Journal of Neuroscience*. doi: 10.1111/ejn.12809

McIntyre, J., Zago, M., Berthoz, A., & Lacquaniti, F. (2001). Does the brain model Newton's laws? *Nature Neuroscience, 4*(7), 693-694. doi: 10.1038/89477

Metzinger, T. (2003). *Being no one*. Boston: MIT Press.

Metzinger, T. (2009). Why are out-of-body experiences interesting for philosophers? The theoretical relevance of OBE research. *Cortex, 45*(2), 256-258. doi: 10.1016/j.cortex.2008.09.004

Metzinger, T. (2013). Why are dreams interesting for philosophers? The example of minimal phenomenal selfhood, plus an agenda for future research. *Frontiers in Psychology, 4*, 746. doi: 10.3389/fpsyg.2013.00746

Palluel, E., Aspell, J. E., & Blanke, O. (2011). Leg muscle vibration modulates bodily self-consciousness: integration of proprioceptive, visual, and tactile signals. *Journal of Neurophysiology, 105*(5), 2239-2247. doi: 10.1152/jn.00744.2010

Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: perceptual illusion of body swapping. *Plos One, 3*(12), e3832. doi: 10.1371/journal.pone.0003832

Pfeiffer, C. (2015). Multisensory spatial mechanisms of the bodily self and social cognition-A commentary on Vittorio Gallese and Valentina Cuccio. In T. Metzinger & J. M. Windt (Eds.), *Open MIND*. Frankfurt: MIND-Group.

Pfeiffer, C., Lopez, C., Schmutz, V., Duenas, J. A., Martuzzi, R., & Blanke, O. (2013). Multisensory origin of the subjective first-person perspective: visual, tactile, and vestibular mechanisms. *Plos One, 8*(4), e61751. doi: 10.1371/journal.pone.0061751

Pfeiffer, C., Schmutz, V., & Blanke, O. (2014). Visuospatial viewpoint manipulation during full-body illusion modulates subjective first-person perspective. *Experimental Brain Research*. doi: 10.1007/s00221-014-4080-0

Pfeiffer, C., Serino, A., & Blanke, O. (2014). The vestibular system: A spatial reference for bodily self-conciousness. *Frontiers in Integrative Neuroscience*. doi: 10.3389/fnint.2014.00031

Romano, D., Pfeiffer, C., Maravita, A., & Blanke, O. (2014). Illusory self-identification with an avatar reduces arousal responses to painful stimuli. *Behavioural Brain Research, 261*, 275-281. doi: 10.1016/j.bbr.2013.12.049

Salomon, R., Lim, M., Pfeiffer, C., Gassert, R., & Blanke, O. (2013). Full body illusion is associated with widespread skin temperature reduction. *Frontiers in Behavioral Neuroscience, 7*, 65. doi: 10.3389/fnbeh.2013.00065

Schwabe, Lars, & Blanke, Olaf. (2008). The vestibular component in out-of-body experiences: a computational approach. *Frontiers in Human Neuroscience, 2*, 17-17. doi: 10.3389/neuro.09.017.2008

Sciutti, A., Demougeot, L., Berret, B., Toma, S., Sandini, G., Papaxanthis, C., & Pozzo, T. (2012). Visual gravity influences arm movement planning. *Journal of Neurophysiology, 107*(12), 3433-3445. doi: 10.1152/jn.00420.2011

Senot, P., Zago, M., Lacquaniti, F., & McIntyre, J. (2005). Anticipating the effects of gravity when intercepting moving objects: differentiating up and down based on nonvisual cues. *Journal of Neurophysiology, 94*(6), 4471-4480. doi: 10.1152/jn.00527.2005

Serino, A., Alsmith, A., Costantini, M., Mandrigin, A., Tajadura-Jimenez, A., & Lopez, C. (2013). Bodily ownership and self-location: Components of bodily self-consciousness. *Consciousness and Cognition, 22*(4), 1239-1252. doi: 10.1016/j.concog.2013.08.013

Suzuki, K., Garfinkel, S. N., Critchley, H. D., & Seth, A. K. (2013). Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion. *Neuropsychologia, 51*(13), 2909-2917. doi: 10.1016/j.neuropsychologia.2013.08.014

Thompson, P. (1980). Margaret Thatcher: a new illusion. *Perception, 9*(4), 483-484.

Tiliket, C., Ventre-Dominey, J., Vighetto, A., & Grochowicki, M. (1996). Room tilt illusion. A central otolith dysfunction. *Archives of Neurology, 53*(12), 1259-1264.

Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology, 31*(1), 80-91. doi: 10.1037/0096-1523.31.1.80

Zago, M., McIntyre, J., Senot, P., & Lacquaniti, F. (2008). Internal models and prediction of visual gravitational motion. *Vision Research, 48*(14), 1532-1538. doi: 10.1016/j.visres.2008.04.005

Part B: Brain dynamics of vestibular contribution to multisensory cortical processing

2.4 Study 4: Vestibular effects on somatosensory cortical processing

Vestibular effects on somatosensory cortical processing

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Abstract

In non-human primates, several brain areas have been identified where individual neurons respond to both vestibular and somatosensory stimulation. Behavioral studies in humans found that vestibular stimulation can improve tactile perception. However, little is known about the neural mechanisms of such vestibular-somatosensory interaction in the human brain. To address this issue, we recorded from 16 healthy participants high-density electroencephalography during median nerve electrical stimulations to obtain Somatosensory Evoked Potentials (SEPs). We analyzed SEPs during vestibular stimulation following sudden decelerations from constant-velocity (90°/s and 60°/s) earth-vertical axis yaw rotations and SEPs during a non-vestibular control period. Electrical neuroimaging analysis of the SEPs revealed two distinct temporal effects of vestibular stimulation: An early effect (24-35ms post-stimulus onset) characterized by vestibular suppression of SEP amplitude that depended on rotation velocity and a later effect (97-112ms post-stimulus) that was rotation velocity-independent and characterized by distinct topographical SEP patterns for the vestibular and control condition. Source estimations localized brain activation for the early effect in the right pre- and postcentral gyrus (including primary somatosensory cortex, S1) and for the late effect in bilateral middle temporal gyrus (MTG), further confirmed by region-of-interest analysis. We discuss these distinct spatial and temporal vestibular effects on somatosensory cortical processing related to the functional neuroanatomy of the primate and human vestibular cortex.

Keywords

EEG; somatosensory evoked potentials; vestibular system; multisensory processing; electrical neuroimaging; somatosensory cortex

Introduction

The vestibular system encodes rotational and linear accelerations of the head in space. The subcortical and cortical structures that process vestibular signals contribute to numerous functions including gaze control (Bertolini, Bockisch, Straumann, Zee, & Ramat, 2008), balance (Alsmith & Longo, 2014; Lacour et al., 1997), self- motion perception (Longo, Schuur, Kammers, Tsakiris, & Haggard, 2008; MacNeilage, Turner, & Angelaki, 2010), spatial cognition (Berthoz, 1991) and bodily aspects of self-consciousness (Blanke, Ortigue, Landis, & Seeck, 2002; Lopez, Lenggenhager, & Blanke, 2010). The vestibular system is unique among all sensory systems because no primary vestibular cortical region has been identified. Instead, several distinct, distributed and interconnected cortical regions receive direct and indirect vestibular inputs from the thalamus. Those are in particular the parieto-insular vestibular cortex (PIVC; Chen, DeAngelis, & Angelaki, 2010; Grüsser, Pause, & Schreiter, 1990a, 1990b), the somatosensory cortical regions Brodmann Area 2v (Buttner & Buettner, 1978; Fredrickson, Scheid, Figge, & Kornhuber, 1966), area 3a (Odkvist, Schwarz, Fredrickson, & Hassler, 1974), the ventral intra-parietal area (VIP; Bremmer, Klam, Duhamel, Ben Hamed, & Graf, 2002; Schlack, Hoffmann, & Bremmer, 2002), the middle superior temporal area (MST; Duffy, 1998), as well as other regions (for reviews see Guldin & Grüsser, 1998; Lopez & Blanke, 2011). It has been proposed that the brain regions PIVC, 2v, 3a from an "inner vestibular circuit" because they receive direct vestibular input from the thalamus, process vestibular signals, are reciprocally connected, and have descending connections to brainstem nuclei (Guldin, Akbarian, and Grüsser, 1992; see also Akbarian, Grüsser, & Guldin, 1993, 1994; Guldin et al., 1992; Vogt & Pandya, 1978). Notably, no neuron of this vestibular cortical network responds exclusively to vestibular stimulation. Instead, vestibular cortical neurons respond also to visual, somatosensory, and auditory signals (for review see Lopez & Blanke, 2011).

Vestibular-somatosensory interactions are particularly prominent as revealed by electrophysiological studies in animals as well as by neuroimaging, clinical, and behavioral studies in humans. For instance, electrophysiological studies in animals revealed that regions receiving direct thalamo-cortical vestibular input (i.e. PIVC, 2v, 3a) also process proprioceptive and cutaneous somatosensory signals. For instance, in a single-cell study in monkeys Fredrickson et al. (Fredrickson et al., 1966) described evoked responses from area 2v not only in response to electrical stimulation of the vestibular nerve, but also to electrical stimulation of the median nerve, or simultaneous stimulation of both nerves. In a different study in humans undergoing pre-surgical epilepsy evaluation, direct electro-cortical stimulation of Brodmann area 2v induced vestibular sensations and somatosensory responses at immediately adjacent sites (Blanke, Perrig, Thut, Landis, & Seeck, 2000; Penfield & Jaspers, 1954). Other evidence for vestibular interactions with somatosensory (i.e., including proprioceptive) processing was provided by studies identifying in subdivisions of area 3a neurons responding to both vestibular input and proprioceptive and deep muscle stimulation at the neck or the limbs (Odkvist et al., 1974).

In humans, functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies using caloric (CVS) or galvanic vestibular stimulation (GVS) observed vestibular-somatosensory interactions. An overlap in brain areas responding to both somatosensory and vestibular stimulation was found at the temporo-parietal junction including the medial and posterior insula and the parietal operculum, generally considered to be the human homologue of PIVC (for discussion see Lopez, Blanke, & Mast, 2012; Mazzola et al., 2014; zu Eulenburg, Caspers, Roski, & Eickhoff, 2012). GVS and CVS have also been shown to modulate activity in S1 and secondary somatosensory cortex (S2; Bense, Stephan, Yousry, Brandt, & Dieterich, 2001; Fasold et al., 2002; Lobel, Kleine, Bihan, Leroy-Willig, & Berthoz, 1998). Reversely, somatosensory (i.e. proprioceptive) stimulation by neck-muscle vibration has been shown to activate the posterior insula (i.e. PIVC) and the somatosensory cortex (i.e. putative area 3a and S2; Fasold, Heinau, Trenner, Villringer, & Wenzel, 2008).

Further support for vestibular-somatosensory interactions came from psychophysical and behavioral studies in humans. In patients with hemianaesthesia and tactile extinction, who show somatosensory perception deficits due to damage to the parietal cortex, CVS or GVS can temporarily ameliorate tactile perception (Bottini et al., 2005; Bottini et al., 1995; Kerkhoff et al., 2011; Vallar, Sterzi, Bottini, Cappa, & Rusconi, 1990). A similar improvement of tactile detection thresholds at the hands was found in healthy subjects during passive whole-body rotation, GVS, or CVS (Ferre, Bottini, & Haggard, 2011; Ferre, Day, Bottini, & Haggard, 2013; Ferre, Kaliuzhna, Herbelin, Haggard, & Blanke, 2014), extending human neuroimaging and animal electrophysiology data on vestibular-somatosensory interactions.

Despite the importance of these studies, these human data are difficult to compare with animal electrophysiology, because entirely different stimulations have been used. Moreover, the underlying brain mechanisms of vestibular-somatosensory interactions in humans remain elusive, because artificial vestibular stimulation techniques such as CVS or GVS not only activate vestibular receptors, but also stimulate tactile, nociceptive, thermal, and gustatory receptors and thus result in activation of many other sensory systems and associated cortical regions (Lopez et al., 2012). This methodological limitation renders the interpretation of vestibular-somatosensory interactions observed based on these methods difficult.

Here we aimed to overcome these methodological limitations by using short sequences of constant-velocity passive whole-body yaw rotations about the earth vertical axis through the head that selectively activate the horizontal semicircular canals of the vestibular system (Bertolini et al., 2011; Prsa, Gale, & Blanke, 2012; van Elk & Blanke, 2013). Based on an earlier study on vestibular effects (using CVS) on somatosensory evoked potentials (SEPs; Ferre, Bottini, & Haggard, 2012), we measured SEPs (see below) during the post-rotational period. SEPs were measured during this period because the vestibular system is activated in this post-rotational period for sustained time periods, although the body does not move (Bertolini et al., 2011; Goldberg & Fernandez, 1971). Because vestibular stimulation was ongoing while the body did not move, we were able to exclude effects of somatosensory co-activation that could accompany the onset of vestibular yaw rotation (Lopez et al., 2012). In addition, we recorded SEPs during vestibular stimulation immediately following decelerations from fast (90 °/s) or slow (60 °/s) constant-velocity yaw rotations and during a later control period without any vestibular stimulation leading to a 2 x 2 factorial design with the factors Condition (vestibular stimulation, control) and Rotation Velocity (fast, slow). We performed electrical neuroimaging analysis (Murray, Brunet, & Michel, 2008) and analyzed whether early (Fredrickson et al., 1966; Odkvist et al., 1974) and/or late SEP components (Ferre et al., 2012) were modulated by vestibular stimulation.

Materials and methods

Participants

Sixteen students from the Ecole Polytechnique Fédérale de Lausanne participated (4 females; mean age = 23.8 years, SD = 4.2 years, range = 19-32 years). All participants were right-handed, had normal balance and unimpaired somatosensation, and no history of psychiatric or neurologic disease. Before inclusion in the study each participant gave informed consent and after having participated each participant received a monetary compensation of 60 Swiss Francs. The experimental protocol was approved by the local ethics committee—La Commission d'Ethique de la Recherche Clinique de la Faculté et de Medicine de l'Université de Lausanne—and was conducted in accordance with the Declaration of Helsinki.

Experimental setup

Figure 1a shows a top view of the experimental setup modified from a similar experimental setup used by us in Prsa et al. (Prsa et al., 2012) and van Elk and Blanke (van Elk and Blanke, 2013). Inside of a faraday cage (Industrial Acoustics Company, Niederkrüchten, Germany), used to shield the experimental setup from external electromagnetic, visual, and auditory signals, a motion platform was installed. A racing car seat was firmly mounted at the axial center of a beam platform (2 m diameter) that was fixated on an electrical engine (PCI-7352 servo control). Platform rotations were controlled with 0.1 angular degree precision at 100 Hz sampling rate using Labview software (version 8.6, National Instruments, Austin, TX, US).

The participant sat comfortably in upright posture with safety belts attached. The participant's head was centered above the trunk and the rotation axis. The participant's head was tilted by 30° forward, which because of the anatomical configuration of the semicircular canals aligned participant's horizontal canals with the yaw rotation plane (Day & Fitzpatrick, 2005). A chin- and forehead-rest were used to stabilize participant's head posture during platform rotation. This setup allowed to apply passive whole-body yaw rotations about an earth-vertical axis through the participant's head center and thus of their horizontal canals. Indeed, we cannot exclude inter-subject variability of head position with respect to the rotation axis that may have also led to additional otolith vestibular stimulation. However, these variations were small and random between subjects and can, therefore, be considered negligible.

A screen (Samsung Syncmaster 2233RZ, Seoul, Korea) with 120 Hz refresh rate and 22-inch diameter was positioned at eye-level in front of the participant and was firmly attached to the motion platform. The screen had 29 cm eye-to-screen distance giving rise to 56° vertical and 80° horizontal visual angles. A white fixation cross was presented at the center of the screen on a black background. Apart from the fixation cross the experiment was conducted in complete darkness, such that no visual signal informed participants whether the platform rotated or not. Furthermore, the participant wore earphones (Sennheiser CX 400, Hannover, Germany) on which white noise (individually adjusted between 40-70 dB loudness) was presented to mask auditory cues from platform rotations. A computer was laterally mounted on the platform that was used to control the visual display (i.e. presenting instructions and a fixation cross) and for scheduling median nerve stimulations.

An electrical stimulator (Grass S48, Astor-Med Inc., West Warwick, RI, US) was installed laterally on the beam platform and was used to generate electrical currents for median nerve stimulation. The electrical stimulator was connected to an isolation unit (Grass SIU5), a constant current stimulus unit (Grass CCU1), and to two disk electrodes (GRASS F-E5GH) attached to the skin at participant's the left wrist above the median nerve. Before the experiment participant's skin at the left wrist was cleaned with alcohol and the electrodes were attached with conducting gel in order to reduce skin resistance. Electrode placement was individually adjusted, such that electrical stimulations induced clearly visible thumb abductions.

Experimental design, procedure and stimuli

The experiment was conducted using a 2 x 2 x 2 full-factorial experimental design with the within-subjects factors Condition (vestibular stimulation, control), Rotation Velocity (fast, slow), and Rotation Direction (clockwise, counterclockwise). Note that with this study we aimed to investigate effects of vestibular stimulation and rotation velocity on somatosensory cortical processing (using a 2 x 2 experimental design). Therefore, we randomized the rotation direction from trial to trial in order to reduce anticipation effects (Bertolini et al., 2008; Prsa et al., 2012; van Elk & Blanke, 2013). After all experimental data was recorded and processed (see below) we conducted initial statistical analysis to evaluate effects of Rotation Direction on our data. We thus performed all analyses mentioned in the Analysis section using the three-factorial design. Because the results of these analyses showed no main effects or interactions with the Rotation Direction factor, it assured us that our experimental results were unlikely to be affected by having used different rotation directions. Therefore, in the following we present the experimental setup and analysis for a pooled experimental design with 2 (Condition: vestibular stimulation, control) x 2 (Rotation Velocity: fast, slow) experimental factors.

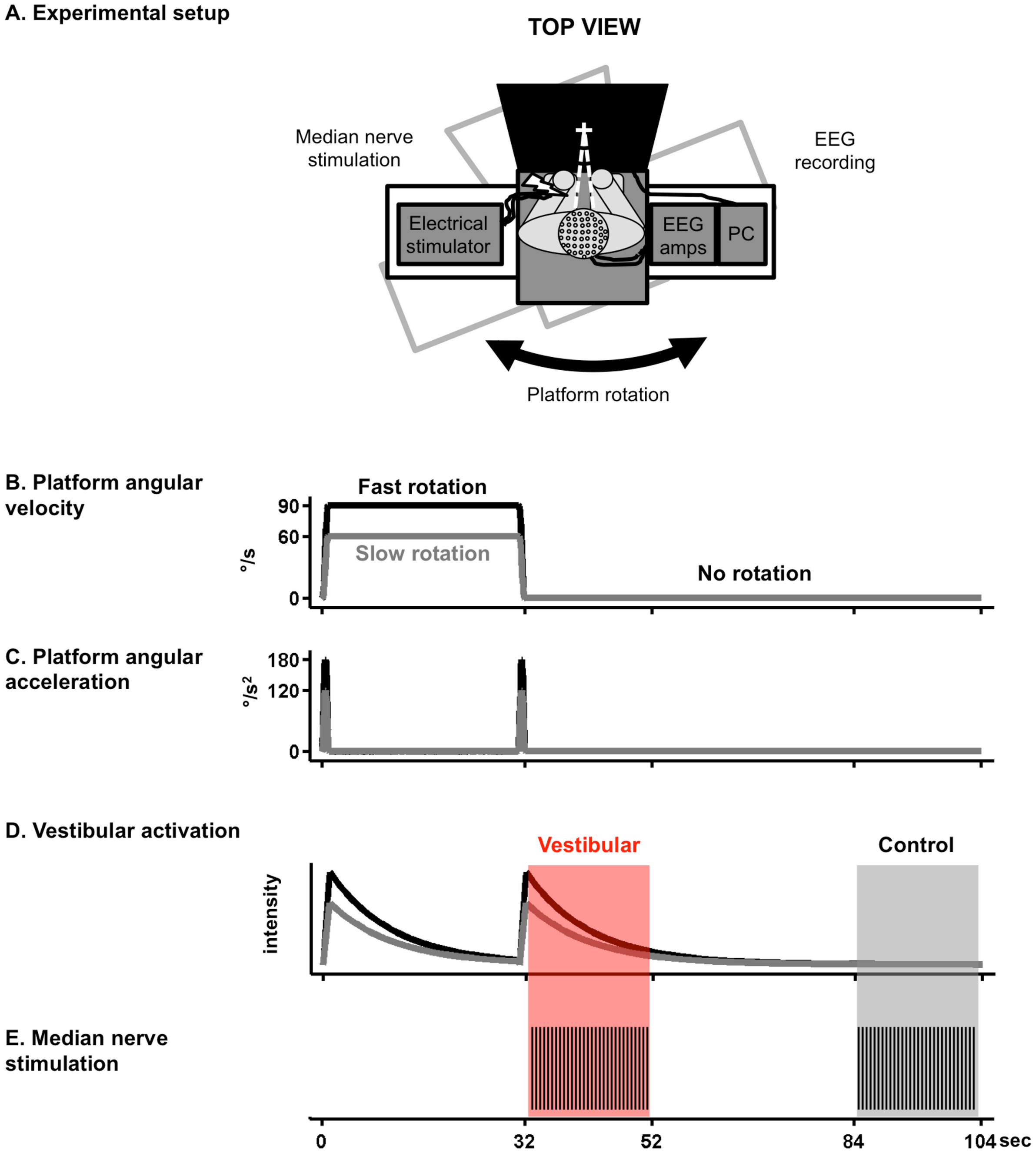

Figure 1 Experimental setup and procedures. (a) Experimental setup viewed from the top showing the participant (image center) equipped with electroencephalography (EEG) recording electrodes (black dots) and median nerve stimulation electrodes (white flash). The participant was seated at the center of an angular motion platform (white rectangle) on which an electrical stimulator, EEG amplifiers (amps), stimulation computer (PC) and a computer screen (black trapezoid) were firmly attached. The participant fixated a central cross (white) presented on the computer screen throughout the experiment. (b-c). Platform motion kinematics during a rotation trial over time began with a 30-sec step of 90°/s (fast rotation; in black) or 60°/s (slow rotation; in gray) constant-velocity rotation followed by 72 sec of no rotation (no rotation; in black). (d). Hypothetical vestibular activation over time following sudden platform accelerations (0 sec) and decelerations (32 sec) related to fast (black) and slow (gray) constant-velocity rotation. Critical EEG data recording periods for the vestibular stimulation condition (in red) and a later non-vestibular control condition (in gray).

Figure 1 (continued) (e) Median nerve stimulations (black vertical lines) over time were presented in trains of 20-sec stimulation at 4 Hz (fixed 250-ms inter-stimulus interval) following platform decelerations during vestibular stimulation (in red) and later during the control period (in gray).

Figure 1b-e show the general sequence of events of an experimental rotation trial. Steps of same-duration (30 sec) constant-velocity rotation were used in order to induce post-rotational vestibular stimulation, i.e. that is vestibular stimulation while the body (and the motion platform) did not move (Bertolini et al., 2011). Initially, the motion platform was static (0°/s velocity) and accelerated during 1 sec to maximum velocity (90°/s in the fast condition, 60°/s in the slow condition) with a cosine-smoothed acceleration profile (Gaussian shape) reaching at 0.5 sec after rotation onset the maximum acceleration (180°/s^2 in the fast condition, 120°/s^2 in the slow condition). This was followed by constant rotation at maximum velocity (i.e. 90°/s or 60°/s according to the experimental condition) during 30 sec. It is known that during constant-velocity rotation, horizontal canal activity habituates over time following an approximately exponential decay (see Figure 1d; a more detailed model can be found in (Bertolini et al., 2011; Raphan, Matsuo, & Cohen, 1979)). Thus, at the end of the constant-velocity rotation there was a minimal amount of vestibular stimulation. This was followed by rapid platform deceleration from maximum velocity to no-motion (0°/s) during 1 sec by means of a cosine-smoothed profile that was the reverse of the profile used for platform accelerations. Such rapid changes in velocity (i.e. accelerations) are known to induce vestibular stimulation in the absence of body motion. In fact, electrophysiological recordings and mathematical models of the vestibular system strongly suggest that using such angular rotation profiles, peri-rotational (following platform acceleration) and post-rotational (following platform deceleration) vestibular stimulation are almost identical and have a time constant of approximately 15 sec with total durations between 10-50 sec (Bertolini et al., 2011; Goldberg & Fernandez, 1971; Laurens & Angelaki, 2011).

SEPs were acquired during two time intervals following a rotation. First, immediately following the sudden platform decelerations, i.e. during post-rotational vestibular stimulation, 80 subsequent median nerve stimulations were presented at 4-Hz frequency with a fixed 250-ms inter-stimulus interval for 20 s (vestibular stimulation condition). Triggers associated with the onset of median nerve stimulation were sent in parallel to the EEG computer for post-hoc analysis of SEPs. Electrical median nerve stimulations were transcutaneous constant-current square wave pulses of 0.15 ms duration and 8-12 mA intensity (i.e. 110% of motor threshold). This was followed by a resting period during which no stimulus was presented and vestibular stimulation habituated. Immediately after that, i.e. during no vestibular stimulation, another series of 80 median nerve stimulations with identical parameters from the first stimulation interval was presented during 20 s (control condition). The total duration of a rotation trial was thus 104 s. Each participant was presented with 12 rotation trials in 2 separate sessions of 6 subsequent rotation trials. A total of 1,920 median nerve stimulations were presented to each participant with 480 stimulations per experimental condition.

In addition to SEP recordings following constant-velocity rotation reported in this manuscript, participants also volunteered for another recording session of SEPs during transient (2 sec) rotations in yaw. Unfortunately, these other data could not further be reported, because SEPs were too strongly contaminated by artifacts from rotational accelerations and decelerations.

EEG acquisition and preprocessing

Continuous EEG was acquired at 2048 Hz with a 64-channel Biosemi ActiveTwo system (Biosemi, Amsterdam, Netherlands, www.biosemi.nl) referenced to a vertex CMS-DRL ground, which serves as a feedback loop driving the average potential across all channels as close as possible to the amplifier zero. Bipolar horizontal EOG was recorded from electrodes attached to the outer canthi and bipolar vertical EOG was recorded from electrodes above and below the right eye. During EEG preparation for each participant the experimenters took care to keep DC offsets below 50 mV for all channels (i.e. for active EEG recording systems DC offset serves as evaluation criterion similar to channel impedances for passive montages). All data was recorded with an online 0.2 - 100 Hz band-pass filter

Offline data pre-processing was conducted using EEGLAB software (http://sccn.ucsd.edu/eeglab/), the FASTER toolbox (http://www.mee.tcd.ie/neuraleng/Research/Faster) implemented in MATLAB software (MathWorks, version R13, http://www.mathworks.ch) and customized MATLAB scripts. In order to correct for slight temporal imprecisions (i.e. on average <5 ms) between computer-scheduled triggers and actual median nerve stimulus onsets, which might have affected the interpretation of early short-latency SEP components, we initially identified in the continuous EEG data for each scheduled event (i.e. stimulation trigger) the related electrical stimulation artifact onset, which became clearly apparent as a short-latency (<5 ms) and high amplitude (>50 mV) electrical artifact in all scalp channels (e.g. see brief waveform deflection by the electrical artifact immediately after stimulus onset in Figure 2b-c and in Figure 5). After having in this way identified stimulation artifact onset latencies we assigned those empirically identified latencies to the stimulus onset triggers further used for evoked potential analysis. Then, continuous raw data was high-pass filtered (1 Hz cut-off, ripple: 0.05 dB, attenuation: 80 dB, transition bandwidth: 0.5 Hz) and notch filtered (48-52 Hz, bandwidth: 3 dB, ripple: 0.05 dB, attenuation: 80 dB, transition bandwidth: 1 Hz) using second-order Butterworth filters. The data was recalculated against the average reference. Artifact electrodes from each participant were identified using a signal variance criterion (3 z-score Hurst exponent). On average, 6 (SD = 3) electrodes were interpolated for each participant using spherical splines (Nolan, Whelan, & Reilly, 2010).

EEG epochs from -50 to 200 ms relative to stimulus onset (i.e., median nerve stimulation) were extracted for each participant and each condition. A pre-stimulus baseline correction from -50 to 0 ms pre-stimulus onset was applied. Physiological artifacts (e.g. muscular artifacts, eye blinks) were removed by semi-automated procedures including independent component analysis (ICA; 63 components, k-value:

25, kurtosis rejection criterion: 3 z-scores), application of a ±100 μV bipolar vertical EOG signal rejection criterion, and by visual inspection. The average number (and standard deviation) of accepted epochs per experimental condition was 415 (63) epochs for vestibular stimulation-fast rotation velocity, 365 (55) epochs for vestibular stimulation-slow rotation velocity, 414 (65) epochs for control-fast rotation velocity and 364 (58) epochs for control-slow rotation velocity. Statistical analysis using a repeated-measures ANOVA on the accepted number of epochs per condition for the participant sample showed no significant main effects or interactions related to the Condition and Rotation Velocity factors (all p-values > 0.1). Thus, we can exclude that our results were due to differences in signal to noise ratio across conditions. For each subject condition-wise averages were calculated (i.e. SEPs) and subjected to further statistical analysis.

EEG analyses and source estimation

Global electric field analyses and source estimation of the SEPs were conducted using CARTOOL software (Functional Brain Mapping Laboratory, Geneva, Switzerland http://www.brainmapping.unige.ch/cartool.htm), STEN software (Laboratory of Investigative Neurophysiology, Lausanne, Switzerland, http://www.unil.ch/line/Sten), RAGU software (http://www.thomaskoenig.ch/Ragu_pkg.exe), and customized scripts in MATLAB software.

Global electrical field analyses. Two reference electrode-independent analyses of the global electrical field strength (global field power, GFP; Murray et al., 2008) and topographical changes (global map dissimilarity, GMD; König and Melie-Garcia, 2010) were conducted. GFP is calculated as the square root of the mean of the squared values recorded at each electrode (versus average reference) and represents the spatial standard deviation of the potentials at all electrodes and at each time point (Lehmann & Skrandies, 1980). This measure indicates the global strength of the response, regardless of its topographic distribution. Changes in GFP were statistically analyzed at each time point from -50 to 200 ms relative to stimulus onset using repeated-measures ANOVAs with the within-subjects factors Condition (vestibular stimulation, control) and Rotation Velocity (fast, slow) with an alpha threshold of $p < 0.05$. Because it is well documented that median nerve SEPs consist of early short-latency potentials (<50 ms post-stimulus) and later long-latency potentials (Allison, McCarthy, Wood, Darcey, et al., 1989; Allison, McCarthy, Wood, Williamson, & Spencer, 1989) we applied a two-step procedure to control for temporal autocorrelation of our statistical effects. First, we applied a 20 contiguous time-point (>10 ms) temporal criterion for the persistence of differential statistical effects for the entire -50 ms to 200 ms peri-stimulus interval (Guthrie & Buchwald, 1991). In order to further increase sensitivity to detect statistical difference for short-latency potentials we applied in a second step a more liberal 8 contiguous time-point (> 4 ms) criterion for the 0-50 ms post-stimulus interval.

Topographic modulations across conditions were identified using global map dissimilarity (GMD; König & Melie-Garcia, 2010), which is calculated as the root mean square of the differences between two strength-normalized vectors (i.e. instantaneous voltage potentials across the electrode montage). The GMD values between four experimental conditions (i.e. factorial combinations of Condition and Rotation Velocity experimental factors) were then compared at each time point with an empirical distribution derived from a bootstrapping procedure (5000 permutations per data point) based on randomly reassigning each participant's data to either one of the four experimental conditions. GMD is independent of the chosen reference electrode and is insensitive to pure amplitude modulations across conditions, i.e. that is GMD modulations are orthogonal to GFP modulations. This analysis is useful in terms of the neurophysiologic interpretability, following the assumption that topographic changes necessarily reflect differences in the configuration of the brain's underlying active generators (Lehmann & Skrandies, 1980). Correction for temporal autocorrelation was performed according to the same procedure used for the GFP analysis, i.e. using first a 20 contiguous time-point criterion for the -50 ms to 200 ms peri-stimulus interval and a more liberal 8 contiguous time-point temporal criterion for the 0-50 ms post-stimulus interval.

Topographical pattern differences, as revealed by GMD analysis, were further evaluated by topographical segmentation and individual subject fitting analyses. Topographical segmentation analysis is based on hierarchical clustering using an atomize and agglomerate approach and was performed over contiguous time periods where significant GMD differences were observed to identify the pattern of predominating topographies (template maps) in the cumulative group averaged data (Murray et al., 2008). This serves as hypothesis generation tool that is subsequently statistically evaluated using single-subject data. Thus, differences in the pattern of maps observed during topographical segmentation between conditions in the group-average data were tested by calculating the spatial correlation between these maps from the group-average data and each time-point of single-subject (referred to as individual subject fitting). This allows extracting for each topographical map the duration of presence (in ms) in the time interval of interest (i.e. 16 subjects x 2 factor levels for Condition x 2 factor levels for Rotation Velocity). Statistical analysis of map presence was performed using a 2 x 2 repeated measures ANOVA for each topographical map.

Source estimations. To identify the intracranial sources generating the GFP and GMD effects, over distinct time periods, we estimated the electrical activity in the brain using a distributed linear inverse solution applying the local autoregressive average regularization approach (LAURA), comprising biophysical laws as constraints (Grave de Peralta Menendez, Gonzalez Andino, Lantz, Michel, & Landis, 2001; Michel et al., 2004). For the lead field matrix calculation, we applied the spherical model with anatomical constraints (SMAC) method (Spinelli, Andino, Lantz, Seeck, & Michel, 2000), which transforms a standard anatomical MRI to the best-fitting sphere using homogeneous transformation operators. It then determines a regular grid of 3005 solution points in the gray matter of this spherical MRI and computes the lead filed matrix using the known analytical solution for a spherical head model with three shells of different conductivities as defined by (Ary, Klein, & Fender, 1981). The results of the global electrical field analysis described above provide an estimation of the two distinct time intervals for conducting separate source estimations.

Statistical analyses of source estimations were performed by first averaging separately for each of the distinct time intervals the SEP data across the period of interest to generate a single data point for each participant and condition. The inverse solutions (16 subjects x 2 factor levels for Condition x 2 factor levels for Rotation Velocity) were then estimated. Regions-of-interest (ROIs) were defined by first averaging condition-wise across subjects the inverse solutions and identifying the peak-activation solution points. Then, the direct neighbors (non-diagonal) were added resulting in 7 contiguous solution points ROI for each experimental condition. Then, for each experimental condition and each subject and activity was extracted from the ROI and averaged across solution points. Statistical analysis on ROI activity data (16 subjects x 2 factor levels for Condition x 2 factor levels for Rotation Velocity) using 2 x 2 repeated measures ANOVAs was performed. The results of the source estimations were rendered on the Montreal Neurologic Institute’s average brain with the Talairach and Tournoux (Talairach and Tournoux, 1988) coordinates.

Results

In order to allow comparison to previous SEP studies, classical single-electrode waveform analysis of SEPs was performed that showed typical SEP waveforms for all four experimental conditions (see Figure 2a, Figure 5 and Appendix). However, all interpretations of experimental results in this study are based on global electrical field analysis and source estimation based on the waveforms recorded in all scalp electrodes.

Global electrical field analysis

GFP analysis revealed a significant Condition x Rotation Velocity interaction in the 24-35 ms post-stimulus interval ($F(1,15) = 9.03$, $p < 0.01$, $\eta^2 = 0.38$). Figure 2f shows the average GFP amplitude for the 24-35 ms post-stimulus interval as a function of experimental condition. Over the 24-35 ms post-stimulus period the GFP amplitude was lower during vestibular stimulation following fast Rotation Velocity as compared to slow Rotation Velocity (paired-samples *t*-test: $t(15) = -2.07$, $p < 0.05$) and the control condition (vestibular stimulation-fast versus control-fast: $t(15) = -2.05$, $p < 0.05$). There was no difference in GFP between the two control conditions (control-fast versus control-slow: $t(15) = 0.68$, $p = 0.52$). These results reveal a vestibular modulation of the SEP global electrical field strength that was rotation velocity-dependent and only followed our fast constant-velocity rotation. The GFP analysis in the same time period showed no main effect of Condition ($F(1,15) = 0.34$, $p = 0.57$, $\eta^2 = 0.02$), no main effect of Rotation Velocity ($F(1,15) = 0.94$, $p = 0.35$, $\eta^2 = 0.06$). No main effects of Condition or Rotation Velocity were observed in the remaining time periods.

Next we performed time-wise topographical pattern analysis. This GMD analysis revealed no statistically significant main effects or interactions in the early periods (<50 ms; *p*-values > 0.1), including the 24-35 ms post-stimulus period that had revealed vestibular effects on GFP. This suggests that early stages of somatosensory cortical processing show no changes in topographical pattern (i.e. no changes in underlying neural generators) related to our experimental manipulations. For later time periods (>50 ms), the same GMD analysis revealed a Condition main effect in the 97-112 ms post-stimulus interval (*p*-values < 0.05). To further analyze this topographical difference we performed a topographical segmentation analysis of the group average SEPs for this period in each condition. This analysis revealed two different SEP maps in the 97-112 ms post-stimulus interval (Figure 2g) that were confirmed by statistical analysis of these two topographical maps (individual subject fitting) in the 97-112 ms period. This analysis revealed that Map_V accounted more for the vestibular stimulation

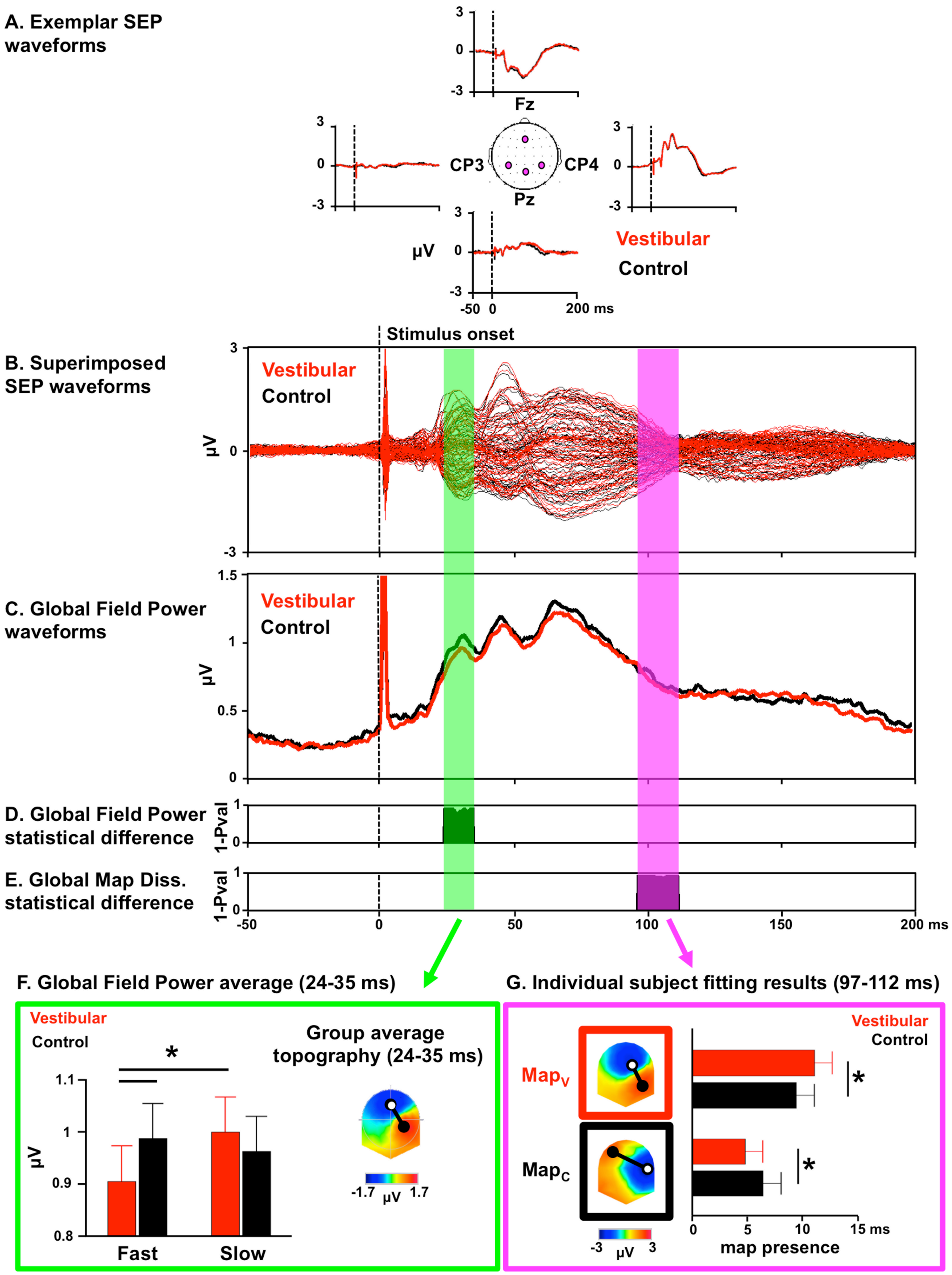

Figure 2 Electrical neuroimaging results. (a) Group averaged (n=16) somatosensory evoked potentials (SEPs) to left median nerve stimulations for exemplar electrodes (Fz, CP3, CP4, Pz) in the vestibular stimulation (in red) and non-vestibular control (in black) conditions. (b) Superimposed SEP waveforms across all electrodes per experimental condition and periods of significant global field power (GFP, green) and topographical pattern modulations (GMD, purple). (c) Global field power waveforms across time in the vestibular stimulation (red) and

Figure 2 (continued) control (black) conditions. (d) Time-wise repeated measures ANOVA results on the GFP (1 - p-value shown) are shown for time periods meeting at least 8 contiguous data points. This analysis revealed a significant Condition x Rotation Velocity interaction ($p<0.05$; in green) at 24-35 ms. (e) The Global Map Dissimilarity (GMD) analysis revealed a significant Condition main effect ($p<0.05$ and >20 contiguous data points; in purple) at 97-112 ms. (f) Barplot shows global field power average over the 24-35 ms period as a function of experimental condition and post-hoc t-test significant differences marked (*, $p< 0.05$). Group-average topography (nasion upward) of the potential field across conditions over the 24-35 ms period with positive (black circle) and negative (white circle) peak electrodes. (g) Segmentation analysis over the 97-112 ms period revealed two topographical maps (nasion upward, peak electrodes highlighted by circles) that differentially accounted for the vestibular stimulation (MapV; in red) and the non-vestibular control (MapC; in black) conditions. This was revealed by individual subject fitting analysis consisting of individual condition-wise extraction of map presence during the 97-112 ms period and subsequent repeated measures ANOVAs showing for each map significant main effects of Condition (* $p<0.05$).

conditions ($p < 0.05$) and Map$_C$ accounted more for the control conditions ($p < 0.05$; Figure 2g). Apart from this Condition main effect in the 97-112 ms post-stimulus period, the GMD analysis revealed no Rotation Velocity main effect and no Condition x Rotation interaction (p-values > 0.05; results not shown).

To summarize, the electrical neuroimaging analysis revealed two distinct time periods during which vestibular stimulation modulated SEPs. We found a rotation velocity-dependent vestibular modulation of SEPs during an early period (i.e. 24-35 ms) without any changes in the underlying neural generators and a rotation velocity-independent vestibular modulation of SEPs during a later period (i.e. 97-112 ms) that revealed the presence of different neural generators for vestibular stimulation versus control conditions (i.e. without any significant global electrical field strength modulations).

Source estimation analysis

LAURA distributed source estimations of SEPs were calculated over the 24-35 ms post-stimulus period where GFP analysis revealed modulations of the global electrical field strength (i.e. Condition x Rotation Velocity interaction) and over the 97-112 ms

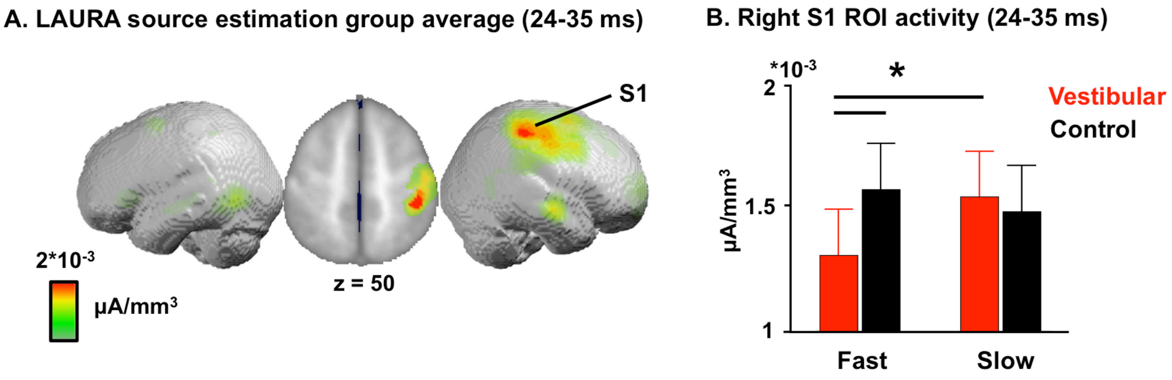

Figure 3 Source estimation results in the 24-35 ms period. (a) Group-average source estimation shows a prominent right hemisphere activation cluster in the precentral, postcentral, and posterior parietal regions including the primary somatosensory cortex (S1). (b) Region-of-interest analysis of right S1 activity with a repeated measures ANOVA showed a significant Condition x Rotation Velocity interaction (p<0.05; post-hoc t-test significant results highlighted: * p<0.05).

post-stimulus period where GMD analysis revealed topographical pattern differences (i.e. Condition main effect).

Source estimation for the early 24-35 ms post-stimulus showed, on the group average and consistently across conditions, a prominent activation cluster in the right hemisphere including the precentral gyrus, the postcentral gyrus and the inferior parietal lobe (Figure 3a). In line with intracranially recorded median nerve SEPs (Allison, McCarthy, Wood, Darcey, et al., 1989; Allison, McCarthy, Wood, Williamson, et al., 1989) the inverse solution showed the same condition-wise activation maxima in the postcentral gyrus [45; -33; 50 mm, BA40] using the coordinate system of Talairach and Tournoux (Talairach and Tournoux, 1988). Additional analysis of ROI activity (i.e. centered on the group-average activation maxima) revealed a Condition x Rotation Velocity interaction ($F(1,15) = 5.37$, $p < 0.05$, $\eta^2 = 0.26$; Figure 3b), reflecting weaker ROI activity during vestibular stimulation following fast rotation as compared to the control condition following fast rotation (paired-samples *t*-test: $t(15) = -1.95$, $p < 0.05$) or vestibular stimulation following slow constant-velocity rotation (vestibular stimulation-fast versus vestibular stimulation-slow: $t(15) = -1.95$, $p < 0.05$). No statistical difference of ROI activity was

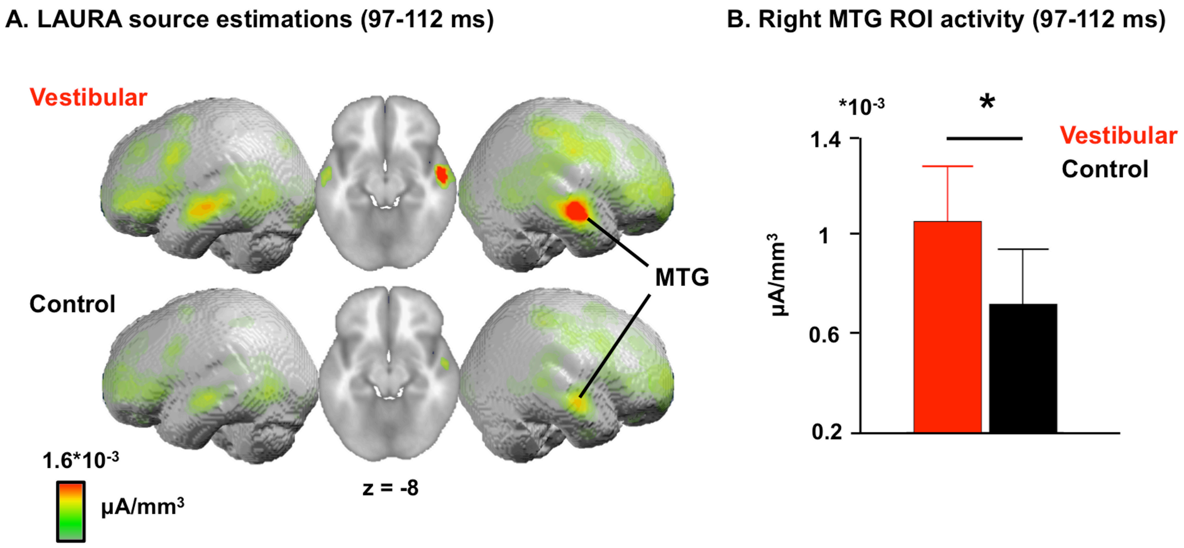

Figure 4 Source estimation results in the 97-112 ms period. (a) Source estimation for the vestibular stimulation (in red) and non-vestibular control (in black) conditions show prominent activations in bilateral middle temporal gyrus (MTG), moreover right precentral, postcentral and posterior parietal and frontal activation. (b) Region-of-interest analysis of right MTG activity in the 97-112 ms period with repeated measures ANOVA revealed a Condition main effect (* p<0.05).

observed between the control conditions (control-fast versus control-slow: $t(15) = 0.71$, $p = 0.49$).

Source estimations over the later 97-112 ms post-stimulus interval showed three prominent activation clusters across conditions, i.e. consisting of a cluster in the right hemisphere pre- and postcentral gyrus, and two clusters in the right- and left middle temporal gyrus (MTG) expanding to the superior temporal gyrus (Figure 4a). Common global activation maxima in all experimental conditions were centered in the right MTG [58; -7; -8 mm, BA21; Talairach coordinates). ROI analysis of the right MTG activity confirmed a Condition main effect ($F(1,15) = 6.66$, $p < 0.05$, $\eta^2 = 0.31$) reflecting higher activity during vestibular stimulation than during control conditions (paired samples *t*-test: $t(15) = 2.16$, $p < 0.05$; Figure 4b). Compatible with the results of topographical pattern analysis, no main effect of Rotation Velocity and no Condition x Rotation Velocity interaction were found (*F*-values < 1).

In sum, source estimation and ROI analysis results were consistent with results from the global electrical field analyses, showing in the early period (i.e. 24-35 ms post-stimulus) a rotation-velocity dependent decrease of activity in the postcentral gyrus and in the later period (i.e. 97-112 ms post-stimulus) an increase of right MTG activity that was found in all vestibular stimulation conditions. Together, these results reveal temporally, functionally, and topographically distinct vestibular modulations of SEPs.

Discussion

Using physiological vestibular stimulation and concurrent median nerve SEP recordings we observed two distinct vestibular effects on somatosensory cortical processing, one early effect (i.e. 24-35 ms post-stimulus period) and a later effect (i.e. 97-112 ms post-stimulus period). In the following we will discuss both effects separately with respect to previous data from animal electrophysiology and human neuroimaging data.

Early rotation velocity-dependent vestibular modulation of SEPs

The early vestibular effect on SEPs was rotation velocity-dependent and consisted of a suppression of the SEP global electrical field strength (GFP) following fast (90°/s), but not slow (60°/s) constant-velocity rotation. This early suppression of SEP amplitude was not associated with topographical pattern difference (GMD) of the SEP reflecting the presence of statistically indistinguishable neural generators in all conditions (Bernasconi et al., 2011). In line with these findings, our source estimations for the brain activity in the early period revealed consistently across all conditions a single right-hemispheric activation cluster with a peak activation in the postcentral gyrus expanding to adjacent precentral and more posterior parietal regions, likely reflecting activation of S1. This postcentral activation with this timing was expected based numerous previous SEP studies using surface EEG recordings in humans (Aspell, Palluel, & Blanke, 2012; Schubert, Blankenburg, Lemm, Villringer, & Curio, 2006; Waberski, Gobbele, Darvas, Schmitz, & Buchner, 2002). The postcentral location of this source estimation is also compatible with intracranial recordings in humans revealing the first cortical response to median nerve stimulation in the 20-35 ms post-stimulus period in S1, likely Brodmann areas 3b and 1 (Allison, McCarthy, Wood, Darcey, et al., 1989). Tracer studies in monkeys showed that both regions are reciprocally connected with area 2v and area 3a (i.e. both are subregions of S1), which are both part of the inner circuit of the vestibular cortex (Guldin et al., 1992). Moreover, area 2v and area 3a receive rotational vestibular input and respond to median nerve somatosensory signals similar to those applied in our study (Fredrickson et al., 1966; Odkvist et al., 1974). Given the spatial resolution of EEG we cannot distinguish whether vestibular stimulation during the early effect modulated activation only in areas 3b/1, only areas 3a/2v, or in all areas jointly (Michel et al., 2004). However, comparing our data with those obtained by electrophysiological recordings from monkey area 2v (Fredrickson et al., 1966) we speculate that the present vestibular-somatosensory interaction during the early period originates from activation of the human homologue of area 2v (Blanke et al., 2000). This is suggested by results observed by Fredrickson et al. (Fredrickson et al., 1966) who found in monkeys that concurrent electrical stimulation of the vestibular and the median nerve suppressed activity in area 2v (compared to the sum of both unimodal stimulations). Moreover, repeated or delayed stimulation drastically decreased the response of vestibular neurons in area 2v. In line with these data we found a vestibular suppression of SEPs when median nerve stimulation immediately followed sudden platform decelerations, but not during later non-vestibular control period. The present SEP suppression in humans is further substantiated by findings in fMRI showing a decreased BOLD signal in S1 following GVS stimulation (Bense et al., 2001). However, because GVS also induces nociceptive somatosensory activation, our results extend the findings by Bense et al. (Bense et al., 2001), because the vestibular effects observed in our study were not confounded by the unavoidable somatosensory co-activations when using GVS (Lopez et al., 2012).

What neural mechanisms cause vestibular suppression of somatosensory activity evoked by electrical median nerve stimulation? Considering earlier observations in animals that bimodal vestibular-somatosensory neurons are activated by vestibular stimulation (Bremmer et al., 2002; Fredrickson et al., 1966; Grüsser et al., 1990a), it is likely that in our experiment the vestibular stimulation following constant-velocity rotation induced ongoing activation of vestibular-somatosensory neurons in S1 including the human homologues of area 2v (and area 3a) and thereby caused a relatively weaker S1 response to intermittent median nerve stimulations, resembling S1 monkey data that showed that median nerve stimulation when associated with vestibular nerve stimulation resulted in smaller response amplitude when compared to median nerve stimulation without vestibular nerve stimulation (Fredrickson et al., 1966). Findings from other human S1 studies are compatible with such S1 activity decreases. For instance, Katayama and Rothwell (Katayama and Rothwell, 2007) found that theta-burst transcranial magnetic stimulation (TMS) over S1 and concurrent or delayed median nerve stimulation induced an SEP amplitude decrease in the 25-35 ms post-stimulus period. Similar results were found by Legon et al. (2014) who used transcranial ultrasound stimulation of S1 and found a decrease of concurrently recorded median nerve SEPs in the 27-35 ms and a later 50-70 ms post-stimulus period. Thus, stimulation of S1 can result in an SEP amplitude decrease in a time period that is highly similar to the present early SEP effect. Such modulations of S1 activity by TMS (for review see Thut and Pascual-Leone, 2010) and ultrasound stimulation (Legon et al., 2014) were also shown to improve tactile detection, resembling behavioral data showing that passive whole-body yaw rotation, as used in our experiment, improved tactile detection (Ferre et al., 2014). Although more work is necessary requiring combined electrophysiological and perceptual studies, we suggest that - based on these data - yaw rotation suppresses S1 activation (most likely area 2v) and that this decreased activation facilitates the processing of ascending somatosensory signals. We further speculate that vestibular suppression of S1 activation might functionally serve to suppress processing of (predicted) somatosensory inputs arising from self-generated movements of head and body, compatible with S1 suppression during self-generated hand movements (i.e. Blanke et al., 2002; Chalmers, 1996; see Blanke & Mohr, 2005 for review). Alternatively, the present early SEP effects may relate to intersensory inhibition during vestibular stimulation that permits shifting the weight from one modality to another (Brandt et al., 2002; Brandt, Strupp, & Dieterich, 2014; Deutschlander et al., 2002).

Another result of our study was that the early SEP modulation was rotation velocity-dependent. SEP amplitudes were significantly decreased following fast (90°/s) but not slow (60 °/s) constant-velocity rotation. Although the slow and fast rotation velocities used in our study are known to both activate the semicircular canals (Goldberg & Fernandez, 1971) and to induce self-motion perception above perceptual threshold (Grabherr, Nicoucar, Mast, & Merfeld, 2008), vestibular stimulation differs in intensity and duration between both rotation profiles. Thus, by increasing head motion velocity the firing rates of neurons in the vestibular nucleus and the vestibular cortex has been reported to increase (Cheyne & Girard, 2009; Goldberg & Fernandez, 1971; Grüsser et al., 1990a) and post-rotational nystagmus as well as self-motion sensations are more pronounced during higher rotation speeds (Bertolini et al., 2011). Accordingly, the fast yaw rotations used in our study likely induced stronger post-rotational vestibular stimulation than the slow yaw rotations, associated with stronger suppression of the SEPs. Second, is known that the duration of post-rotational vestibular stimulation is variable (Laurens & Angelaki, 2011; Laurens, Meng, & Angelaki, 2013; Raphan et al., 1979) and may have been shorter during slow vestibular constant-velocity rotation, and thus leading to weaker SEP suppression. Notably, our experimental design focused on well-controlled timing of SEP recordings that allowed for the same number of median nerve stimulations between conditions in order to obtain comparable signal-to-noise ratios (for discussion see Cruccu et al., 2008). As such, we cannot distinguish whether vestibular intensity or duration or both contributed to our results, which will be an important issue to address in future studies.

Late rotation velocity-independent vestibular modulation of SEPs

Our results also showed that vestibular stimulation modulated SEPs during a later 97-112 ms post-stimulus period. However, this finding differed from the early effect. In fact, we observed differences in the topographical pattern (i.e. GMD) between vestibular stimulation versus a control condition but found that the global electrical field (i.e. GFP) had similar strength across conditions (Bernasconi et al., 2011). This suggests that different neural generators were activated in vestibular stimulation conditions versus control conditions, independent of whether subjects received fast (90°/s) or slow (60°/s) constant-velocity rotations. We found two distinct topographical maps, one accounting more for SEPs during vestibular stimulation and another accounting more for the non-vestibular control condition. Source estimations over this time period localized the likely neural generators in the bilateral middle temporal gyri (MTG) and in the right postcentral gyrus (likely S1). Across the whole brain, peak activation for this time period was located in the right MTG region where further region of interest analysis showed increased activation when the SEP followed vestibular stimulation.

The latency of this later effect (97-112 ms) suggests involvement of the S2 (i.e. in association or separately from S1) as previously reported by surface (Cullen, 2012; Waberski et al., 2002) and intracranial recordings (Allison, McCarthy, Wood, Williamson, et al., 1989; Cullen, 2012; Garcia-Larrea, Lukaszewicz, & Mauguiere, 1995). The human S2 region is located in the upper wall of the sylvian sulcus, thus somewhat more superior to the MTG region as revealed by our source estimation. However, bearing in mind the limited spatial resolution of EEG, the limited number of electrodes (i.e. 64 electrodes) and the fact that a previous SEP study often attributed MTG sources in this time period to functional processing in S2 (Waberski et al., 2002), and intracranial human data (Allison, McCarthy, Wood, Williamson, et al., 1989), it is likely that the late effect also relates to neural generators in S2. Compatible with such a proposal we note further that S2 processes cutaneous and proprioceptive somatosensory signals (Burton & Sinclair, 1991; Disbrow, Litinas, Recanzone, Padberg, & Krubitzer, 2003) and has reciprocal connections with both S1 and PIVC (Guldin et al., 1992; Guldin & Grüsser, 1998). Although S2 does not belong to the vestibular cortex (Guldin & Grüsser, 1998), in humans neck-muscle vibration may activate S2 and the medial-posterior insula, i.e. the human homologue of PIVC (Bottini et al., 2001; Fasold et al., 2008). Our data also extend recent observations by

Ferre et al. (Ferre et al., 2012) who reported vestibular modulation (CVS) of SEPs and linked these effects to putative S2. These authors found that SEPs recorded several minutes after CVS showed increased amplitudes of a slowly rising SEP component at about 80 ms when compared to SEPs recorded before CVS. Ferre et al. (Ferre et al. 2012) have argued that such activity changes in the somatosensory cortex may underlie the perceptual effects of vestibular stimulation on tactile processing in neurological patients and healthy subjects (Bottini et al., 2005; Bottini et al., 1995; Ferre, Bottini, et al., 2011; Ferre et al., 2013; Ferre et al., 2014; Kerkhoff et al., 2011; Vallar et al., 1990). The present SEP data suggest that such effects may be caused by vestibular-somatosensory mechanisms in S1, S2, or both that may also be effective at different time periods.

In addition, the fact that our source estimations showed activation in the MTG may indicate vestibular effects on multisensory stimulus attention. Previously, fMRI and EEG studies related processing in area MTG to attention capture (bottom-up) due to changing patterns of somatosensory, visual, or auditory stimulation (Downar, Crawley, Mikulis, & Davis, 2000) or due to sudden visual stimulation during ongoing auditory processing (Desimone & Duncan, 1995). MTG processing was also related to selective spatial attention (top-down) to body parts to which somatosensory stimulation was subsequently applied (Waberski et al., 2002). Thus, the MTG activation in our study may be related to anticipatory attention modulation by the ongoing vestibular stimulation regarding upcoming somatosensory stimulation, similar to visual modulation of ongoing auditory processing in MTG observed by Desimone and Duncan (Desimone and Duncan, 1995). This is in line with previous behavioral studies showing that ongoing vestibular stimulation can improve tactile detection (Ferre et al., 2013; Ferre et al., 2014; Ferre, Sedda, Gandola, & Bottini, 2011).

Conclusion

Whereas in earlier studies in humans, vestibular-somatosensory effects were based on artificial vestibular stimulations co-activating thermal, nociceptive, or acoustic receptors (Lopez et al., 2012) and using low temporal resolution neuroimaging techniques (Bense et al., 2001; Bottini et al., 1994), our combination of a motion platform with high-density EEG allowed us to measure brain responses to yaw rotations. We observed two distinct vestibular effects on somatosensory cortical processing induced in humans by yaw rotations. One early process in S1 (including vestibular areas 2v and 3a) was susceptible to rotation velocity differences and associated with suppression of SEP global electrical field amplitude; and one late process showed topographical differences of the evoked brain activation that involved enhanced activation in the right MTG/S2 region by vestibular stimulation independent of the rotation velocity. These results show that vestibular signals differently affect multiple processing stages of the hierarchically organized somatosensory cortical processing. For instance by modulating somatosensory input due to self-motion during the early period (Downar et al., 2000; Ehrsson, 2007) and later by enhancing the processing of higher-level somatosensory stimulus features (Ferre, Bottini, et al., 2011; Legon et al., 2014). We speculate that the first process serves to rapidly integrate vestibular signals with concurrent somatosensory inputs in S1 and that the second process reflects higher-level aspects of vestibular-somatosensory perception in MTG and/or S2. These electrophysiological results in humans are highly similar to observations in animal studies that several distinct and interconnected cortical areas host neurons that respond to vestibular and somatosensory simulation (Fredrickson et al., 1966; Grüsser et al., 1990b; Odkvist et al., 1974).

Appendix

Complementary SEP waveform analysis. A positive peak-activation channel was identified by calculating the group-average condition-average SEP over the 20-35 ms post-stimulus period, i.e. when the first cortical response to median nerve stimulation was expected (Allison, McCarthy, Wood, Darcey, et al., 1989). As expected, this revealed the CP4 channel in a posterior location on the right hemisphere approximately above the primary somatosensory cortex (Figure 5). Following the method by Schubert et al. (Schubert et al., 2006), positive and negative waveform voltage peaks were identified in the group-average time-wise data in the CP4 channel. All classical SEP components were observed, which depending on their polarity (i.e. N for negative, P for positive) and latency were denoted as N20, P26, N35, P45, N60, P80, and N120 components. Condition-wise component peak-latencies and peak-to-peak amplitudes were extracted by automated search within non-overlapping time-windows around the group average component peak. Search windows (in brackets) for each component were: N20 (18-22 ms), P26 (23-29 ms), N35 (30-40 ms), P45 (40-50 ms), N60 (50-70 ms), P80 (70-90 ms), N120 (100-140 ms). Statistical analysis using separate 2 x 2 repeated measures ANOVAs was performed for peak-latencies and peak-to-peak amplitudes per SEP component (alpha threshold of 0.05, uncorrected for

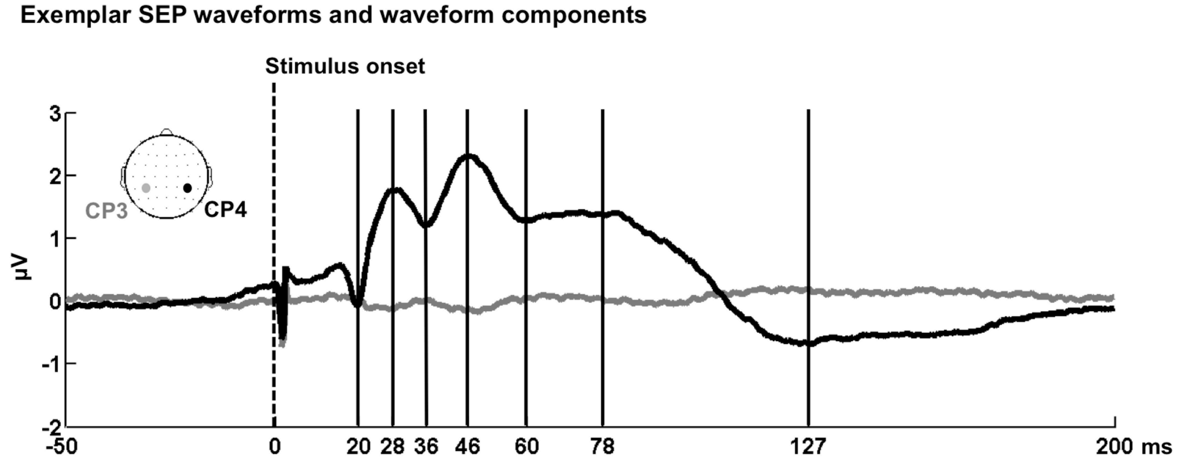

Figure 5 Group-average SEP waveforms to left median nerve stimulations (Stimulus onset) shown for the contralateral right-hemispheric CP4 (black trace) and the ipsilateral left-hemispheric CP3 (gray trace) electrodes. Vertical bars represent latencies of CP4 waveform peaks and troughs used for complementary SEP component analysis.

multiple comparisons). As expected, the group-average SEPs showed highest amplitudes for the N20 component in fronto-parietal EEG channels that were placed contralateral to the stimulated median nerve (Figure 2a). Figure 5 illustrates typical SEP components that were observed at electrode CP4 over the contralateral somatosensory cortex (Cruccu et al., 2008). For comparison, the same SEP at electrode CP3 (over ipsilateral somatosensory cortex) showed no such SEP components. Table 1 summarizes the latencies and amplitudes for the different SEP components recorded at scalp electrode CP4. Visual inspection of component-wise group-average latencies and peak-to-peak amplitudes showed that standard median nerve SEPs were evoked during vestibular stimulation and control conditions. Component-wise statistical analysis by separate 2 x 2 ANOVAs for these SEP component latencies and amplitudes showed not significant differences (all *p*-values > 0.05).

Table 1 *SEP waveform component summarized (CP4 electrode).*

	Latency							Amplitude					
	N20 Lat. ms	**P28 Lat. ms**	**N35 Lat. ms**	**P45 Lat. ms**	**N60 Lat. ms**	**P80 Lat. ms**	**N120 Lat. ms**	**N20-P28 Amp. mV**	**P28-N35 Amp. mV**	**N35-P45 Amp. mV**	**P45-N60 Amp. mV**	**N60-P80 Amp. mV**	**P80-N120 Amp. mV**
Vest.	19.9	27.4	35.4	45.8	60.4	78.2	127.9	2.6	1.6	2.3	2.1	1.1	3.0
Fast	(1.6)	(2.8)	(2.8)	(5.1)	(6.2)	(7.4)	(10.4)	(1.6)	(1.0)	(1.2)	(1.2)	(0.8)	(1.1)
Vest.	19.7	27.3	35.6	46.3	61.0	77.0	127.3	2.7	1.6	2.2	2.1	1.1	3.2
Slow	(1.7)	(3.0)	(3.3)	(5.5)	(6.1)	(6.5)	(10.9)	(1.7)	(1.0)	(1.2)	(1.2)	(0.9)	(1.2)
Ctrl.	19.7	26.8	35.5	46.3	61.6	78.2	127.1	2.6	1.6	2.2	2.0	1.2	3.1
Fast	(1.3)	(3.1)	(3.2)	(5.8)	(6.8)	(6.4)	(11.6)	(1.5)	(0.9)	(1.2)	(1.2)	(0.7)	(1.4)
Ctrl.	19.6	27.8	36.0	45.9	59.2	76.8	127.1	2.6	1.6	2.1	2.1	1.1	3.1
Slow	(1.6)	(2.9)	(3.0)	(5.4)	(5.3)	(6.0)	(11.7)	(1.7)	(0.9)	(1.1)	(1.2)	(0.8)	(1.2)

Values are means; numbers in brackets are standard deviations; SEP, somatosensory evoked potential; Vest., Vestibular Stimulation; Ctrl., Control

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References

Akbarian, S., Grüsser, O. J., & Guldin, W. O. (1993). Corticofugal projections to the vestibular nuclei in squirrel monkeys: further evidence of multiple cortical vestibular fields. *The Journal of Comparative Neurology, 332*(1), 89-104. doi: 10.1002/cne.903320107

Akbarian, S., Grüsser, O. J., & Guldin, W. O. (1994). Corticofugal connections between the cerebral cortex and brainstem vestibular nuclei in the macaque monkey. *The Journal of Comparative Neurology, 339*(3), 421-437. doi: 10.1002/cne.903390309

Allison, T., McCarthy, G., Wood, C. C., Darcey, T. M., Spencer, D. D., & Williamson, P. D. (1989). Human cortical potentials evoked by stimulation of the median nerve. I. Cytoarchitectonic areas generating short-latency activity. *Journal of Neurophysiology, 62*(3), 694-710.

Allison, T., McCarthy, G., Wood, C. C., Williamson, P. D., & Spencer, D. D. (1989). Human cortical potentials evoked by stimulation of the median nerve. II. Cytoarchitectonic areas generating long-latency activity. *Journal of Neurophysiology, 62*(3), 711-722.

Alsmith, A. J., & Longo, M. R. (2014). Where exactly am I? Self-location judgements distribute between head and torso. *Consciousness and Cognition, 24*, 70-74. doi: 10.1016/j.concog.2013.12.005

Ary, J. P., Klein, S. A., & Fender, D. H. (1981). Location of sources of evoked scalp potentials: corrections for skull and scalp thicknesses. *IEEE Transactions on Biomedical Engineering, 28*(6), 447-452. doi: 10.1109/TBME.1981.324817

Aspell, J. E., Palluel, E., & Blanke, O. (2012). Early and late activity in somatosensory cortex reflects changes in bodily self-consciousness: an evoked potential study. *Neuroscience, 216*, 110-122. doi: 10.1016/j.neuroscience.2012.04.039

Bense, S., Stephan, T., Yousry, T. A., Brandt, T., & Dieterich, M. (2001). Multisensory cortical signal increases and decreases during vestibular galvanic stimulation (fMRI). *Journal of Neurophysiology, 85*(2), 886-899.

Bernasconi, F., De Lucia, M., Tzovara, A., Manuel, A. L., Murray, M. M., & Spierer, L. (2011). Noise in brain activity engenders perception and influences discrimination sensitivity. *The Journal of Neuroscience, 31*(49), 17971-17981. doi: 10.1523/JNEUROSCI.3715-11.2011

Berthoz, A. (1991). Reference frames for the perception and control of movement. In J. Paillard (Ed.), *Brain and Space* (pp. 81-111). New York: Oxford University Press.

Bertolini, G., Bockisch, C. J., Straumann, D., Zee, D. S., & Ramat, S. (2008). Estimating the time constant of pitch rVOR by separation of otoliths and semicircular canals contributions. *Conference Proceedings: IEEE Engineering in Medicine and Biology Society, 2008*, 1060-1063. doi: 10.1109/IEMBS.2008.4649342

Bertolini, G., Ramat, S., Laurens, J., Bockisch, C. J., Marti, S., Straumann, D., & Palla, A. (2011). Velocity storage contribution to vestibular self-motion perception in healthy human subjects. *Journal of Neurophysiology, 105*(1), 209-223. doi: 10.1152/jn.00154.2010

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience, 13*(8), 556-571. doi: 10.1038/nrn3292

Blanke, O., Landis, T., Spinelli, L., & Seeck, M. (2004). Out-of-body experience and autoscopy of neurological origin. *Brain, 127*, 243-258. doi: 10.1093/brain/awh040

Blanke, O., & Mohr, C. (2005). Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin Implications for neurocognitive mechanisms of corporeal awareness and self-consciousness. *Brain Research Reviews 50*(1), 184-199. doi: 10.1016/j.brainresrev.2005.05.008

Blanke, O., Ortigue, S., Landis, T., & Seeck, M. (2002). Stimulating illusory own-body perceptions. *Nature, 419*(6904), 269-270. doi: 10.1038/419269a

Blanke, O., Perrig, S., Thut, G., Landis, T., & Seeck, M. (2000). Simple and complex vestibular responses induced by electrical cortical stimulation of the parietal cortex in humans. *Journal of Neurology, Neurosurgery, and Psychiatry, 69*(4), 553-556.

Bottini, G., Karnath, H. O., Vallar, G., Sterzi, R., Frith, C. D., Frackowiak, R. S., & Paulesu, E. (2001). Cerebral representations for egocentric space: Functional-anatomical evidence from caloric vestibular stimulation and neck vibration. *Brain, 124*(Pt 6), 1182-1196.

Bottini, G., Paulesu, E., Gandola, M., Loffredo, S., Scarpa, P., Sterzi, R., . . . Vallar, G. (2005). Left caloric vestibular stimulation ameliorates right hemianesthesia. *Neurology, 65*(8), 1278-1283. doi: 10.1212/01.wnl.0000182398.14088.e8

Bottini, G., Paulesu, E., Sterzi, R., Warburton, E., Wise, R. J., Vallar, G., . . . Frith, C. D. (1995). Modulation of conscious experience by peripheral sensory stimuli. *Nature, 376*(6543), 778-781. doi: 10.1038/376778a0

Bottini, G., Sterzi, R., Paulesu, E., Vallar, G., Cappa, S. F., Erminio, F., . . . Frackowiak, R. S. (1994). Identification of the central vestibular projections in man: a positron emission tomography activation study. *Experimental Brain Research, 99*(1), 164-169.

Brandt, T., Glasauer, S., Stephan, T., Bense, S., Yousry, T. A., Deutschlander, A., & Dieterich, M. (2002). Visual-vestibular and visuovisual cortical interaction: new insights from fMRI and pet. *Annals of the New York Academy of Sciences, 956*, 230-241.

Brandt, T., Strupp, M., & Dieterich, M. (2014). Towards a concept of disorders of "higher vestibular function". *Frontiers in Integregrative Neuroscience, 8*, 47. doi: 10.3389/fnint.2014.00047

Bremmer, F., Klam, F., Duhamel, J. R., Ben Hamed, S., & Graf, W. (2002). Visual-vestibular interactive responses in the macaque ventral intraparietal area (VIP). *The European Journal of Neuroscience, 16*(8), 1569-1586.

Burton, H., & Sinclair, R. J. (1991). Second somatosensory cortical area in macaque monkeys: 2. Neuronal responses to punctate vibrotactile stimulation of glabrous skin on the hand. *Brain Research, 538*(1), 127-135.

Buttner, U., & Buettner, U. W. (1978). Parietal cortex (2v) neuronal activity in the alert monkey during natural vestibular and optokinetic stimulation. *Brain Research, 153*(2), 392-397.

Chalmers, D. J. (1996). *The conscious mind: In search of a fundamental theory*. Oxford: Oxford University Press.

Chen, A., DeAngelis, G. C., & Angelaki, D. E. (2010). Macaque parieto-insular vestibular cortex: responses to self-motion and optic flow. *The Journal of Neuroscience, 30*(8), 3022-3042. doi: 10.1523/JNEUROSCI.4029-09.2010

Cheyne, J. A., & Girard, T. A. (2009). The body unbound: vestibular-motor hallucinations and out-of-body experiences. *Cortex, 45*(2), 201-215. doi: 10.1016/j.cortex.2007.05.002

Cruccu, G., Aminoff, M. J., Curio, G., Guerit, J. M., Kakigi, R., Mauguiere, F., . . . Garcia-Larrea, L. (2008). Recommendations for the clinical use of somatosensory-evoked potentials. *Clinical Neurophysiology, 119*(8), 1705-1719. doi: 10.1016/j.clinph.2008.03.016

Cullen, K. E. (2012). The vestibular system: multimodal integration and encoding of self-motion for motor control. *Trends in Neurosciences, 35*(3), 185-196. doi: 10.1016/j.tins.2011.12.001

Day, B. L., & Fitzpatrick, R. C. (2005). Virtual head rotation reveals a process of route reconstruction from human vestibular signals. *The Journal of Physiology, 567*(Pt 2), 591-597. doi: 10.1113/jphysiol.2005.092544

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Reviews in Neuroscience, 18*, 193-222. doi: 10.1146/annurev.ne.18.030195.001205

Deutschlander, A., Bense, S., Stephan, T., Schwaiger, M., Brandt, T., & Dieterich, M. (2002). Sensory system interactions during simultaneous vestibular and visual stimulation in PET. *Human Brain Mapping, 16*(2), 92-103.

Disbrow, E., Litinas, E., Recanzone, G. H., Padberg, J., & Krubitzer, L. (2003). Cortical connections of the second somatosensory area and the parietal ventral area in macaque monkeys. *The Journal of Comparative Neurology, 462*(4), 382-399. doi: 10.1002/cne.10731

Downar, J., Crawley, A. P., Mikulis, D. J., & Davis, K. D. (2000). A multimodal cortical network for the detection of changes in the sensory environment. *Nature Neuroscience, 3*(3), 277-283. doi: 10.1038/72991

Duffy, C. J. (1998). MST neurons respond to optic flow and translational movement. *Journal of neurophysiology, 80*(4), 1816-1827.

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science, 317*(5841), 1048. doi: 10.1126/science.1142175

Fasold, O., Heinau, J., Trenner, M. U., Villringer, A., & Wenzel, R. (2008). Proprioceptive head posture-related processing in human polysensory cortical areas. *Neuroimage, 40*(3), 1232-1242. doi: 10.1016/j.neuroimage.2007.12.060

Fasold, O., von Brevern, M., Kuhberg, M., Ploner, C. J., Villringer, A., Lempert, T., & Wenzel, R. (2002). Human vestibular cortex as identified with caloric stimulation in functional magnetic resonance imaging. *Neuroimage, 17*(3), 1384-1393.

Ferre, E. R., Bottini, G., & Haggard, P. (2011). Vestibular modulation of somatosensory perception. *The European Journal of Neuroscience, 34*(8), 1337-1344. doi: 10.1111/j.1460-9568.2011.07859.x

Ferre, E. R., Bottini, G., & Haggard, P. (2012). Vestibular inputs modulate somatosensory cortical processing. *Brain Structure and Function, 217*(4), 859-864. doi: 10.1007/s00429-012-0404-7

Ferre, E. R., Day, B. L., Bottini, G., & Haggard, P. (2013). How the vestibular system interacts with somatosensory perception: a sham-controlled study with galvanic vestibular stimulation. *Neuroscience Letters, 550*, 35-40. doi: 10.1016/j.neulet.2013.06.046

Ferre, E. R., Kaliuzhna, M., Herbelin, B., Haggard, P., & Blanke, O. (2014). Vestibular-somatosensory interactions: effects of passive whole-body rotation on somatosensory detection. *Plos One, 9*(1), e86379. doi: 10.1371/journal.pone.0086379

Ferre, E. R., Sedda, A., Gandola, M., & Bottini, G. (2011). How the vestibular system modulates tactile perception in normal subjects: a behavioural and physiological study. *Experimental Brain Research, 208*(1), 29-38. doi: 10.1007/s00221-010-2450-9

Fredrickson, J. M., Scheid, P., Figge, U., & Kornhuber, H. H. (1966). Vestibular nerve projection to the cerebral cortex of the rhesus monkey. *Experimental Brain Research, 2*(4), 318-327.

Garcia-Larrea, L., Lukaszewicz, A. C., & Mauguiere, F. (1995). Somatosensory responses during selective spatial attention: The N120-to-N140 transition. *Psychophysiology, 32*(6), 526-537.

Goldberg, J. M., & Fernandez, C. (1971). Physiology of peripheral neurons innervating semicircular canals of the squirrel monkey. I. Resting discharge and response to constant angular accelerations. *J Neurophysiol, 34*(4), 635-660.

Grabherr, L., Nicoucar, K., Mast, F. W., & Merfeld, D. M. (2008). Vestibular thresholds for yaw rotation about an earth-vertical axis as a function of frequency. *Experimental Brain Research, 186*(4), 677-681. doi: 10.1007/s00221-008-1350-8

Grave de Peralta Menendez, R., Gonzalez Andino, S., Lantz, G., Michel, C. M., & Landis, T. (2001). Noninvasive localization of electromagnetic epileptic activity. I. Method descriptions and simulations. *Brain Topography, 14*(2), 131-137.

Grüsser, O. J., Pause, M., & Schreiter, U. (1990a). Localization and responses of neurones in the parieto-insular vestibular cortex of awake monkeys (Macaca fascicularis). *The Journal of Physiology, 430*, 537-557.

Grüsser, O. J., Pause, M., & Schreiter, U. (1990b). Vestibular neurones in the parieto-insular cortex of monkeys (Macaca fascicularis): visual and neck receptor responses. *The Journal of Physiology, 430*, 559-583.

Guldin, W. O., Akbarian, S., & Grüsser, O. J. (1992). Cortico-cortical connections and cytoarchitectonics of the primate vestibular cortex: a study in squirrel monkeys (Saimiri sciureus). *The Journal of Comparative Neurology, 326*(3), 375-401. doi: 10.1002/cne.903260306

Guldin, W. O., & Grüsser, O. J. (1998). Is there a vestibular cortex? *Trends in Neurosciences, 21*(6), 254-259.

Guthrie, D., & Buchwald, J. S. (1991). Significance testing of difference potentials. *Psychophysiology, 28*(2), 240-244.

Katayama, T., & Rothwell, J. C. (2007). Modulation of somatosensory evoked potentials using transcranial magnetic intermittent theta burst stimulation. *Clin Neurophysiol, 118*(11), 2506-2511. doi: 10.1016/j.clinph.2007.08.011

Kerkhoff, G., Hildebrandt, H., Reinhart, S., Kardinal, M., Dimova, V., & Utz, K. S. (2011). A long-lasting improvement of tactile extinction after galvanic vestibular stimulation: two Sham-stimulation controlled case studies. *Neuropsychologia, 49*(2), 186-195. doi: 10.1016/j.neuropsychologia.2010.11.014

Koenig, T., & Melie-Garcia, L. (2010). A method to determine the presence of averaged event-related fields using randomization tests. *Brain Topography, 23*(3), 233-242. doi: 10.1007/s10548-010-0142-1

Lacour, M., Barthelemy, J., Borel, L., Magnan, J., Xerri, C., Chays, A., & Ouaknine, M. (1997). Sensory strategies in human postural control before and after unilateral vestibular neurotomy. *Experimental Brain Research, 115*(2), 300-310.

Laurens, J., & Angelaki, D. E. (2011). The functional significance of velocity storage and its dependence on gravity. *Experimental Brain Research, 210*(3-4), 407-422. doi: 10.1007/s00221-011-2568-4

Laurens, J., Meng, H., & Angelaki, D. E. (2013). Computation of linear acceleration through an internal model in the macaque cerebellum. *Nature Neuroscience, 16*(11), 1701-1708. doi: 10.1038/nn.3530

Legon, W., Sato, T. F., Opitz, A., Mueller, J., Barbour, A., Williams, A., & Tyler, W. J. (2014). Transcranial focused ultrasound modulates the activity of primary somatosensory cortex in humans. *Nature Neuroscience, 17*(2), 322-329. doi: 10.1038/nn.3620

Lehmann, D., & Skrandies, W. (1980). Reference-free identification of components of checkerboard-evoked multichannel potential fields. *Electroencephalography and Clinical Neurophysiology, 48*(6), 609-621.

Lobel, E., Kleine, J. F., Bihan, D. L., Leroy-Willig, A., & Berthoz, A. (1998). Functional MRI of galvanic vestibular stimulation. *Journal of Neurophysiology, 80*(5), 2699-2709.

Longo, M. R., Schuur, F., Kammers, M. P., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition, 107*(3), 978-998. doi: 10.1016/j.cognition.2007.12.004

Lopez, C., & Blanke, O. (2011). The thalamocortical vestibular system in animals and humans. *Brain Research Reviews, 67*(1-2), 119-146. doi: 10.1016/j.brainresrev.2010.12.002

Lopez, C., Blanke, O., & Mast, F. W. (2012). The human vestibular cortex revealed by coordinate-based activation likelihood estimation meta-analysis. *Neuroscience, 212*, 159-179. doi: 10.1016/j.neuroscience.2012.03.028

Lopez, C., Lenggenhager, B., & Blanke, O. (2010). How vestibular stimulation interacts with illusory hand ownership. *Consciousness and Cognition, 19*(1), 33-47. doi: 10.1016/j.concog.2009.12.003

MacNeilage, P. R., Turner, A. H., & Angelaki, D. E. (2010). Canal-otolith interactions and detection thresholds of linear and angular components during curved-path self-motion. *Journal of Neurophysiology, 104*(2), 765-773. doi: 10.1152/jn.01067.2009

Mazzola, L., Lopez, C., Faillenot, I., Chouchou, F., Mauguiere, F., & Isnard, J. (2014). Vestibular responses to direct stimulation of the human insular cortex. *Ann Neurol.* doi: 10.1002/ana.24252

Michel, C. M., Murray, M. M., Lantz, G., Gonzalez, S., Spinelli, L., & Grave de Peralta, R. (2004). EEG source imaging. *Clinical Neurophysiology, 115*(10), 2195-2222. doi: 10.1016/j.clinph.2004.06.001

Murray, M. M., Brunet, D., & Michel, C. M. (2008). Topographic ERP analyses: a step-by-step tutorial review. *Brain Topography, 20*(4), 249-264. doi: 10.1007/s10548-008-0054-5

Nolan, H., Whelan, R., & Reilly, R. B. (2010). FASTER: Fully Automated Statistical Thresholding for EEG artifact Rejection. *Journal of Neuroscience Methods, 192*(1), 152-162. doi: 10.1016/j.jneumeth.2010.07.015

Odkvist, L. M., Schwarz, D. W., Fredrickson, J. M., & Hassler, R. (1974). Projection of the vestibular nerve to the area 3a arm field in the squirrel monkey (saimiri sciureus). *Experimental Brain Research, 21*(1), 97-105.

Penfield, W., & Jaspers, H. (1954). *Epilepsy and the functional anatomy of the human brain.* Boston: Little Brown & Co.

Prsa, M., Gale, S., & Blanke, O. (2012). Self-motion leads to mandatory cue fusion across sensory modalities. *Journal of Neurophysiology, 108*(8), 2282-2291. doi: 10.1152/jn.00439.2012

Raphan, T., Matsuo, V., & Cohen, B. (1979). Velocity storage in the vestibulo-ocular reflex arc (VOR). *Experimental Brain Research, 35*(2), 229-248.

Schlack, A., Hoffmann, K. P., & Bremmer, F. (2002). Interaction of linear vestibular and visual stimulation in the macaque ventral intraparietal area (VIP). *The European Journal of Neuroscience, 16*(10), 1877-1886.

Schubert, R., Blankenburg, F., Lemm, S., Villringer, A., & Curio, G. (2006). Now you feel it--now you don't: ERP correlates of somatosensory awareness. *Psychophysiology, 43*(1), 31-40. doi: 10.1111/j.1469-8986.2006.00379.x

Spinelli, L., Andino, S. G., Lantz, G., Seeck, M., & Michel, C. M. (2000). Electromagnetic inverse solutions in anatomically constrained spherical head models. *Brain Topography, 13*(2), 115-125.

Talairach, J, & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.

Thut, G., & Pascual-Leone, A. (2010). A review of combined TMS-EEG studies to characterize lasting effects of repetitive TMS and assess their usefulness in cognitive and clinical neuroscience. *Brain Topogr, 22*(4), 219-232. doi: 10.1007/s10548-009-0115-4.

Vallar, G., Sterzi, R., Bottini, G., Cappa, S., & Rusconi, M. L. (1990). Temporary remission of left hemianesthesia after vestibular stimulation. A sensory neglect phenomenon. *Cortex, 26*(1), 123-131.

van Elk, M., & Blanke, O. (2013). Imagined own-body transformations during passive self-motion. *Psychological Research*. doi: 10.1007/s00426-013-0486-8

Vogt, B. A., & Pandya, D. N. (1978). Cortico-cortical connections of somatic sensory cortex (areas 3, 1 and 2) in the rhesus monkey. *The Journal of Comparative Neurology, 177*(2), 179-191. doi: 10.1002/cne.901770202

Waberski, T. D., Gobbele, R., Darvas, F., Schmitz, S., & Buchner, H. (2002). Spatiotemporal imaging of electrical activity related to attention to somatosensory stimulation. *Neuroimage, 17*(3), 1347-1357.

zu Eulenburg, P., Caspers, S., Roski, C., & Eickhoff, S. B. (2012). Meta-analytical definition and functional connectivity of the human vestibular cortex. *Neuroimage, 60*(1), 162-169. doi: 10.1016/j.neuroimage.2011.12.032

2.5 Study 5: Vestibular effects on visual cortical processing

Vestibular effects on visual cortical processing

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Abstract

Visual perception not only depends on visual signals but also on multisensory information including vestibular signals about the accelerations of the head in space. For instance, visual-vestibular signal integration critically contributes to self-motion perception. However, the specific contributions of vestibular signals to visual processing remain poorly understood. Here we investigated the spatiotemporal brain mechanisms underlying the modulation of visual processing by vestibular stimulation. Participants received steps of constant-velocity whole-body yaw rotation eliciting natural vestibular stimulation. Electrical neuroimaging analyses were applied to visual evoked potentials induced by checkerboard reversals, during vestibular stimulation and a non-vestibular control period. Vestibular stimulation modulated the response strength (i.e. global field power) and topographical pattern (i.e. global map dissimilarity) in the interval 83-119 ms and 178-205 ms after stimulus onset. Distributed source estimation over these time intervals revealed that vestibular stimulation modulated the neural activity in the right posterior insula cortex (i.e. a core region of the vestibular cortical network) and occipital, parietal and temporal regions of the visual processing pathway. Analysis of the temporal decay of vestibular effects showed longer duration of the vestibular ocular reflex (time constant of 14 s) than for the global field power differences (time constants of 8.7 s and 4.6 s) suggesting less dependence of visual-vestibular interactions on prior subcortical afferent processing. Collectively these results indicate temporal-specific effects of vestibular stimulation on visual cortical processing relevant to self-motion processing.

Keywords

Vestibular system; EEG; VEP; Insula; PIVC; velocity storage

Abbreviations

ANOVA	Analysis of variance
CVS	Caloric vestibular stimulation
EEG	Electroencephalography
fMRI	Functional magnetic resonance imaging
FG	Fusiform gyrus
FPV	Fast phase velocity
GFP	Global field power
GMD	Global map dissimilarity
GVS	Galvanic vestibular stimulation
ICA	Independent component analysis
LAURA	Local autoregressive average regularization approach
MOG	Middle occipital gyrus
MSTd	Medial superior temporal dorsal region
PCN	Precuneus
PET	Positron emission tomography
PHD	Parahippocampal gyrus
PIVC	Parieto-insular vestibular cortex
SCC	Semicircular canal
SMAC	Spherical model with anatomical constraints
SPV	Slow phase velocity
TC	Time constant
VEP	Visual evoked potential
VIP	Ventral intraparietal region
VN	Vestibular nucleus
VOR	Vestibular ocular reflex
VPS	Visual posterior sylvian region
VSM	Velocity storage mechanism

Introduction

The vestibular system encodes rotational and linear accelerations of the head. Vestibular signals not only contribute to visual perception by gaze stabilization, but also by supporting the discrimination between visual inputs from self- and object-motion, as well as to the perception of the subjective visual vertical. These important functions critically depend on visual-vestibular signals integration in the brain. However, data is lacking about the spatiotemporal neural mechanisms by which vestibular signals contribute to visual processing in humans.

Electrophysiological studies in non-human primates identified visual-vestibular convergence zones at the cortical and subcortical level. For instance in monkeys, the medial superior temporal dorsal region (MSTd), ventral intraparietal region (VIP), visual posterior sylvian area (VPS) host bimodal and trimodal neurons that encode visual (mostly optokinetic stimuli) and vestibular signals tuned to motion direction, which are thought to underlie self-motion related processing (Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005; Bremmer, Klam, Duhamel, Ben Hamed, & Graf, 2002; A. Chen, DeAngelis, & Angelaki, 2011; X. Chen, Deangelis, & Angelaki, 2013a, 2013b; Colby, Duhamel, & Goldberg, 1993; Duhamel, Bremmer, Ben Hamed, & Graf, 1997; Fetsch, Wang, Gu, Deangelis, & Angelaki, 2007; Graziano & Cooke, 2006). Also the core vestibular cortical regions in the parieto-insular vestibular cortex (PIVC; Grüsser, Pause, & Schreiter, 1990a, 1990b) and the primary somatosensory cortex, i.e. area 2v (Buttner & Buettner, 1978; Fredrickson, Scheid, Figge, & Kornhuber, 1966) and area 3a (Odkvist, Schwarz, Fredrickson, & Hassler, 1974; Phillips, Powell, & Wiesendanger, 1971) respond to visual, vestibular, and multimodal signals related to body movement. Visual signals from the cortex further modulate subcortical vestibular processing in the vestibular nucleus of the brain stem involved in relaying vestibular signals to the cortex and reflexive gaze control (Akbarian, Grüsser, & Guldin, 1993; Waespe & Henn, 1978) and in processing of vestibular afferents by a velocity storage mechanism (VSM; see Leigh & Zee, 2006, for a review) contributing to self motion perception (Bertolini et al., 2011; Cohen, Henn, Raphan, & Dennett, 1981; Laurens &

Angelaki, 2011; Raphan, Matsuo, & Cohen, 1979). These data from animal studies show considerable contributions of visual signals to central vestibular processing.

Neuroimaging studies in humans using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) showed that vestibular stimulation induced distributed cortical activations comparable to the animal data. Consistently across different vestibular stimulation techniques, vestibular stimulation activated an area in the posterior insula and the parietal operculum (OP2 region), which is thought of being the human homologue of the monkey PIVC (Lopez, Blanke, & Mast, 2012; zu Eulenburg, Caspers, Roski, & Eickhoff, 2012). Several studies found that such vestibular stimulation not only activated the vestibular cortical network, but also deactivated visual cortical regions, i.e. the parietal-occipital cortex and precuneus (PCN; Della-Justina et al., 2015; Deutschlander et al., 2002). In the same subjects, in turn, optokinetic visual stimulation activated these visual cortical regions and simultaneously deactivated the human PIVC (Brandt, Bartenstein, Janek, & Dieterich, 1998; Brandt et al., 2002; Deutschlander et al., 2004; Wenzel et al., 1996). This pattern of reciprocal visual-vestibular inhibition has been proposed to reflect underlying multisensory signal weighting serving to optimize self-motion perception (Brandt et al., 1998). However, it is currently not clear whether visual-vestibular inhibition depend on specific stimulation parameters or neuroimaging method used, because other fMRI studies found no modulation or even further activation of the human PIVC by visual stimulation (Frank, Baumann, Mattingley, & Greenlee, 2014; Kovacs, Raabe, & Greenlee, 2008). Similarly controversial are the data about visual responses of PIVC neurons in the monkey (compare Grüsser et al., 1990a, 1990b, to Chen, DeAngelis, & Angelaki, 2010).

Most of the currently available data about visual-vestibular interaction in the human brain was based on fMRI and PET recordings (Lopez et al., 2012; zu Eulenburg et al., 2012). To our knowledge, only two electroencephalography (EEG) studies addressed this issue. Ferre, Bottini, & Haggard (Ferre, Bottini, & Haggard, 2012) recorded visual evoked potentials (VEPs) immediately before and several minutes after caloric vestibular stimulation (CVS) and observed no modulation of the evoked responses in a single EEG channel above the occipital cortex. A different study by Cheron et al. (Cheron et al., 2014) compared VEPs recorded in microgravity and on earth—thus, analyzing the contribution of otolithic vestibular signals to visual cortical processing. Gravity modulated the neural oscillations in the theta-alpha band when the visual stimulus was relevant to a subsequent virtual navigation task.

No study has investigated the spatiotemporal neural dynamics of how visual processing depends on vestibular stimulation in humans. This might be attributed to the low temporal resolution of fMRI and PET, the fact that the magnetic field of the MR scanner constantly innervates the peripheral vestibular organs (Antunes, Glover, Li, Mian, & Day, 2012; Roberts et al., 2011), and the fact that PET and fMRI require head fixation and the use of artificial vestibular stimulation techniques, i.e. by CVS, galvanic vestibular stimulation (GVS), and auditory vestibular stimulation, which unselectively stimulate the vestibular receptors and induce co-activation of thermal, nociceptive, or auditory sensory signals (Lopez et al., 2012; zu Eulenburg et al., 2012).

To address these issues, we aimed at identifying the spatiotemporal dynamics of the effects vestibular stimulation on visual processing. Passive whole-body yaw rotations about an earth-vertical axis through the center of the head selectively stimulated the horizontal semicircular canals (SCC; Ferre, Kaliuzhna, Herbelin, Haggard, & Blanke, 2014; Prsa, Gale, & Blanke, 2012; Michiel van Elk & Blanke, 2012). To isolate vestibular stimulation from confounding sensory co-activation, steps of constant-velocity whole-body rotation were used inducing vestibular stimulation following accelerations and decelerations related to constant-velocity rotation. Electrical neuroimaging analysis of the VEPs elicited by checkerboard reversals was compared between vestibular stimulation to and non-vestibular control periods. Reference-independent analyses were conducted of response strength (i.e. global field power, GFP) and spatial configuration of putative underlying neural sources (i.e. global map dissimilarity, GMD; Lehmann & Skrandies, 1980; Murray, Brunet, & Michel, 2008). We asked: whether, when, and how vestibular stimulation would affect visual cortical processing. In line with previous studies in animals and humans, we hypothesized vestibular effects of mid-late processing stages involving extrastriate, parietal, and temporal regions. We addressed this hypothesis by additional source estimation of the underlying neural generators (Michel et al., 2004). In addition, we hypothesized that any visual-vestibular interaction found should follow the exponential decay function for post-rotational vestibular stimulation intensity that can be estimated by analysis of the vestibular ocular reflex (VOR; Bertolini et al., 2011; Goldberg & Fernandez, 1971), and that the temporal decay could serve as a measure of the specific contributions of VSM to visual-vestibular interactions.

Materials and methods

Participants

Thirteen right-handed students from the Ecole Polytechnique Fédérale de Lausanne participated (3 females; mean age: 23.7 years, SD: 4.3 years, range: 18-30 years). All had normal or corrected-to-normal vision and no known visual, vestibular, or neurologic disease. Participants gave their written informed consent before the experiment and received a monetary compensation of 60 Swiss Francs after the experiment. The experimental protocol was approved by the local ethics committee—La Commission d'Ethique de la Recherche Clinique de la Faculté et de Medicine de l'Université de Lausanne—and was conducted in accordance the Declaration of Helsinki.

Experimental setup

A motion platform was installed inside of a faraday cage (Industrial Acoustics Company, Niederkrüchten, Germany), used to shield the experimental setup from external electromagnetic, visual, and auditory signals. Figure 1a shows the

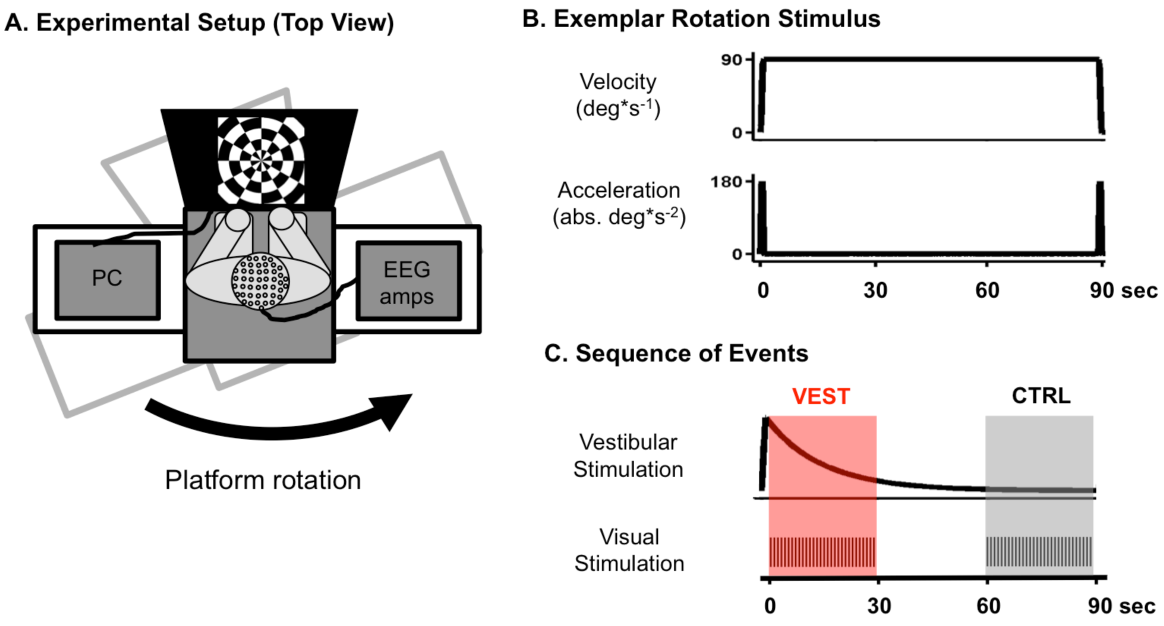

Figure 1 Experimental setup and procedures. (a) Experimental setup viewed from the top showing the participant (image center) equipped with electroencephalography (EEG) recording electrodes (black dots). The participant was seated at the center of an angular motion platform (white rectangle) on which a stimulation computer (PC), computer screen (black trapezoid) and EEG amplifiers (amps) were firmly attached. The participant fixated the central point of large-field checkerboard images presented on the computer screen. (b) Platform motion kinematics for an exemplar step of 90 °/s constant-velocity rotation for 90 s. (c) Hypothetical vestibular stimulation following sudden platform acceleration or deceleration from constant-velocity rotation. Critical EEG data recording periods for the Vestibular Stimulation condition (VEST; in red) and the non-vestibular Control condition (CTRL; in gray). (d) Checkerboard reversals (black vertical lines) over time were presented within trains of 30-sec stimulation at 1 Hz (fixed 1-s interstimulus interval) following platform accelerations and decelerations during VEST and later CTRL periods.

experimental setup modified from Prsa et al. (Prsa et al., 2012) and van Elk and Blanke (van Elk and Blanke, 2013). A beam platform (2 m diameter) was fixated on an electrical engine (PCI-7352 servo control) that controlled angular platform rotations with 0.1 ° precision at 100 Hz sampling rate using Labview software (version 8.6, National Instruments, Austin, TX, US). The participant sat in an upright posture with safety belts attached with the head at the axial center of platform rotations. The participant's head was tilted by 30 ° forward to align participant's horizontal SCCs to the yaw rotation plane (Day & Fitzpatrick, 2005). A chin- and forehead-rest fixated the participant's head posture during platform rotation.

A screen (Samsung Syncmaster 2233RZ, Seoul, Korea) with 120 Hz refresh rate and 22-inch diameter was firmly attached to the motion platform and centered at eye-level in front of the participant at 29 cm distance from the eyes resulting in 56 ° vertical and 80 ° horizontal visual angles (Figure 1a). On earphones (Sennheiser CX 400, Hannover, Germany) participants were presented with white noise (individually adjusted between 40-70 dB loudness) masking any auditory cues from platform rotations. Thus, no auditory or visual cues informed the participants whether the platform actually rotated. A computer was laterally mounted on the platform used for visual stimulus presentation and written task instructions. A photodiode was attached to the screen for recording visual stimulus onset via an additional photodiode channel of the EEG recording system at 2048 Hz sampling rate.

Experimental design and rotation procedure

A 2 x 2 x 2 full-factorial experimental design was used with three within-subjects factors Stimulation (vestibular, control), Rotation (constant-velocity, post-rotation), and Direction (clockwise, counterclockwise). Vestibular Stimulation was the critical factor for the aim of the study, i.e. identifying the effects of vestibular stimulation on visual processing. The additional factors were included for the following reasons. First, in order to maximize the number of trials, we presented visual stimuli both during constant-velocity rotation and during the post-rotation period (Rotation factor). This was based on previous evidences in animal and human studies (Bertolini et al., 2011; Goldberg & Fernandez, 1971; Laurens & Angelaki, 2011) showing that vestibular signals following sudden accelerations to constant velocity are highly similar to those following decelerations from constant-velocity (i.e. given constant-velocity rotation was sufficiently long, i.e. > 30 s, to induce SCC habituation). Second, in order to reduce habituation effects by identical repeated rotation stimuli and because of the fact that vestibular signals following accelerations are directed opposite to those following decelerations (i.e. endolymph flow inside the SCC, reflexive eye movements, and feeling of self-motion) we presented an equal numbers of clockwise and counterclockwise rotations in random order to each subject (Rotation factor).

Because the Vestibular Stimulation factor was the main manipulation of the present study, and because initial data analysis using the three-factorial design showing no significant interactions between Vestibular Stimulation and the Rotation or Direction factor, we will present analysis and results for the one-factorial design using Vestibular Stimulation only, collapsed over Rotation and Direction

Each participant received 24 rotation stimuli presented in 6 runs of 4 rotations (i.e. 2 clockwise, 2 counterclockwise in random order). Each run had 12 min 13 s duration and participants were allowed pauses between runs in which the light was switched on and the experimenter got in contact with the participant. Figure 1b shows the sequence of events for an exemplar rotation stimulus. Initially, the motion platform accelerated from static (0 °/s velocity) to constant-velocity rotation (90 °/s velocity) during 1 s. The acceleration had a cosine-smoothed (Gaussian) profile and reach 180 $°/s^2$ peak acceleration 500 ms after rotation onset. Constant 90 °/s velocity rotation was presented during 90 s, during which initial vestibular stimulation (see below) fully habituated. This was followed by platform deceleration from constant-velocity (90 °/s) to static (0 °/s velocity) during 1 s. The deceleration profile was the inverse of the acceleration profile (i.e. 180 $°/s^2$ peak acceleration). This was followed by no rotation during 90 s, during which, similar to constant-velocity rotation, there was initial vestibular stimulation (induced by the sudden deceleration) that habituated over time before the next rotation stimulus was presented.

Stimuli and sequence of events

Vestibular stimulation following sudden accelerations to (/decelerations from) constant-velocity rotation as used in the present study are approximated by an exponential decay function (Cohen et al., 1981; Raphan et al., 1979; see Figure 1c) as in Equation 1:

$$y = A * e^{-t/TC} \tag{1}$$

where A is the amplitude, t is time, and and TC the time constant. This has been shown for the firing rates from vestibular nerve neurons, for reflexive eye movements induced by vestibular stimulation, and for the perception of self-motion in darkness (Bertolini et al., 2011; Clement, Tilikete, & Courjon, 2008; Sinha et al., 2008). Yaw rotations about an earth-vertical axis as used here induce vestibular processing with a time constant (TC_{VSM} between 15-20 s; Cohen et al., 1981; Raphan et al., 1979) that exceed the peripheral SCC activation (TC_{SCC} between 4-6 s; Buttner & Waespe, 1981; Goldberg & Fernandez, 1971), which is attributed to subcortical vestibular afferent processing by the VSM. Given these time constants, during constant-velocity rotation vestibular stimulation should have considerably habituated after about 60 s following sudden rotational accelerations / decelerations (Figure 1c).

Accordingly, the sequence of events for the visual stimulations was as follows. Immediately following platform acceleration (/deceleration) during intense vestibular stimulation, a sequence of 30 visual stimuli was presented during 30 s and for each visual stimulus onset a trigger was sent to the EEG system for later evoked potential analysis. Participants were instructed to suppress reflexive eye movements by fixating on a central point. This was followed by the presentation of a black screen and a central fixation point for a 30-s resting period allowing full habituation of the vestibular stimulation. This was followed by a sequence of 30 visual stimuli during 30 s (i.e. Control condition; event triggers were sent to the EEG system) that terminated before the end of the constant-velocity (/no) rotation period. This allowed us to compare the effects of vestibular stimulation (versus no-vestibular control) on visual processing and to control for any general effects of rotation on our data, i.e. because an equal number of visual stimulations were presented during constant-velocity rotation and during the post-rotational period for the Vestibular Stimulation and Control conditions.

The visual stimulus was a checkerboard image consisting of five concentric rings with equal diameter that were each segmented into 12 patches thus consisted of a total of 60 patches (30 black and 30 white; Figure 1a). The stimulus subtended 56 ° (w) x 56 ° (h) visual angles and thus stimulated foveal and extrafoveal retinal fields. The stimulus contrast was 100% and stimulation consisted of initial presentation of the stimulus and subsequent pattern reversals (i.e. contrast change of black and white patches) at 1 Hz with a fixed 1 s inter-stimulus interval for 30 s. We did not distinguish between the initial stimulus onset and both checkerboard reversal patterns in our analyses, but considered them alike as visual stimulus events. Thus, per visual stimulation period 30 stimuli were presented, and in total each participant received 2,880 visual stimulations across experimental conditions.

Data acquisition

Continuous EEG was acquired at 2048 Hz with a 64-channel Biosemi ActiveTwo system (Biosemi, Amsterdam, Netherlands, www.biosemi.nl) referenced to the vertex common mode sense (active electrode), which serves as a feedback loop driving the average potential across all channels as close as possible to the amplifier zero. Bipolar horizontal EOG was recorded from electrodes attached to the outer canthi and bipolar vertical EOG was recorded from electrodes above and below the right eye. In addition, a screen-attached photodiode recorded luminance of the visual stimulus at 2048 Hz in register with the EEG data. During EEG preparation for each participant the experimenters took care to keep DC offsets below 50 mV for all channels, i.e. for active EEG recording systems DC offset serves as evaluation criterion similar to channel impedances for passive montages. All data was recorded with an online band-pass filter (0.2 - 100 Hz).

VOR analysis

Analysis of eye movement data was conducted offline in MATLAB (version 8.4, The Mathworks, Natick, MA, http://www.mathworks.ch). Raw continuous bipolar horizontal EOG data was extracted and re-referenced against the Afz channel from EEG, located centrally on the forehead (Marmor et al., 2011). The data was then low-pass filtered (10 Hz cut-off, ripple: 0.05 dB, attenuation: 80 dB, transition bandwidth:

0.5 Hz) using the FIR filter implemented in EEGLAB (Bertolini, Bockisch, Straumann, Zee, & Ramat, 2008). Then, the difference between the left and right horizontal EOG channel was calculated, which approximates horizontal eye position. Then, the first derivative of these data was calculated, which approximated eye velocity. These data was then segmented in epochs from 0 s to 30 s (Vestibular Stimulation) and from 60 s to 90 s (Control) relative to the onset of constant-velocity rotation / the post-rotation phases. Note that the epochs comprised the total 30-s visual stimulation periods (Figure 1c). Because vestibular stimulation-related eye movements depend on the direction of the vestibular stimulus, we multiplied the segmented data from counterclockwise Direction trials by -1 to obtain positive values for the slow phase velocity (SPV) and negative values for the fast phase velocity (FPV) of eye movements. This was followed by semi-automated removal of the FPV (Bertolini et al., 2008; Bertolini et al., 2011). No interpolation of FPV was applied because this might have affected subsequent exponential fitting. This resulted in continuous SPV data for horizontal eye movements. Visual inspection of the data revealed in 2 out of 11 subjects no characteristic VOR SPV-FPV patterns, suggesting these subjects were able to suppress the VOR for all experimental trials. The VOR data from these subjects was not further analyzed, but coded as missing data in subsequent analyses. For the remaining 11 subjects, we quantified the vestibular stimulation-related decay of the SPV by calculating the average of all epochs for the Vestibular Stimulation condition and then performed an exponential function fitting (Figure 3a; using equation **Eq. 1** above) using as free parameters TC (i.e. parameter of interest) and A (i.e. parameter of non-interest, which is necessary to account for individual variability in signal amplitude but which was not further analyzed). This resulted for each subject in a TC estimate for the VOR (i.e. TC_{VOR})—i.e. a proxy of vestibular stimulus intensity—which had longer duration than the time constants from EEG analysis (see below).

EEG analyses and source estimation

EEG data was analyzed using the MATLAB toolboxes EEGLAB (http://sccn.ucsd.edu/eeglab/) and FASTER (http://www.mee.tcd.ie/neuraleng/Research/Faster), as well as CARTOOL software (Functional Brain Mapping Laboratory, Geneva, Switzerland http://www.brainmapping.unige.ch/cartool.htm), STEN software (Laboratory of Investigative Neurophysiology, Lausanne, Switzerland, http://www.unil.ch/line/Sten), and RAGU software (http://www.thomaskoenig.ch/Ragu_pkg.exe).

EEG data pre-processing included the following steps. First, we corrected for latency jitters (on average 10 ms) between computer-generated event triggers and actual stimulus presentations on the screen due to the refresh rate of the screen. For this we extracted from the continuous recording of the screen-attached photodiode the raw signal and calculated the first derivative of the signal reflecting changes in visual contrast due to checkerboard reversal. We then moved the scheduled event triggers to the latencies identified in the photodiode recording. The continuous raw EEG data was band-pass filtered (1 Hz low cut-off, 40 Hz high cut-off, ripple: 0.05 dB, attenuation: 80 dB, transition bandwidth: 0.5 Hz) and using second-order Butterworth FIR filter implemented in EEGLAB. The data was recalculated against the average reference. Artifact electrodes from each participant were identified using a signal variance criterion (3 z-score Hurst exponent). On average, 8.23 (SD= 1.72) electrodes were interpolated for each participant using spherical splines (Nolan, Whelan, & Reilly, 2010). The EEG data was resampled to 512 Hz. EEG epochs from -100 to 500 ms relative to stimulus onset (i.e. checkerboard reversal) were extracted for each participant and each condition. A pre-stimulus baseline correction from -100 to 0 ms pre-stimulus onset was applied. Physiological artifacts (e.g. muscular artifacts, eye blinks) were removed by semi-automated procedures including independent component analysis (ICA; 63 components, k-value: 25, kurtosis rejection criterion: 3 z-scores), application of a ±100 μV bipolar vertical EOG signal rejection criterion, and by visual inspection. The average number (and standard deviation) of accepted epochs per experimental condition was 1.312 (160) epochs for the Vestibular Stimulation condition and 1.275 (172) epochs for the Control condition. Statistical analysis using a paired samples t-test on the accepted number of epochs per condition for the participant sample showed no significant effect ($t(12) = 2$, $p > 0.05$). Thus, we can exclude that our results are due to differences in signal to noise ratio across conditions. For each subject condition-wise averages were calculated (i.e. VEPs) and subjected to further statistical analysis.

Global electrical field analyses. Two reference electrode-independent analyses of the global electrical field strength (i.e. GFP; Murray et al. (2008)) and topographical changes (i.e. GMD; Koenig and Melie-Garcia, 2010) were conducted. GFP is calculated as the square root of the mean of the squared values recorded at each electrode (versus average reference) and represents the spatial standard deviation of the potentials at all electrodes and at each time point (Lehmann & Skrandies, 1980). This measure indicates the global strength of the response, regardless of its topographic distribution. Changes in GFP were statistically analyzed at each time point from -100 to 500 ms relative to stimulus onset using repeated-measures analysis-of-variance (ANOVAs) with the within-subjects factor Condition (Vestibular Stimulation, Control) with an alpha threshold of $p < 0.01$. We controlled for temporal autocorrelation of our statistical effects by application of a 10 contiguous time-point (> 20 ms) temporal criterion for the persistence of differential statistical effects (Guthrie & Buchwald, 1991).

Topographic modulations across conditions were identified using GMD (Koenig & Melie-Garcia, 2010), which is calculated as the root mean square of the differences between two strength-normalized vectors (i.e. instantaneous voltage potentials across the electrode montage). The GMD values between two experimental conditions (i.e. vestibular activation, control) were then compared at each time point with an empirical distribution derived from a bootstrapping procedure (5000 permutations per data point) based on randomly reassigning each participant’s data to either one of the two experimental conditions. GMD is independent of the chosen reference electrode and is insensitive to pure amplitude modulations across conditions, i.e. that is GMD modulations are orthogonal to GFP modulations. This analysis is useful in terms of the neurophysiologic interpretability, following the assumption that topographic changes necessarily reflect differences in the configuration of the brain's underlying active generators (Lehmann & Skrandies, 1980). Correction for temporal autocorrelation was performed according to the same procedure used for the GFP analysis, i.e. using a 10 contiguous time-point (> 20 ms) criterion for the persistence of differential statistical effects.

Source estimations. To identify the intracranial sources generating over distinct time periods the GFP and GMD effects we estimated the electrical activity in the brain using a distributed linear inverse solution applying the local autoregressive average regularization approach (LAURA), comprising biophysical laws as constraints (Grave de Peralta Menendez, Gonzalez Andino, Lantz, Michel, & Landis, 2001; Michel et al., 2004). For the lead field matrix calculation, we applied the spherical model with anatomical constraints (SMAC) method (Spinelli, Andino, Lantz, Seeck, & Michel, 2000), which transforms a standard anatomical MRI to the best-fitting sphere using homogeneous transformation operators. It then determines a regular grid of 3005 solution points in the gray matter of this spherical MRI and computes the lead filed matrix using the known analytical solution for a spherical head model with three shells of different conductivities as defined by (Ary, Klein, & Fender, 1981). The results of the global electrical field analysis described above provide an estimation of the two distinct time intervals for conducting separate source estimations.

Statistical analyses of source estimations were performed by first averaging separately for each of the distinct time intervals the VEP data across the period of interest to generate a single data point for each participant and condition. The inverse solutions (13 subjects x 2 factor levels for Condition) were then estimated. Sources calculated for the vestibular activation and control conditions were then submitted to repeated measures ANOVA with the within-subjects factor Condition (vestibular activation, control) with a spatial criterion for at least 9 contiguous solutions points and a significance threshold of $p < 0.005$ at the single node level. The results of the source estimations were rendered on the Montreal Neurologic Institute's average brain with the Talairach and Tournoux (Talairach and Tournoux, 1988) coordinates.

Time constant analysis

Because the vestibular stimulus used in the present study is known to approximately follows an exponential decay (see equation **Eq. 1** above), we hypothesized that any vestibular stimulation-related differences in EEG should follow a similar exponential decay. Moreover, no study has estimated the time constants of visual-vestibular interactions to identify whether they resemble rather to the SCC time constant (4-6 s) or the VSM time constant (15-20 s).

In order for this, we re-calculated VEPs for 15 time bins (2 s duration and 192 stimuli per bin) of subsequent of visual stimuli, i.e. including thus both patterns of checkerboard reversal into each time bin. We accordingly calculated condition averages for 2 (Stimulation: Vestibular, Control) x 15 (Time: 0-30 s in steps of 2 s bins). The GFP was calculated and averaged over time periods of interest, revealed by the main analysis. We then calculated the difference in GFP between Vestibular Stimulation and Control condition for each time bin. These data was then subjected to exponential function fitting (Figure 3c) to extract the time constants for GFP Vestibular Stimulation versus Control condition differences for each period of interest.

Thus, together with the data from eye movement analysis we time constant estimates for the VOR, the early GFP effect (83-119 ms), and the late GFP effect (178-205 ms) for each subject. We statistically tested for differences between these time constants using separate paired-samples t-test (alpha threshold < 0.05).

Results

VOR analysis

Visual inspection of EOG data from the Vestibular Stimulation condition showed in most of the subjects characteristic VOR slow and fast phases for Vestibular Stimulation which were absent for the Control condition. Figure 3a shows the VOR SPV of an exemplar representative subject, showing a clearly exponential decay of SPV for Vestibular Stimulation, which was absent for the Control condition. Exponential fitting on the SPV showed on average a TC_{VOR} = 14 s (SD = 9.3 s; Figure 3d), indicating that the vestibular stimulus had reached 50% intensity at 14 s following motion platform acceleration / deceleration.

Event-related potentials

The VEP waveforms from four exemplar electrodes and the superimposed VEP waveforms from the Vestibular Stimulation and the Control conditions are depicted in Figure 2a-b to allow the reader to compare our signal to previous studies using similar VEP recordings. Note that interpretations of the data in our study are based on the reference-independent analysis of the global electrical field of the VEPs.

Global electrical field analysis

Analysis of GFP identified two periods of significant differences ($p < 0.01$ during contiguous period > 20 ms) between the Vestibular Stimulation and Control conditions. There was a first GFP modulation in the 83-119 ms post-stimulus period and a second GFP modulation in the 178-205 ms post-stimulus interval which both showed lower GFP in the Vestibular Stimulation than Control condition (Figure 2c-d).

The topographic analysis of GMD identified three time periods of significant topographic modulations ($p < 0.01$ during contiguous period > 20 ms) between

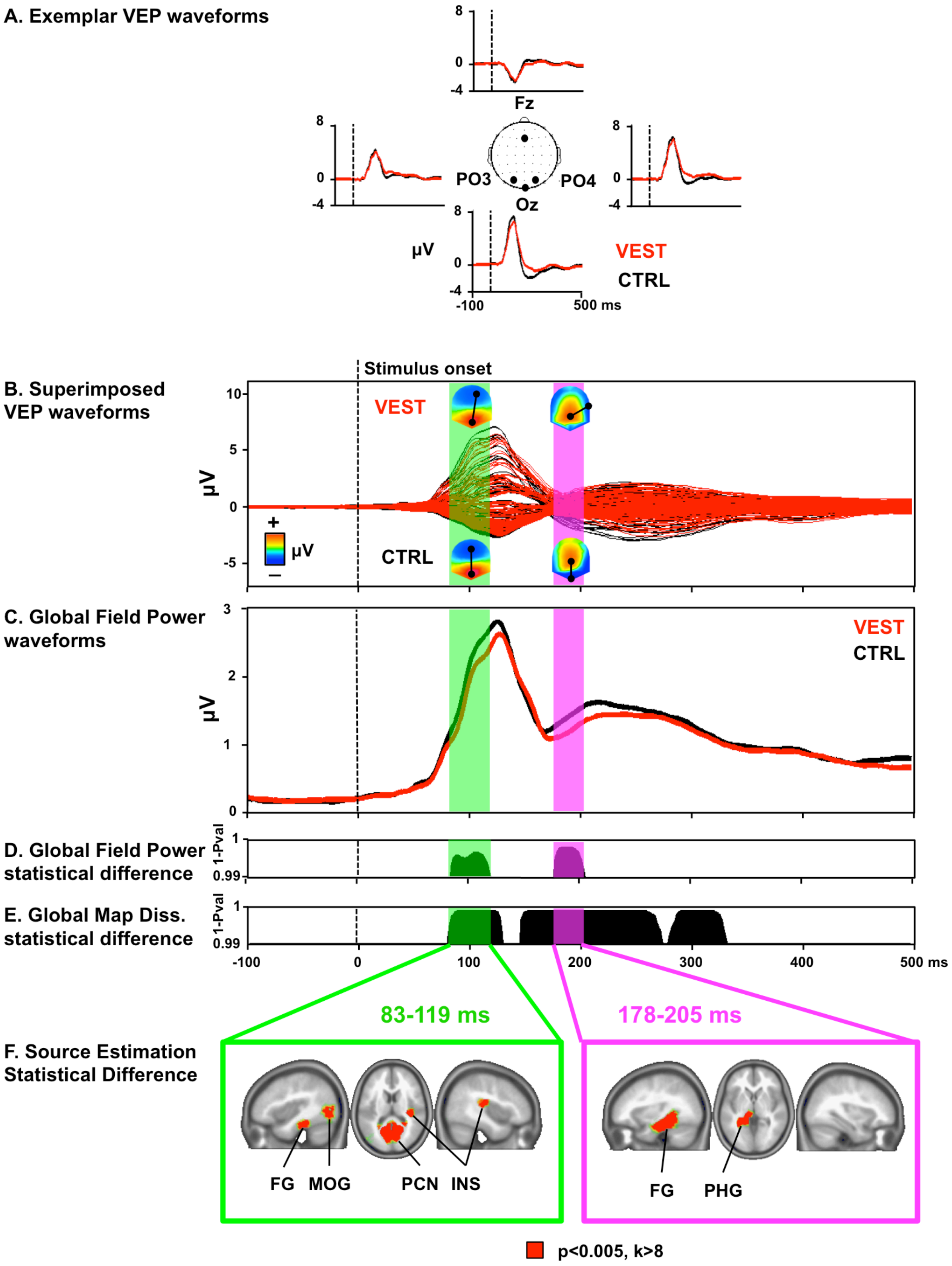

Figure 2 Electrical neuroimaging results. (a) Group averaged (n=13) visual evoked potentials (VEPs) to checkerboard reversals for exemplar electrodes (Fz, PO3, PO4, Oz) for Vestibular Stimulation (VEST, red) and non-vestibular Control (CTRL, black) conditions. (b) Superimposed VEP waveforms across all electrodes for the experimental conditions with topographies of the potential field (nasion upward) for the two conditions in distinct time periods (green and purple) that showed statistical differences of response strength

Figure 2 (continued) (i.e. global field power, GFP) and spatial distribution of underlying neural generators (i.e. global map dissimilarity, GMD). (c) GFP waveforms across time for the VEST (red) and the CTRL (black) conditions. (d) Time-wise repeated measures ANOVA on the GFP revealed two intervals where significant differences VEST<CTRL were observed, i.e. at 83-119 ms ($p < 0.01$ for at least 20 ms contiguously; in green) and at 178-205 ms ($p < 0.01$, duration > 20 ms; in purple). (e) GMD analysis revealed significant Vestibular Activation main effects ($p < 0.01$, duration > 20 ms) over the same time periods (in green and purple). (f) Results of repeated measures ANOVAs on the source estimations for two distinct time periods with significant GFP and GMD modulations (83-119 ms, in green; 178-205 ms, in purple). Results of the ANOVAs (significant activation differences: $p < 0.005$, at least 8 contiguous solution points) are projected on a template brain for these two time periods showing collectively less activity during the VEST condition as compared to the CTRL condition. Significant modulations were observed in the right posterior Insula (INS), bilateral precuneus (PCN) and cuneus, and in left middle occipital gyrus (MOG), fusiform gyrus (FG), and parahippocampal gyrus (PHG).

Vestibular Stimulation and Control conditions: 82-130 ms and the 148-270 ms, and 278- 334 ms (Figure 2e).

There were thus two time periods where the analysis revealed vestibular modulations of the VEP global electrical field strength (GFP) and topographic pattern (GMD): 83-119 ms and 178-205 ms post-stimulus onset.

Source estimation analysis

Source estimations for two distinct time intervals (83-119 ms, 178-205 ms) for which modulations of both GFP and GMD were observed revealed significant differences ($p < 0.005$, cluster size $k > 8$ nodes) between Vestibular Stimulation and Control in several distinct cortical regions. The significant solution points are represented on a template brain separately for the two distinct time periods.

The significant difference in the 83-119 ms post-stimulus period showed activation differences between Vestibular Stimulation and Control condition in the right posterior insula cortex (highest significance level), a cluster including bilateral parts of the PCN and cuneus, the left fusiform gyrus (FG) and the left middle occipital gyrus (MOG; Figure 2f).

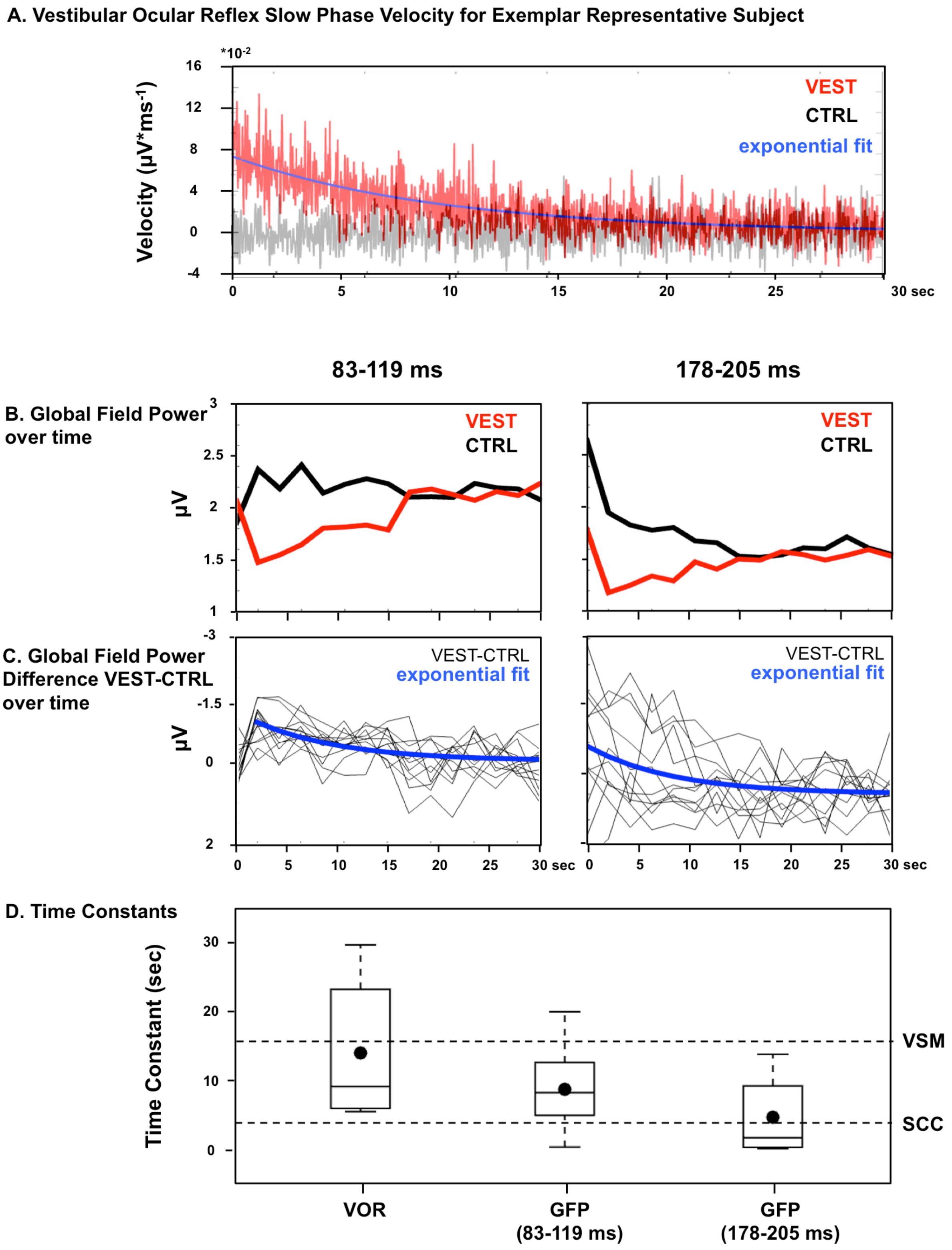

Figure 3 Time constant analyses. (a) Slow phase velocity from vestibular ocular reflex (VOR) recorded in EOG for the VEST and CTRL conditions for an exemplar representative subject. Exponential function fit to the data from the VEST condition served for extracting the time constant TC_{VOR}. (b) GFP in two temporal intervals of interest, that in our previous analysis showed vestibular modulation of visual processing, plotted as a function of time in the 30-sec visual stimulation period for the VEST and CTRL conditions.

Figure 3 (continued) (c) GFP difference VEST-CTRL over time. Exponential function fit (shown here for the group average) was performed for individual subject data to extract TC_{EARLY} (i.e. on GFP differences from the 83-119 ms post-stimulus interval) and TC_{LATE} (i.e. on GFP differences from the 178-205 ms post-stimulus interval). (d) Time constant estimate distribution across the subject sample compared for estimates based on VOR, and the GFP effects. Boxplot box whiskers show the upper and lower quartiles, vertical bars the medians, black circles the mean. Dashed lines show time constants for the SCC activation and velocity storage mechanism (VSM), identified in previous studies, for comparison.

The significant difference in the 178-205 ms post-stimulus period showed differences between Vestibular Stimulation and Control condition in the left FG and left parahippocampal gyrus (PHG, Figure 2f).

Time constant analysis

Visual inspection of time-wise GFP data for the distinct periods of interest (i.e. “early” interval: 83-119 ms; “late” interval 178-205 ms post-stimulus onset) showed Vestibular Stimulation versus Control condition differences during the first half of the 30-s visual stimulation period, when vestibular stimulation was intense, but no differences during the remainder of visual stimulation when vestibular stimulation had considerably decayed (Figure 3a).

Statistical analysis of time constants fitted on the SPV (see above) and the early and late GFP data by a repeated-measures one-way ANOVA with the within-subjects factor Time Constant (levels: VOR, early GFP, late GFP) showed a significant effect of Time Constant ($F(1,9) = 5.87$, $p = 0.01$, $\eta^2 = 0.39$; Fig) reflected in a higher TC_{VOR} ($M = 14$ s, $SD = 9.3$ s) than $TC_{EARLY} = 8.7$ s ($SD = 5.9$ s) and $TC_{LATE} = 4.6$ s ($SD = 5.2$ s). Moreover, Figure 3d shows the distribution of time constants across the tested subjects. It can be seen that the TC_{VOR} from all subjects was always longer than the TC_{SCC} (i.e. 4-6 s) and corresponded on average highly to the TC_{VSM} (i.e. 15-20 s) identified in previously. By contrast, the TC_{LATE} was always shorter than the TC_{VSM} and resembled more to the TC_{SCC}. The TC_{EARLY} was in between TC_{VSM} and TC_{SCC}. This indicates that vestibular effects on GFP elicited by visual stimulation showed a temporal decay more similar to the signals from the SCCs, with little contribution of the VSM.

Discussion

In summary, vestibular stimulation modulated response strength (i.e. GFP) and the spatial configuration of the underlying neural generators (i.e. GMD) in the 83-119 ms and the 178-205 ms post-stimulus interval. Distributed source estimation over these time intervals revealed that vestibular stimulation modulated the brain activity evoked by visual stimulation in the occipital, parieto-temporal, and posterior insula cortex. Moreover, effects of vestibular stimulation on GFP decayed faster (TC_{EARLY} = 8.7 s, TC_{LATE} = 4.6 s) than vestibular processing-related reflexive eye movements (TC_{VOR} = 14 s), suggesting both processes differently depended on subcortical afferent processing by VSM. Together, these results reflect temporal specific effects of vestibular modulation of visual cortical processing.

Temporal specificity of vestibular effects on visual processing

Vestibular stimulation modulated checkerboard VEPs in specific time intervals, later than 83 ms post-stimulus onset. If one wants to compare the timing of these effects with previous VEP studies, it should be borne in mind that these studies often reported data recorded from single electrodes. However, interpretability of such data is problematic because of their dependence on the chosen electrode and reference montage (Murray et al., 2008) and because such data remains uninformative about the underlying neural processes (Michel et al., 2004). Here, we used reference-independent analysis of the global electrical field and distributed source estimations based on data from all scalp electrodes (i.e. with single electrode data in average reference (Murray et al., 2008). Using this approach, our electrical neuroimaging analysis revealed temporal-specific vestibular effects on VEP that compare to the P1 (80-100 ms) and the N1 component (170-200 ms) from single electrode analysis in previous studies. In our study, vestibular stimulation did not affect earlier periods, such as for the C1 component (60-80 ms) identified in single electrodes and presumably reflecting local primary visual cortex activity (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Slotnick, Klein, Carney, Sutter, & Dastmalchi, 1999). Based on the timing of our results, it seems that vestibular stimulation affected mainly higher-order visual processing in extrastriate temporal and parietal visual cortical centers—further confirmed by inverse solution results (Figure 2f). This is in line with single cell recordings in monkeys, that traced the top-down vestibular contributions to visual processing from the PIVC, via the VPS, to the VIP, and the MSTd region, but not further down to earliest visual cortical regions (A. Chen et al., 2011; Duffy & Wurtz, 1991; Grüsser et al., 1990a; Gu, DeAngelis, & Angelaki, 2007). Likewise, in human fMRI studies vestibular stimulation modulated the activity in the extrastriate parieto-occipital but not the primary visual cortex (Bense, Stephan, Yousry, Brandt, & Dieterich, 2001; Brandt & Dieterich, 1999; Della-Justina et al., 2015; Frank et al., 2014). This absence of vestibular effects on primary visual cortical processing differs from the very early effects of visual information on vestibular processing, i.e. processing in core vestibular cortical input regions (i.e. PIVC, area 2v, are 3a) and subcortical vestibular centers (Dieterich & Brandt, 2015; Lopez & Blanke, 2011) is modulated by visual signals. This difference between visual effects on vestibular processing and vice versa, might be related to the different informational content in the respective sensory input. Specifically, vestibular input signals are head-centered and directly inform about the acceleration and tilt of the head in three-dimensional space, whereas visual input is eye-centered and informs about the distribution of light on the retina. Thus, functionally meaningful combination of these signals requires preprocessing of vestibular inputs to derive information about, e.g. coherent motion of a large field of visual input signaling self-motion, or the tilt of parallel lines informing about the visual vertical. Thus, upon initial processing, visual information can thus be functionally integrated with vestibular signals—and our results show this to happen not earlier than 83 ms after stimulus onset.

Neural sources of visual-vestibular convergence

Distributed source analysis over the significant temporal periods in which vestibular stimulation modulated response strength (i.e. GFP) and spatial configuration of underlying neural generators (i.e. GMD) localized these differences to activation differences in a cortical network including the right posterior insula, the bilateral PCN and cuneus, the left MOG, FG, and PHG.

Activation differences by vestibular stimulation had the highest level of significance in the right posterior insula. This region corresponds to the human PIVC (i.e. posterior insula cortex and parietal operculum; Lopez et al., 2012; zu Eulenburg et al., 2012) identified in numerous PET and fMRI studies in humans. There is evidence for predominantly ipsilateral activation of the posterior insula dependent on the handedness of the subjects (Dieterich et al., 2003). This matches to the results observed here: because out experimental subjects were right-handed and vestibular stimulation affected processing in the right (ipsilateral) posterior insula (Figure 2f). This result cannot be attributed to a specific rotation direction or stimulus attention differences, because equal amounts of clockwise and counterclockwise rotations were presented and the centrally presented visual stimulus extended across the left and right visual hemifield and was left-right symmetric (Figure 1a). It is currently not clear why there is hemispheric dominance for vestibular cortical processing, because, vestibular information already crosses three times before reaching the cortex (Dieterich & Brandt, 2015). This might be related to the functional relevance of vestibular information to body- and self-related processing, encoded in right-hemispheric networks (Astafiev, Stanley, Shulman, & Corbetta, 2004; Blanke, 2012; Limanowski, Lutti, & Blankenburg, 2014). In addition, we found activation modulation in the posterior part, but not in the medial or anterior part, or the insula, corresponds to the results from direct electrocortical insula stimulation showing only for stimulation in the posterior part vestibular sensation reported by the patient (Mazzola et al., 2014). In fMRI studies, visual stimulation deactivated or activated the posterior insula cortex (Bense et al., 2001; Della-Justina et al., 2015; Frank et al., 2014), further suggesting visual-vestibular convergence in this core vestibular cortical region. Our results extend previous results by showing that visual-vestibular signals converge in the posterior insula in a specific temporal interval (i.e. 83-119 ms post-stimulus interval) but not in a later period.

Source estimation analysis also showed vestibular contributions to activation in occipital, parietal and temporal regions that correspond to neural generators identified in previous checkerboard VEP studies (Di Russo et al., 2002). These significant activations largely overlap with the visual patieto-medial temporal pathway in monkeys (Kravitz, Saleem, Baker, & Mishkin, 2011), encoding of different visuo-spatial frames of references during whole-body motion, involved in distant-space perception, and memory-related spatial navigation.

We found visual-vestibular convergence in the bilateral PCN and cuneus. Resting-state functional connectivity in fMRI showed that the PCN functionally connects with all the regions found activated in the present study (Margulies et al., 2009). Specifically, the PCN posterior part is connected with the visual cortex, the anterior part is connected with the posterior and medial insula cortex, and the inferior part is connected with the PHG (Margulies et al., 2009). The PCN might thus be the hub of distributing upstream vestibular signals to distributed visual cortical regions. Previous fMRI studies found the PCN activated by optokinetic stimulation, which together with vestibular signals are relevant to self-motion processing (Cardin & Smith, 2010). This is supported by an fMRI study, that found the PCN and cuneus deactivated by combined visual-vestibular stimulation (Della-Justina et al., 2015). Functionally, the PCN has been linked to visuo-spatial imagery, episodic memory retrieval, and self-related functions including as visuo-spatial perspective taking and agency (Cavanna & Trimble, 2006; Freton et al., 2013). These functions might thus be supported by rapid (i.e. > 83 ms post-stimulus onset in our study) visual and vestibular signal integration in the PCN. Here we show that even passive motions of the body and simple visual stimulation without any specific cognitive task automatically activate the PCN, this corresponds to the functional connectivity data from the PCN at rest (Margulies et al., 2009). Our result might provide a ground for future experimental studies on the visual-vestibular contribution to PCN processing-related functions, i.e. perspective taking and agency in particular (see Deroualle & Lopez, 2014; Lenggenhager & Lopez, 2015; Pfeiffer, 2015, for reviews).

Source estimations also showed vestibular modulation of two neighboring regions: the FG and PHG. Both regions are the terminal of the visual parieto-medial temporal pathway relevant for visuo-spatial transformations, spatial navigation and episodic memory (Kravitz et al., 2011). Previous inverse solution results for static checkerboard VEPs of the P1 and N1 found the FG (Di Russo et al., 2002). The FG also encodes optokinetic stimulation (de Jong, Shipp, Skidmore, Frackowiak, & Zeki, 1994) and has been proposed a self-motion sensitive visual region (Deutschlander et al., 2004). In patients with vestibular loss, as compared to individuals with an intact vestibular system, the FG shows stronger activation for optokinetic stimuli, suggesting a role of the FG in visual substitution of lost vestibular function (Dieterich, Bauermann, Best, Stoeter, & Schlindwein, 2007). Similarly, the PHG showed visual-vestibular training-dependent changes of gray matter volume in slackliners (Hufner et al., 2011). In addition, the FG encoding socially relevant stimuli, i.e. the identity of face images, depending on the spatial configuration of the image, i.e. body inversion effect, thatcher illusion (Minnebusch, Keune, Suchan, & Daum, 2010; Reed, Stone, Bozova, & Tanaka, 2003; Thompson, 1980), which might be related to vestibular processing—a hypothesis no study has tested so far.

Visual-vestibular interaction: Independence of velocity storage?

To minimize non-vestibular sensory co-activations and mechanical noise in the recording equipment by platform accelerations and decelerations, our design focused on the constant-velocity rotation and the post-rotational periods when sensory inputs and noise levels were constant. Vestibular stimulation following sudden accelerations or decelerations decays exponentially over time and when evaluated in terms of the VOR and the perception of self motion has a TC_{VSM} of 15-20 s (Clement et al., 2008;

Cohen et al., 1981; Raphan et al., 1979) attributed to subcortical vestibular afferent processing (Goldberg & Fernandez, 1971; Meng, May, Dickman, & Angelaki, 2007). This duration exceeds the duration of inertial forces activating the peripheral vestibular organs (TC_{SCC} = 4-6 s; Buttner & Waespe, 1981; Fernandez & Goldberg, 1971). This particular stimulus decay function allowed us to confirm such a progressive decay of vestibular stimulation effects on GFP related to visual stimulation, and for estimating the time constants of the GFP effects to evaluate the dependence on VSM and SCC information processing respectively.

This analysis showed that vestibular effects on GFP decayed faster (TC_{EARLY} = 8.7 s, TC_{LATE} = 4.6 s) and thereby resembled the T_{SCC} (i.e. 4-6 s) rather than vestibular stimulation induced reflexive eye movements (TC_{VOR} = 14 s)—which resembled more to the previous estimates of the VSM time constant (Bertolini et al., 2011). This suggests that VSM might make little contributions to visual-vestibular interactions at the cortical level.

This is in line with previous evidences for visual inhibition of the feeling of self-motion related to VSM (Laurens & Angelaki, 2011). Moreover, it has been argued, that VSM directly contributes subcortical control of the VOR without the involvement of cortical processing (Bertolini et al., 2008). On the other hand, during constant-velocity rotation in darkness VSM contributes to self-motion perception that strongly depends on cortical processing. It is currently unknown what are the exact contributions of VSM to higher vestibular functions involving cortical processing. Our data suggests, however that basic visual-vestibular interactions seem to be relatively independent of prior vestibular afferent processing by VSM. We speculate, because two routes relay vestibular signals reach the cortex i.e. a thalamic and a non-thalamic projection (Dieterich & Brandt, 2015), our results might be based on vestibular inputs along the faster, non-thalamic, projection that might bypasses time-consuming afferent computations (i.e. VSM) in order to be rapidly available for multisensory cortical processing.

Limitations and outlook

Our study exploited the combination of natural selective stimulation of the horizontal SCCs and the high temporal resolution of EEG. However, we did not study visual-vestibular interactions during head acceleration/deceleration, which activates the SCCs, but we focused on the time periods following acceleration/deceleration for sensory confound control. The resulting vestibular stimulus consisted of both residual SCC activation and VSM, which cannot be fully dissociated in our study. Future work should also study visual-vestibular interactions during head accelerations to study the selective contribution of SCC signals to visual processing.

Furthermore, although participants were instructed to suppress the VOR by focusing on a central fixation point, the strong vestibular stimuli (i.e. 180 $°/s^2$) used here induced the VOR in most of the subjects resulting in jitter of the visual input to the retina. This might have affected our results. However, it is unlikely that our results could be entirely explained by eye movements independent of vestibular effects on visual processing. This is the case because the VOR was not time locked to the visual stimulation presentation reflected that event-related EOG analysis showed no significant differences between the vestibular and control condition. Furthermore, eye movement artifacts were removed from the EEG data by ICA and by amplitude thresholds. Finally, the fact that the inverse solution found activation in the insula cortex, which is a key vestibular region, reassures that our result were based on vestibular contributions to visual processing.

Conclusion

This study combined natural vestibular stimulation with electrical neuroimaging of visual cortical processing in humans. Electrical neuroimaging analysis showed that vestibular stimulation modulated the response strength (i.e. GFP) and topographical pattern (i.e. GMD) of VEPs as early as 83 ms after stimulus onset. Distributed source estimations localized these vestibular effects on visual processing to the right posterior insula cortex—a core vestibular input region to the cortex—and several regions of the parieto-medial temporal visual pathway involved in self-motion processing and spatial navigation. These vestibular effects on visual processing decayed rapidly (TC_{EARLY} = 8.7 s and TC_{LATE} = 4.6 s) resembling thus the temporal dynamics of afferent vestibular input from the SCCs, which was distinct from the prolonged decay of the VOR, related to subcortical vestibular processing. Collectively these results indicate temporal-specific effects of natural vestibular stimulation on visual cortical processing relevant to self-motion processing.

References

Akbarian, S., Grüsser, O. J., & Guldin, W. O. (1993). Corticofugal projections to the vestibular nuclei in squirrel monkeys: further evidence of multiple cortical vestibular fields. *The Journal of Comparative Neurology, 332*(1), 89-104. doi: 10.1002/cne.903320107

Antunes, A., Glover, P. M., Li, Y., Mian, O. S., & Day, B. L. (2012). Magnetic field effects on the vestibular system: calculation of the pressure on the cupula due to ionic current-induced Lorentz force. *Physics in Medicine and Biology, 57*(14), 4477-4487. doi: 10.1088/0031-9155/57/14/4477

Ary, J. P., Klein, S. A., & Fender, D. H. (1981). Location of sources of evoked scalp potentials: corrections for skull and scalp thicknesses. *IEEE Transactions on Biomedical Engineering, 28*(6), 447-452. doi: 10.1109/TBME.1981.324817

Astafiev, S. V., Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience, 7*(5), 542-548. doi: 10.1038/nn1241

Avillac, M., Deneve, S., Olivier, E., Pouget, A., & Duhamel, J. R. (2005). Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience, 8*(7), 941-949. doi: 10.1038/nn1480

Bense, S., Stephan, T., Yousry, T. A., Brandt, T., & Dieterich, M. (2001). Multisensory cortical signal increases and decreases during vestibular galvanic stimulation (fMRI). *Journal of Neurophysiology, 85*(2), 886-899.

Bertolini, G., Bockisch, C. J., Straumann, D., Zee, D. S., & Ramat, S. (2008). Estimating the time constant of pitch rVOR by separation of otoliths and semicircular canals contributions. *Conference Proceedings: IEEE Engineering in Medicine and Biology Society, 2008*, 1060-1063. doi: 10.1109/IEMBS.2008.4649342

Bertolini, G., Ramat, S., Laurens, J., Bockisch, C. J., Marti, S., Straumann, D., & Palla, A. (2011). Velocity storage contribution to vestibular self-motion perception in healthy human subjects. *Journal of Neurophysiology, 105*(1), 209-223. doi: 10.1152/jn.00154.2010

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience, 13*(8), 556-571. doi: 10.1038/nrn3292

Brandt, T., Bartenstein, P., Janek, A., & Dieterich, M. (1998). Reciprocal inhibitory visual-vestibular interaction. Visual motion stimulation deactivates the parieto-insular vestibular cortex. *Brain, 121 (Pt 9)*, 1749-1758.

Brandt, T., & Dieterich, M. (1999). The vestibular cortex. Its locations, functions, and disorders. *Annals of the New York Academy of Sciences, 871*, 293-312.

Brandt, T., Glasauer, S., Stephan, T., Bense, S., Yousry, T. A., Deutschlander, A., & Dieterich, M. (2002). Visual-vestibular and visuovisual cortical interaction: new insights from fMRI and pet. *Annals of the New York Academy of Sciences, 956*, 230-241.

Bremmer, F., Klam, F., Duhamel, J. R., Ben Hamed, S., & Graf, W. (2002). Visual-vestibular interactive responses in the macaque ventral intraparietal area (VIP). *The European Journal of Neuroscience, 16*(8), 1569-1586.

Buttner, U., & Buettner, U. W. (1978). Parietal cortex (2v) neuronal activity in the alert monkey during natural vestibular and optokinetic stimulation. *Brain Research, 153*(2), 392-397.

Buttner, U., & Waespe, W. (1981). Vestibular nerve activity in the alert monkey during vestibular and optokinetic nystagmus. *Experimental Brain Research, 41*(3-4), 310-315.

Cardin, V., & Smith, A. T. (2010). Sensitivity of human visual and vestibular cortical regions to egomotion-compatible visual stimulation. *Cerebral Cortex, 20*(8), 1964-1973. doi: 10.1093/cercor/bhp268

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: a review of its functional anatomy and behavioural correlates. *Brain, 129*(Pt 3), 564-583. doi: 10.1093/brain/awl004

Chen, A., DeAngelis, G. C., & Angelaki, D. E. (2010). Macaque parieto-insular vestibular cortex: responses to self-motion and optic flow. *The Journal of Neuroscience, 30*(8), 3022-3042. doi: 10.1523/JNEUROSCI.4029-09.2010

Chen, A., DeAngelis, G. C., & Angelaki, D. E. (2011). Convergence of vestibular and visual self-motion signals in an area of the posterior sylvian fissure. *The Journal of Neuroscience, 31*(32), 11617-11627. doi: 10.1523/JNEUROSCI.1266-11.2011

Chen, X., Deangelis, G. C., & Angelaki, D. E. (2013a). Diverse Spatial Reference Frames of Vestibular Signals in Parietal Cortex. *Neuron*. doi: 10.1016/j.neuron.2013.09.006

Chen, X., Deangelis, G. C., & Angelaki, D. E. (2013b). Eye-centered representation of optic flow tuning in the ventral intraparietal area. *The Journal of Neuroscience, 33*(47), 18574-18582. doi: 10.1523/JNEUROSCI.2837-13.2013

Cheron, G., Leroy, A., Palmero-Soler, E., De Saedeleer, C., Bengoetxea, A., Cebolla, A. M., . . . McIntyre, J. (2014). Gravity influences top-down signals in visual processing. *Plos One, 9*(1), e82371. doi: 10.1371/journal.pone.0082371

Clement, G., Tilikete, C., & Courjon, J. H. (2008). Retention of habituation of vestibulo-ocular reflex and sensation of rotation in humans. *Experimental Brain Research, 190*(3), 307-315. doi: 10.1007/s00221-008-1471-0

Cohen, B., Henn, V., Raphan, T., & Dennett, D. (1981). Velocity storage, nystagmus, and visual-vestibular interactions in humans. *Annals of the New York Academy of Sciences, 374*, 421-433.

Colby, C. L., Duhamel, J. R., & Goldberg, M. E. (1993). Ventral intraparietal area of the macaque: anatomic location and visual response properties. *Journal of Neurophysiology, 69*(3), 902-914.

Day, B. L., & Fitzpatrick, R. C. (2005). Virtual head rotation reveals a process of route reconstruction from human vestibular signals. *The Journal of Physiology, 567*(Pt 2), 591-597. doi: 10.1113/jphysiol.2005.092544

de Jong, B. M., Shipp, S., Skidmore, B., Frackowiak, R. S., & Zeki, S. (1994). The cerebral activity related to the visual perception of forward motion in depth. *Brain, 117 (Pt 5)*, 1039-1054.

Della-Justina, H. M., Gamba, H. R., Lukasova, K., Nucci-da-Silva, M. P., Winkler, A. M., & Amaro, E., Jr. (2015). Interaction of brain areas of visual and vestibular simultaneous activity with fMRI. *Experimental Brain Research, 233*(1), 237-252. doi: 10.1007/s00221-014-4107-6

Deroualle, D., & Lopez, C. (2014). Toward a vestibular contribution to social cognition. *Frontiers in Integrative Neuroscience, 8*, 16. doi: 10.3389/fnint.2014.00016

Deutschlander, A., Bense, S., Stephan, T., Schwaiger, M., Brandt, T., & Dieterich, M. (2002). Sensory system interactions during simultaneous vestibular and visual stimulation in PET. *Human Brain Mapping, 16*(2), 92-103.

Deutschlander, A., Bense, S., Stephan, T., Schwaiger, M., Dieterich, M., & Brandt, T. (2004). Rollvection versus linearvection: comparison of brain activations in PET. *Human Brain Mapping, 21*(3), 143-153. doi: 10.1002/hbm.10155

Di Russo, F., Martinez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping, 15*(2), 95-111.

Dieterich, M., Bauermann, T., Best, C., Stoeter, P., & Schlindwein, P. (2007). Evidence for cortical visual substitution of chronic bilateral vestibular failure (an fMRI study). *Brain, 130*(Pt 8), 2108-2116. doi: 10.1093/brain/awm130

Dieterich, M., Bense, S., Lutz, S., Drzezga, A., Stephan, T., Bartenstein, P., & Brandt, T. (2003). Dominance for vestibular cortical function in the non-dominant hemisphere. *Cerebral Cortex, 13*(9), 994-1007.

Dieterich, M., & Brandt, T. (2015). The bilateral central vestibular system: its pathways, functions, and disorders. *Annals of the New York Academy of Sciences*. doi: 10.1111/nyas.12585

Duffy, C. J., & Wurtz, R. H. (1991). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *Journal of neurophysiology, 65*(6), 1329-1345.

Duhamel, J. R., Bremmer, F., Ben Hamed, S., & Graf, W. (1997). Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature, 389*(6653), 845-848. doi: 10.1038/39865

Fernandez, C., & Goldberg, J. M. (1971). Physiology of peripheral neurons innervating semicircular canals of the squirrel monkey. II. Response to sinusoidal stimulation and dynamics of peripheral vestibular system. *Journal of Neurophysiology, 34*(4), 661-675.

Ferre, E. R., Bottini, G., & Haggard, P. (2012). Vestibular inputs modulate somatosensory cortical processing. *Brain Structure and Function, 217*(4), 859-864. doi: 10.1007/s00429-012-0404-7

Ferre, E. R., Kaliuzhna, M., Herbelin, B., Haggard, P., & Blanke, O. (2014). Vestibular-somatosensory interactions: effects of passive whole-body rotation on somatosensory detection. *Plos One, 9*(1), e86379. doi: 10.1371/journal.pone.0086379

Fetsch, C. R., Wang, S., Gu, Y., Deangelis, G. C., & Angelaki, D. E. (2007). Spatial reference frames of visual, vestibular, and multimodal heading signals in the dorsal subdivision of the medial superior temporal area. *The Journal of Neuroscience, 27*(3), 700-712. doi: 10.1523/JNEUROSCI.3553-06.2007

Frank, S. M., Baumann, O., Mattingley, J. B., & Greenlee, M. W. (2014). Vestibular and visual responses in human posterior insular cortex. *Journal of Neurophysiology, 112*(10), 2481-2491. doi: 10.1152/jn.00078.2014

Fredrickson, J. M., Scheid, P., Figge, U., & Kornhuber, H. H. (1966). Vestibular nerve projection to the cerebral cortex of the rhesus monkey. *Experimental Brain Research, 2*(4), 318-327.

Freton, M., Lemogne, C., Bergouignan, L., Delaveau, P., Lehericy, S., & Fossati, P. (2013). The eye of the self: precuneus volume and visual perspective during autobiographical memory retrieval. *Brain Structure and Function*. doi: 10.1007/s00429-013-0546-2

Goldberg, J. M., & Fernandez, C. (1971). Physiology of peripheral neurons innervating semicircular canals of the squirrel monkey. I. Resting discharge and response to constant angular accelerations. *Journal of Neurophysiology, 34*(4), 635-660.

Grave de Peralta Menendez, R., Gonzalez Andino, S., Lantz, G., Michel, C. M., & Landis, T. (2001). Noninvasive localization of electromagnetic epileptic activity. I. Method descriptions and simulations. *Brain Topography, 14*(2), 131-137.

Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia, 44*(6), 845-859. doi: 10.1016/j.neuropsychologia.2005.09.009

Grüsser, O. J., Pause, M., & Schreiter, U. (1990a). Localization and responses of neurones in the parieto-insular vestibular cortex of awake monkeys (Macaca fascicularis). *The Journal of Physiology, 430*, 537-557.

Grüsser, O. J., Pause, M., & Schreiter, U. (1990b). Vestibular neurones in the parieto-insular cortex of monkeys (Macaca fascicularis): visual and neck receptor responses. *The Journal of Physiology, 430*, 559-583.

Gu, Y., DeAngelis, G. C., & Angelaki, D. E. (2007). A functional link between area MSTd and heading perception based on vestibular signals. *Nature Neuroscience, 10*(8), 1038-1047. doi: 10.1038/nn1935

Guthrie, D., & Buchwald, J. S. (1991). Significance testing of difference potentials. *Psychophysiology, 28*(2), 240-244.

Hufner, K., Binetti, C., Hamilton, D. A., Stephan, T., Flanagin, V. L., Linn, J., . . . Brandt, T. (2011). Structural and functional plasticity of the hippocampal formation in professional dancers and slackliners. *Hippocampus, 21*(8), 855-865. doi: 10.1002/hipo.20801

Koenig, T., & Melie-Garcia, L. (2010). A method to determine the presence of averaged event-related fields using randomization tests. *Brain Topography, 23*(3), 233-242. doi: 10.1007/s10548-010-0142-1

Kovacs, G., Raabe, M., & Greenlee, M. W. (2008). Neural correlates of visually induced self-motion illusion in depth. *Cerebral Cortex, 18*(8), 1779-1787. doi: 10.1093/cercor/bhm203

Kravitz, D. J., Saleem, K. S., Baker, C. I., & Mishkin, M. (2011). A new neural framework for visuospatial processing. *Nature Reviews Neuroscience, 12*(4), 217-230. doi: 10.1038/nrn3008

Laurens, J., & Angelaki, D. E. (2011). The functional significance of velocity storage and its dependence on gravity. *Experimental Brain Research, 210*(3-4), 407-422. doi: 10.1007/s00221-011-2568-4

Lehmann, D., & Skrandies, W. (1980). Reference-free identification of components of checkerboard-evoked multichannel potential fields. *Electroencephalography and Clinical Neurophysiology, 48*(6), 609-621.

Leigh, R. J., & Zee, D. S. (2006). *The neurology of eye movements*. Oxford: Oxford University Press.

Lenggenhager, B., & Lopez, C. (2015). Vestibular contributions to the sense of body, self, and others. In T. Metzinger & J. M. Windt (Eds.), *Open MIND*. Frankfurt: MIND-Group.

Limanowski, J., Lutti, A., & Blankenburg, F. (2014). The extrastriate body area is involved in illusory limb ownership. *Neuroimage, 86*, 514-524. doi: 10.1016/j.neuroimage.2013.10.035

Lopez, C., & Blanke, O. (2011). The thalamocortical vestibular system in animals and humans. *Brain Research Reviews, 67*(1-2), 119-146. doi: 10.1016/j.brainresrev.2010.12.002

Lopez, C., Blanke, O., & Mast, F. W. (2012). The human vestibular cortex revealed by coordinate-based activation likelihood estimation meta-analysis. *Neuroscience, 212*, 159-179. doi: 10.1016/j.neuroscience.2012.03.028

Margulies, D. S., Vincent, J. L., Kelly, C., Lohmann, G., Uddin, L. Q., Biswal, B. B., . . . Petrides, M. (2009). Precuneus shares intrinsic functional architecture in humans and monkeys. *Proceedings of the National Academy of Sciences, 106*(47), 20069-20074. doi: 10.1073/pnas.0905314106

Marmor, M. F., Brigell, M. G., McCulloch, D. L., Westall, C. A., Bach, M., & International Society for Clinical Electrophysiology of, Vision. (2011). ISCEV standard for clinical electro-oculography (2010 update). *Documenta Ophthalmologica, 122*(1), 1-7. doi: 10.1007/s10633-011-9259-0

Mazzola, L., Lopez, C., Faillenot, I., Chouchou, F., Mauguiere, F., & Isnard, J. (2014). Vestibular responses to direct stimulation of the human insular cortex. *Annals of Neurology, 76*(4), 609-619. doi: 10.1002/ana.24252

Meng, H., May, P. J., Dickman, J. D., & Angelaki, D. E. (2007). Vestibular signals in primate thalamus: properties and origins. *The Journal of Neuroscience, 27*(50), 13590-13602. doi: 10.1523/JNEUROSCI.3931-07.2007

Michel, C. M., Murray, M. M., Lantz, G., Gonzalez, S., Spinelli, L., & Grave de Peralta, R. (2004). EEG source imaging. *Clinical Neurophysiology, 115*(10), 2195-2222. doi: 10.1016/j.clinph.2004.06.001

Minnebusch, D. A., Keune, P. M., Suchan, B., & Daum, I. (2010). Gradual inversion affects the processing of human body shapes. *Neuroimage, 49*(3), 2746-2755. doi: 10.1016/j.neuroimage.2009.10.046

Murray, M. M., Brunet, D., & Michel, C. M. (2008). Topographic ERP analyses: a step-by-step tutorial review. *Brain Topography, 20*(4), 249-264. doi: 10.1007/s10548-008-0054-5

Nolan, H., Whelan, R., & Reilly, R. B. (2010). FASTER: Fully Automated Statistical Thresholding for EEG artifact Rejection. *Journal of Neuroscience Methods, 192*(1), 152-162. doi: 10.1016/j.jneumeth.2010.07.015

Odkvist, L. M., Schwarz, D. W., Fredrickson, J. M., & Hassler, R. (1974). Projection of the vestibular nerve to the area 3a arm field in the squirrel monkey (saimiri sciureus). *Experimental Brain Research, 21*(1), 97-105.

Pfeiffer, C. (2015). Multisensory spatial mechanisms of the bodily self and social cognition-A commentary on Vittorio Gallese and Valentina Cuccio. In T. Metzinger & J. M. Windt (Eds.), *Open MIND*. Frankfurt: MIND-Group.

Phillips, C. G., Powell, T. P., & Wiesendanger, M. (1971). Projection from low-threshold muscle afferents of hand and forearm to area 3a of baboon's cortex. *The Journal of Physiology, 217*(2), 419-446.

Prsa, M., Gale, S., & Blanke, O. (2012). Self-motion leads to mandatory cue fusion across sensory modalities. *Journal of Neurophysiology, 108*(8), 2282-2291. doi: 10.1152/jn.00439.2012

Raphan, T., Matsuo, V., & Cohen, B. (1979). Velocity storage in the vestibulo-ocular reflex arc (VOR). *Experimental Brain Research, 35*(2), 229-248.

Reed, C. L., Stone, V. E., Bozova, S., & Tanaka, J. (2003). The body-inversion effect. *Psychological Science, 14*(4), 302-308.

Roberts, D. C., Marcelli, V., Gillen, J. S., Carey, J. P., Della Santina, C. C., & Zee, D. S. (2011). MRI magnetic field stimulates rotational sensors of the brain. *Current Biology, 21*(19), 1635-1640. doi: 10.1016/j.cub.2011.08.029

Sinha, N., Zaher, N., Shaikh, A. G., Lasker, A. G., Zee, D. S., & Tarnutzer, A. A. (2008). Perception of self motion during and after passive rotation of the body around an earth-vertical axis. *Progress in Brain Research, 171*, 277-281. doi: 10.1016/S0079-6123(08)00639-0

Slotnick, S. D., Klein, S. A., Carney, T., Sutter, E., & Dastmalchi, S. (1999). Using multi-stimulus VEP source localization to obtain a retinotopic map of human primary visual cortex. *Clinical Neurophysiology, 110*(10), 1793-1800.

Spinelli, L., Andino, S. G., Lantz, G., Seeck, M., & Michel, C. M. (2000). Electromagnetic inverse solutions in anatomically constrained spherical head models. *Brain Topography, 13*(2), 115-125.

Talairach, J, & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.

Thompson, P. (1980). Margaret Thatcher: a new illusion. *Perception, 9*(4), 483-484.

van Elk, M., & Blanke, O. (2013). Imagined own-body transformations during passive self-motion. *Psychological Research*. doi: 10.1007/s00426-013-0486-8

van Elk, Michiel, & Blanke, Olaf. (2012). Balancing bistable perception during self-motion. *Experimental Brain Research, 222*(3), 219-228. doi: 10.1007/s00221-012-3209-2

Waespe, W., & Henn, V. (1978). Conflicting visual-vestibular stimulation and vestibular nucleus activity in alert monkeys. *Experimental Brain Research, 33*(2), 203-211.

Wenzel, R., Bartenstein, P., Dieterich, M., Danek, A., Weindl, A., Minoshima, S., . . . Brandt, T. (1996). Deactivation of human visual cortex during involuntary ocular oscillations. A PET activation study. *Brain, 119 (Pt 1)*, 101-110.

zu Eulenburg, P., Caspers, S., Roski, C., & Eickhoff, S. B. (2012). Meta-analytical definition and functional connectivity of the human vestibular cortex. *Neuroimage, 60*(1), 162-169. doi: 10.1016/j.neuroimage.2011.12.032

3 General discussion

In this final section I will summarize the main results of my thesis and discuss their methodological and theoretical implications.

3.1 Summary of results

In Part A (Studies 1-3), for studying multisensory mechanisms of 1PP we developed a novel experimental platform that allowed for systematic, well-controlled, and replicable induction of the FBI in more than 200 participants leading to 5 publications (i.e. 3 papers from Studies 1-3, and Appendix 1-2).

Using this virtual reality and robotics platform, we achieved experimental manipulations of the 1PP by multisensory conflict between visual, vestibular, and somatosensory signals. This showed that subjective 1PP experience is malleable und depends on the integration of multisensory signals, in particular on visual and vestibular gravity cues. Globally, our studies showed that experimental manipulations of 1PP were functionally related to self-location changes (Study 1 and 3), but distinct from self-identification changes induced by our experimental manipulations (Studies 1-3).

In Part B (Studies 4-5), we were the first to combine natural vestibular stimulation with non-invasive electrical neuroimaging of multisensory (i.e. somatosensory and visual) cortical processing in humans.

Results from the EEG studies of my thesis showed temporal-specific vestibular effects on somatosensory and visual cortical processing. Vestibular stimulation modulated early somatosensory cortical processing (> 24 ms post-stimulus) related to processing in primary somatosensory cortex (Study 4), mid-late visual cortical processing (> 83 ms post-stimulus) related to extrastriate but not primary visual cortical processing, and higher-tier somatosensory (> 97 ms post-stimulus) and visual (> 178 ms post-stimulus) cortical processing steps. The temporal characteristics of these multisensory effects (i.e. time constant comparison) were highly similar to the temporal decay of peripheral vestibular input from vestibular stimulations, confirming a vestibular origin of the effects recorded in EEG. Thus, with our method we were able to identify the temporal characteristics of vestibular contribution to multisensory cortical processing.

Inverse solution localized these effects to the posterior insula cortex (Study 5), a core vestibular cortical input region in line with previous fMRI studies, and two multisensory regions in the middle temporal gyrus (Study 4) and the precuneus (Study 5), extending previous fMRI studies.

3.2 First-person perspective: Visual-vestibular contributions

What novel insight have we gained from our studies on 1PP? First of all, we showed that visual signals are highly relevant to 1PP experience. In Study 1, visual dependence in subjective visual vertical ratings correlated with visual-stimulus congruent 1PP experience during the FBI. In Study 2, the combined visuo-spatial viewpoint and visual body stimulus information induced viewpoint-congruent changes of 1PP experience. Finally, in Study 3 the direction of visual gravity motion congruently affected the experienced direction of the 1PP. This suggests that visual-spatial and in particular visual-gravitational signals strongly contributed 1PP experience.

However, it is unlikely that these effects were based only on judgments about the visual stimuli, because individual differences of 1PP in Study 1 were found for the exact same visual stimulus. Indeed, participants were asked to judge their subjective visual experience, however, with respect to an invisible external environment to which they had access only by vestibular and somatosensory signals. In addition, blind people or in sighted people in darkness persist experiencing a centered and spatially directed 1PP that under these conditions more likely depends on non-visual multisensory cues, such as auditory, proprioceptive, and vestibular cues.

Another important result of this thesis is that 1PP depended on vestibular otolithic information, i.e. on visual-vestibular integration in particular (Study 1). However, we did not manipulate vestibular inputs during these studies, but kept them constant throughout our experiments on 1PP. This raises the question whether vestibular stimulation might induce changes of 1PP experience similar to those evoked by visual

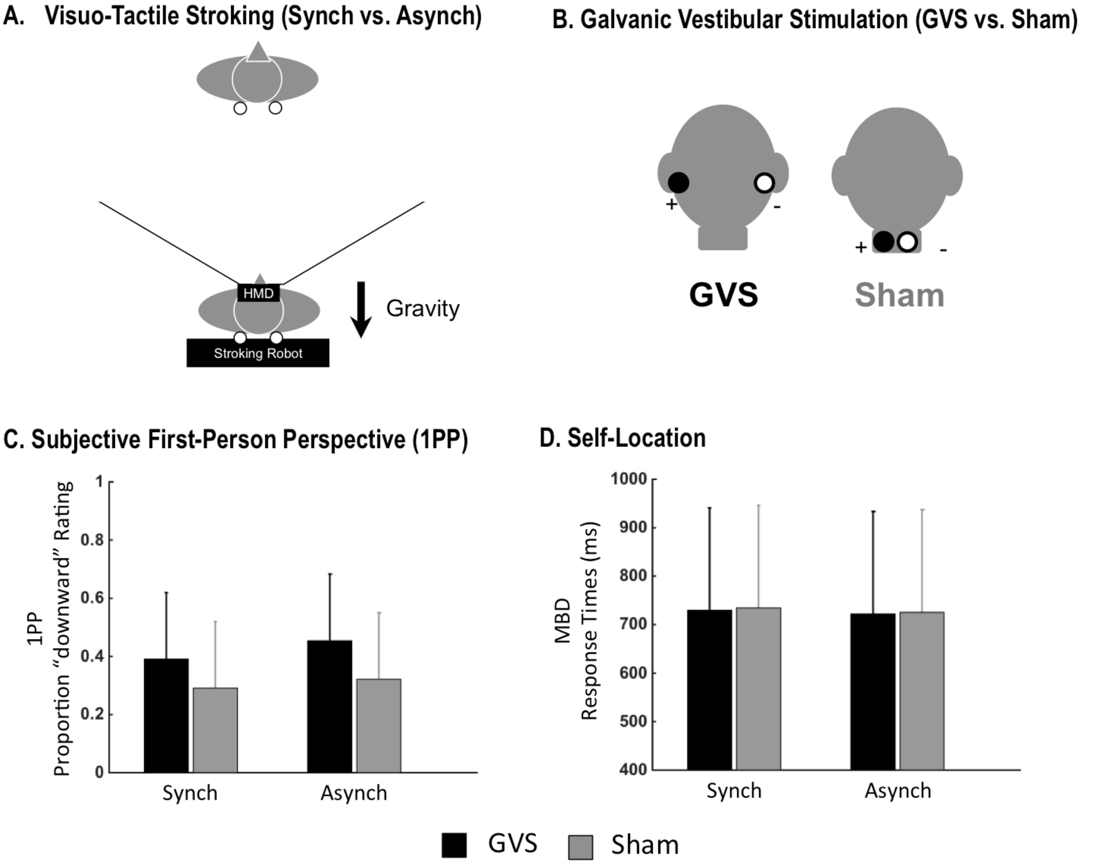

Figure 8 FBI study in 16 healthy subjects (a) the same virtual reality – robotics based experimental platform and experimental procedure of the FBI studies in Studies 1-3 was used. Synchronous (Synch) versus asynchronous (Asynch) visuo-tactile stroking were paired with (b) left-anodal right-cathodal bipolar GVS or identical stimulation at the neck that does not activate the vestibular system (Sham). (c-d) The analysis using repeated measures ANOVAs showed no main effects and no significant ($p > .05$) interactions between Stroking and Vestibular Stimulation for 1PP ratings, for self-location, and self-identification (not shown here; *unpublished study, collaborators: Pfeiffer C, Grivaz P, Blanke O., personal contribution: Experimental design, data analysis*).

manipulations. We tested this prediction in an additional study using GVS (**Figure 8**). We found no effects of GVS on 1PP or self-location. In fact, no basic changes of self-location or 1PP were induced when comparing the GVS and the Sham condition. We think this was related to the fact that GVS primarily induces rotational vestibular signals by activation of the semicircular canals, giving rise to the perception of rotational roll motion (Day & Fitzpatrick, 2005). This contrasts with our results from Studies 1-3 where linear acceleration signals related to gravity, i.e. involving otolith organs, affected 1PP. This might indicate, that under the motionless conditions on the robotic device, primarily gravitational signals contribute to 1PP, though we cannot rule out semicircular canal contributions to other conditions not tested here when the body is in motion.

Another explanation for the absence of effects in this study might be related to the fact that both the GVS and the Sham stimulation are co-activating the somatosensory system. Thus, it is likely that the absence of differential effects of GVS versus Sham can be attributed to the somatosensory stimulations that abolished the induction of the FBI, i.e. which depend on the visual-somatosensory integration.

Thus, our data provide positive evidence for the contribution of constant gravitational vestibular signals to 1PP, but we did not address how rotational vestibular signals or changes in vestibular input affect 1PP, which remains open for future studies.

3.3 Vestibular EEG: Spatio-temporal mapping of the human vestibular cortex

Using natural vestibular stimulation during high-density EEG recordings allowed us to identify the temporal signatures of vestibular contribution to multisensory processing. Vestibular stimulation influenced early somatosensory and visual processing by reduction of the evoked response amplitude. This might reflect an inhibition mechanism that assigns less weight to unexpected sensory signals during ongoing vestibular inputs in order to improve the perception of self-motion, e.g. by suppressing processing of signals related to the own body movements (Brandt et al., 1998). Here we support the findings of vestibular inhibition of visual processing from fMRI showing when these interactions happen in the brain.

The source estimation analysis of our EEG data provided a satisfying spatial resolution, certainly below those of fMRI, but still sufficient to identify a key vestibular cortical input region in the posterior insula, underlying the vestibular effects on visual evoked responses. We thus extend previous human fMRI approaches, by information about the temporal resolution of the multisensory processing in the vestibular cortex. Meta analysis in fMRI data showed that the parietal operculum (OP2 region) and the posterior insula are the main hubs of vestibular input to the human cortex (Lopez, Blanke, et al., 2012; zu Eulenburg et al., 2012). My thesis shows in addition that posterior insula engages visual-vestibular signals integration as early as 83 ms post-stimulus onset.

Moreover, source estimations localized vestibular effects to the middle temporal gyrus and precuneus, two regions relevant to multisensory processing, and spatial navigation (Della-Justina et al., 2015; Freton et al., 2013; Kravitz, Saleem, Baker, & Mishkin, 2011; Margulies et al., 2009). We showed that these regions also integrated vestibular and multisensory inputs during passive sensory stimulations unrelated to specific cognitive tasks.

3.4 Vestibular contribution to first- and second-person perspective

Our data from healthy subjects shows neural evidence for automatic rapid integration of visual, somatosensory, and visual signals, collectively contributing to 1PP, an important aspect of consciousness and subjectivity. Recently, several authors have proposed that multisensory signal integration also is a fundamental basis of inter-subjectivity, i.e. the second person perspective or social cognition.

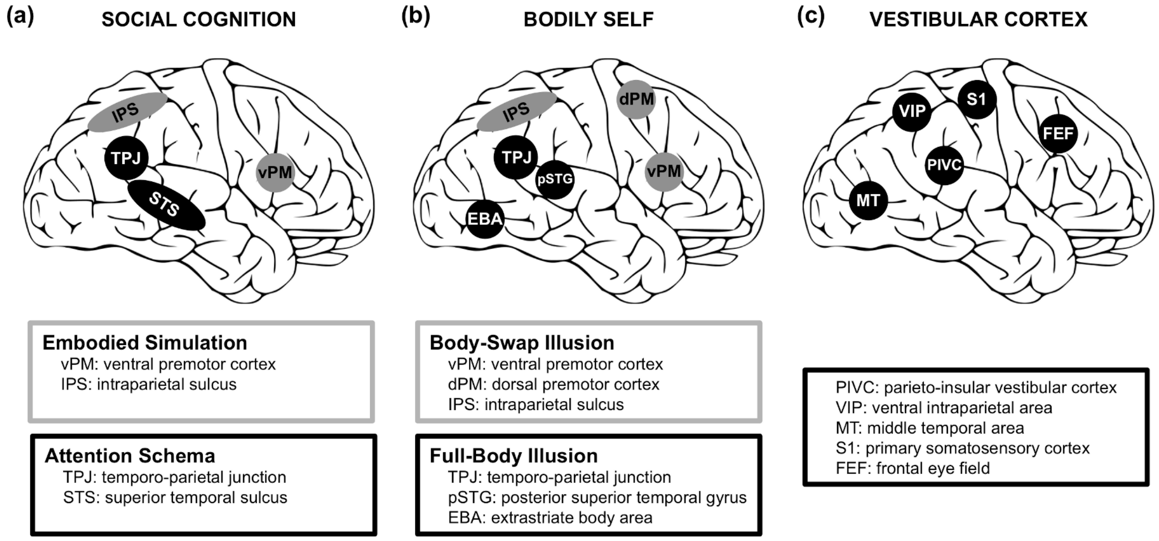

Figure 9 Summary of cortical brain regions involved in social cognition, BSC (*bodily self*), and vestibular processing. (a) Whereas for *social cognition* there is little overlap between the brain regions proposed relevant for the *attention schema* (in black) and *embodied simulation* (in gray), both sets of brain regions overlap with (b) the brain network of the BSC as identified by FBI experiments (*full-body illusion*) manipulating self-location and 1PP (in black) and the body-swap illusion manipulating mainly body ownership (in gray). (c) The human vestibular cortical regions (in black) are widely distributed and overlap with several regions relevant to both the BSC and social cognition (Pfeiffer, 2015).

For instance, according to the embodied simulation theory (Gallese & Sinigaglia, 2011) the brain maps the actions and sensations observed in others to the sensorimotor system of the observer and thereby infers the action goals, and intentions, of the other. This theory capitalizes on mirror neurons, i.e. canonical neurons activated for executing or observing actions, in the ventral premotor cortex and intraparietal sulcus (**Figure 9**a). A totally different set of brain regions has been proposed relevant to social cognition according to the attention schema theory (see Introduction), according to which we understand others by monitoring their states of attention (Graziano & Kastner, 2011a, 2011b). This mechanism supposedly draws on superior-temporal and temporo-parietal cortical regions (**Figure 9**a).

Interestingly, both different sets of brain mechanisms involved in embodied simulation and the attention schema overlap with the brain networks encoding experimentally induced changes of 1PP and self-location (during FBI, **Figure 9**b) and of self-identification (during body-swap illusion, i.e. a different type of visuo-tactile stroking-induced illusion induced without spatial conflict between the virtual body and the participant's body location; Petkova, Bjornsdotter, et al., 2011; **Figure 9**b). Thus social cognition (i.e. the second-person perspective) draws on neural processing involved in the first-person experiences of BSC. Importantly, my thesis shows, that the vestibular system contributes to BSC (see also overlap between **Figure 9**b and c). Accordingly, given the clear neuroanatomical overlap of BSC and social cognition, I predict hat vestibular information not only contributes to BSC, but also strongly contributes to social cognition (see Deroualle & Lopez, 2014; Lenggenhager & Lopez, 2015; Pfeiffer, 2015, for reviews). Vestibular signals might play a particularly potent role for decoding and dissociating the whole-body movements observed in others from the own body movements. In addition, vestibular processing might strongly contribute to routinely perform mental spatial transformations of the visuo-spatial perspective that help "putting oneself in the shoes of the other"—in line with work showing vestibular signals affect mental own-body transformations (Falconer & Mast, 2012; van Elk & Blanke, 2013). Thus, future research should further explore how BSC relates to social cognition and vestibular processing. The results of my thesis provide a good starting point for such an approach, by revealing the neural signatures of vestibular contributions to multisensory processing, and by showing that vestibular signals strongly contribute to spatial aspects of BSC

Bibliography

Adam, C., & Tannery, P. (1964). *Oeuvres de Descartes*. Paris.

Adler, D., Herbelin, B., Similowski, T., & Blanke, O. (2014). Breathing and sense of self: visuo-respiratory conflicts alter body self-consciousness. *Respiratory Physiology and Neurobiology, 203*, 68-74. doi: 10.1016/j.resp.2014.08.003

Alsmith, A. J., & Longo, M. R. (2014). Where exactly am I? Self-location judgements distribute between head and torso. *Consciousness and Cognition, 24*, 70-74. doi: 10.1016/j.concog.2013.12.005

Angelaki, D. E., & Cullen, K. E. (2008). Vestibular system: the many facets of a multimodal sense. *Annual Review of Neuroscience, 31*, 125-150. doi: 10.1146/annurev.neuro.31.060407.125555

Angelaki, D. E., Merfeld, D. M., & Hess, B. J. (2000). Low-frequency otolith and semicircular canal interactions after canal inactivation. *Experimental Brain Research, 132*(4), 539-549.

Antunes, A., Glover, P. M., Li, Y., Mian, O. S., & Day, B. L. (2012). Magnetic field effects on the vestibular system: calculation of the pressure on the cupula due to ionic current-induced Lorentz force. *Physics in Medicine and Biology, 57*(14), 4477-4487. doi: 10.1088/0031-9155/57/14/4477

Aspell, J. E., Heydrich, L., Marillier, G., Lavanchy, T., Herbelin, B., & Blanke, O. (2013). Turning Body and Self Inside Out: Visualized Heartbeats Alter Bodily Self-Consciousness and Tactile Perception. *Psychological Science*. doi: 10.1177/0956797613498395

Aspell, J. E., Lavanchy, T., Lenggenhager, B., & Blanke, O. (2010). Seeing the body modulates audiotactile integration. *The European Journal of Neuroscience, 31*(10), 1868-1873. doi: 10.1111/j.1460-9568.2010.07210.x

Aspell, J. E., Lenggenhager, B., & Blanke, O. (2009). Keeping in touch with one's self: multisensory mechanisms of self-consciousness. *Plos One, 4*(8), e6488. doi: 10.1371/journal.pone.0006488

Baars, B. J. (1988). *A cognitive theory of consciousness*. New York: Cambridge University Press.

Bense, S., Stephan, T., Yousry, T. A., Brandt, T., & Dieterich, M. (2001). Multisensory cortical signal increases and decreases during vestibular galvanic stimulation (fMRI). *Journal of Neurophysiology, 85*(2), 886-899.

Bertolini, G., Ramat, S., Laurens, J., Bockisch, C. J., Marti, S., Straumann, D., & Palla, A. (2011). Velocity storage contribution to vestibular self-motion perception in healthy human subjects. *Journal of Neurophysiology, 105*(1), 209-223. doi: 10.1152/jn.00154.2010

Bertossa, F., Besa, M., Ferrari, R., & Ferri, F. (2008). Point zero: a phenomenological inquiry into the seat of consciousness. *Perceptual and Motor Skills, 107*(2), 323-335. doi: 10.2466/pms.107.2.323-335

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience, 13*(8), 556-571. doi: 10.1038/nrn3292

Blanke, O., Landis, T., Spinelli, L., & Seeck, M. (2004). Out-of-body experience and autoscopy of neurological origin. *Brain, 127*, 243-258. doi: 10.1093/brain/awh040

Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences, 13*(1), 7-13. doi: 10.1016/j.tics.2008.10.003

Blanke, O., & Mohr, C. (2005). Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin Implications for neurocognitive mechanisms of corporeal awareness and self-consciousness. *Brain Research Reviews 50*(1), 184-199. doi: 10.1016/j.brainresrev.2005.05.008

Blanke, O., Ortigue, S., Landis, T., & Seeck, M. (2002). Stimulating illusory own-body perceptions. *Nature, 419*(6904), 269-270. doi: 10.1038/419269a

Bottini, G., Paulesu, E., Gandola, M., Loffredo, S., Scarpa, P., Sterzi, R., . . . Vallar, G. (2005). Left caloric vestibular stimulation ameliorates right hemianesthesia. *Neurology, 65*(8), 1278-1283. doi: 10.1212/01.wnl.0000182398.14088.e8

Bottini, G., Paulesu, E., Sterzi, R., Warburton, E., Wise, R. J., Vallar, G., . . . Frith, C. D. (1995). Modulation of conscious experience by peripheral sensory stimuli. *Nature, 376*(6543), 778-781. doi: 10.1038/376778a0

Bottini, G., Sterzi, R., Paulesu, E., Vallar, G., Cappa, S. F., Erminio, F., . . . Frackowiak, R. S. (1994). Identification of the central vestibular projections in man: a positron emission tomography activation study. *Experimental Brain Research, 99*(1), 164-169.

Botvinick, M. (2004). Neuroscience. Probing the neural basis of body ownership. *Science, 305*(5685), 782-783. doi: 10.1126/science.1101836

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature, 391*(6669), 756. doi: 10.1038/35784

Brandt, T., Bartenstein, P., Janek, A., & Dieterich, M. (1998). Reciprocal inhibitory visual-vestibular interaction. Visual motion stimulation deactivates the parieto-insular vestibular cortex. *Brain, 121 (Pt 9)*, 1749-1758.

Brandt, T., & Dieterich, M. (1999). The vestibular cortex. Its locations, functions, and disorders. *Annals of the New York Academy of Sciences, 871*, 293-312.

Brandt, T., Glasauer, S., Stephan, T., Bense, S., Yousry, T. A., Deutschlander, A., & Dieterich, M. (2002). Visual-vestibular and visuovisual cortical interaction: new insights from fMRI and pet. *Annals of the New York Academy of Sciences, 956*, 230-241.

Bremmer, F., Klam, F., Duhamel, J. R., Ben Hamed, S., & Graf, W. (2002). Visual-vestibular interactive responses in the macaque ventral intraparietal area (VIP). *The European Journal of Neuroscience, 16*(8), 1569-1586.

Bremmer, F., Kubischik, M., Pekel, M., Lappe, M., & Hoffmann, K. P. (1999). Linear vestibular self-motion signals in monkey medial superior temporal area. *Annals of the New York Academy of Sciences, 871*, 272-281.

Chalmers, D. J. (1996). *The conscious mind: In search of a fundamental theory*. Oxford: Oxford University Press.

Chen, A., DeAngelis, G. C., & Angelaki, D. E. (2010). Macaque parieto-insular vestibular cortex: responses to self-motion and optic flow. *The Journal of Neuroscience, 30*(8), 3022-3042. doi: 10.1523/JNEUROSCI.4029-09.2010

Chen, X., Deangelis, G. C., & Angelaki, D. E. (2013a). Diverse Spatial Reference Frames of Vestibular Signals in Parietal Cortex. *Neuron*. doi: 10.1016/j.neuron.2013.09.006

Chen, X., Deangelis, G. C., & Angelaki, D. E. (2013b). Eye-centered representation of optic flow tuning in the ventral intraparietal area. *The Journal of Neuroscience, 33*(47), 18574-18582. doi: 10.1523/JNEUROSCI.2837-13.2013

Cheyne, J. A., & Girard, T. A. (2009). The body unbound: vestibular-motor hallucinations and out-of-body experiences. *Cortex, 45*(2), 201-215. doi: 10.1016/j.cortex.2007.05.002

Clemens, I. A., De Vrijer, M., Selen, L. P., Van Gisbergen, J. A., & Medendorp, W. P. (2011). Multisensory processing in spatial orientation: an inverse probabilistic approach. *The Journal of Neuroscience, 31*(14), 5365-5377. doi: 10.1523/JNEUROSCI.6472-10.2011

Crick, F., & Koch, C. (1990). Some reflections on visual awareness. *Cold Spring Harbor Symposia on Quantitative Biology, 55*, 953-962.

Cullen, K. E. (2012). The vestibular system: multimodal integration and encoding of self-motion for motor control. *Trends in Neurosciences, 35*(3), 185-196. doi: 10.1016/j.tins.2011.12.001

David, N., Bewernick, B. H., Cohen, M. X., Newen, A., Lux, S., Fink, G. R., . . . Vogeley, K. (2006). Neural representations of self versus other: visual-spatial perspective taking and agency in a virtual ball-tossing game. *Journal of Cognitive Neuroscience, 18*(6), 898-910. doi: 10.1162/jocn.2006.18.6.898

Day, B. L., & Fitzpatrick, R. C. (2005). Virtual head rotation reveals a process of route reconstruction from human vestibular signals. *The Journal of Physiology, 567*(Pt 2), 591-597. doi: 10.1113/jphysiol.2005.092544

De Ridder, D., Van Laere, K., Dupont, P., Menovsky, T., & Van de Heyning, P. (2007). Visualizing out-of-body experience in the brain. *The New England Journal of Medicine, 357*(18), 1829-1833. doi: 10.1056/NEJMoa070010

De Saedeleer, C., Vidal, M., Lipshits, M., Bengoetxea, A., Cebolla, A. M., Berthoz, A., . . . McIntyre, J. (2013). Weightlessness alters up/down asymmetries in the perception of self-motion. *Experimental Brain Research, 226*(1), 95-106. doi: 10.1007/s00221-013-3414-7

de Vignemont, F. (2011). Embodiment, ownership and disownership. *Consciousness and Cognition, 20*(1), 82-93. doi: 10.1016/j.concog.2010.09.004

Della-Justina, H. M., Gamba, H. R., Lukasova, K., Nucci-da-Silva, M. P., Winkler, A. M., & Amaro, E., Jr. (2015). Interaction of brain areas of visual and vestibular simultaneous activity with fMRI. *Experimental Brain Research, 233*(1), 237-252. doi: 10.1007/s00221-014-4107-6

Dennett, D. C. (1991). *Consciousness explained*: Penguin Books.

Deroualle, D., & Lopez, C. (2014). Toward a vestibular contribution to social cognition. *Frontiers in Integrative Neuroscience, 8*, 16. doi: 10.3389/fnint.2014.00016

Dickman, J. D., & Angelaki, D. E. (2002). Vestibular convergence patterns in vestibular nuclei neurons of alert primates. *Journal of Neurophysiology, 88*(6), 3518-3533. doi: 10.1152/jn.00518.2002

Dieterich, M., & Brandt, T. (2015). The bilateral central vestibular system: its pathways, functions, and disorders. *Annals of the New York Academy of Sciences*. doi: 10.1111/nyas.12585

Ehrsson, H. H. (2012). The concept of body ownership and it's relationship to multisensory integration. In Barry Stein (Ed.), *The New Handbook of Multisensory Processes*. Cambridge MA: MIT Press.

Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science, 305*(5685), 875-877. doi: 10.1126/science.1097011

Ehrsson, H. H., Wiech, K., Weiskopf, N., Dolan, R. J., & Passingham, R. E. (2007). Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proceedings of the National Academy of Sciences, 104*(23), 9828-9833. doi: 10.1073/pnas.0610011104

Einstein, Albert. (1907). Über das Relativitätsprinzip und die aus demselben gezogenen Folgerungen. *Jahrbuch der Radioaktivität und Elektronik 4*, 411-462.

Engel, A. K., Fries, P., Konig, P., Brecht, M., & Singer, W. (1999). Temporal binding, binocular rivalry, and consciousness. *Consciousness and Cognition, 8*(2), 128-151. doi: 10.1006/ccog.1999.0389

Falconer, C. J., & Mast, F. W. (2012). Balancing the mind: vestibular induced facilitation of egocentric mental transformations. *Experimental Psychology, 59*(6), 332-339. doi: 10.1027/1618-3169/a000161

Fasold, O., von Brevern, M., Kuhberg, M., Ploner, C. J., Villringer, A., Lempert, T., & Wenzel, R. (2002). Human vestibular cortex as identified with caloric stimulation in functional magnetic resonance imaging. *Neuroimage, 17*(3), 1384-1393.

Fernandez, C., & Goldberg, J. M. (1971). Physiology of peripheral neurons innervating semicircular canals of the squirrel monkey. II. Response to sinusoidal stimulation and dynamics of peripheral vestibular system. *Journal of Neurophysiology, 34*(4), 661-675.

Ferre, E. R., Bottini, G., & Haggard, P. (2011). Vestibular modulation of somatosensory perception. *The European Journal of Neuroscience, 34*(8), 1337-1344. doi: 10.1111/j.1460-9568.2011.07859.x

Ferre, E. R., Bottini, G., & Haggard, P. (2012). Vestibular inputs modulate somatosensory cortical processing. *Brain Structure and Function, 217*(4), 859-864. doi: 10.1007/s00429-012-0404-7

Ferre, E. R., Bottini, G., Iannetti, G. D., & Haggard, P. (2013). The balance of feelings: vestibular modulation of bodily sensations. *Cortex, 49*(3), 748-758. doi: 10.1016/j.cortex.2012.01.012

Ferre, E. R., Day, B. L., Bottini, G., & Haggard, P. (2013). How the vestibular system interacts with somatosensory perception: a sham-controlled study with galvanic vestibular stimulation. *Neuroscience Letters, 550*, 35-40. doi: 10.1016/j.neulet.2013.06.046

Ferre, E. R., Kaliuzhna, M., Herbelin, B., Haggard, P., & Blanke, O. (2014). Vestibular-somatosensory interactions: effects of passive whole-body rotation on somatosensory detection. *Plos One, 9*(1), e86379. doi: 10.1371/journal.pone.0086379

Ferre, E. R., Sedda, A., Gandola, M., & Bottini, G. (2011). How the vestibular system modulates tactile perception in normal subjects: a behavioural and physiological study. *Experimental Brain Research, 208*(1), 29-38. doi: 10.1007/s00221-010-2450-9

Ferre, E. R., Vagnoni, E., & Haggard, P. (2013). Vestibular contributions to bodily awareness. *Neuropsychologia, 51*(8), 1445-1452. doi: 10.1016/j.neuropsychologia.2013.04.006

Fetsch, C. R., DeAngelis, G. C., & Angelaki, D. E. (2013). Bridging the gap between theories of sensory cue integration and the physiology of multisensory neurons. *Nature Reviews Neuroscience, 14*(6), 429-442. doi: 10.1038/nrn3503

Fredrickson, J. M., Scheid, P., Figge, U., & Kornhuber, H. H. (1966). Vestibular nerve projection to the cerebral cortex of the rhesus monkey. *Experimental Brain Research, 2*(4), 318-327.

Freton, M., Lemogne, C., Bergouignan, L., Delaveau, P., Lehericy, S., & Fossati, P. (2013). The eye of the self: precuneus volume and visual perspective during autobiographical memory retrieval. *Brain Structure and Function*. doi: 10.1007/s00429-013-0546-2

Gale, S. (2015). *Vestibular processing and its cortical signature in humans.* EPFL, Lausanne.

Gallagher, S. (2005). *How the body shapes the mind*: Oxford University Press.

Gallese, V., & Sinigaglia, C. (2011). What is so special about embodied simulation? *Trends in Cognitive Sciences, 15*(11), 512-519. doi: 10.1016/j.tics.2011.09.003

Gentile, G., Bjornsdotter, M., Petkova, V. I., Abdulkarim, Z., & Ehrsson, H. H. (2015). Patterns of neural activity in the human ventral premotor cortex reflect a whole-body multisensory percept. *Neuroimage*. doi: 10.1016/j.neuroimage.2015.01.008

Goldberg, J. M. (2012). *The vestibular system: A sixth sense*. New York: Oxford University Press.

Goldberg, J. M., & Fernandez, C. (1971). Physiology of peripheral neurons innervating semicircular canals of the squirrel monkey. I. Resting discharge and response to constant angular accelerations. *Journal of Neurophysiology, 34*(4), 635-660.

Graybiel, A., & Kellogg, R. S. (1967). Inversion illusion in parabolic flight: its probable dependence on otolith function. *Aerospace Medicine, 38*(11), 1099-1103.

Graziano, M. S., & Kastner, S. (2011a). Awareness as a perceptual model of attention. *Cognitive Neuroscience, 2*(2), 125-127. doi: 10.1080/17588928.2011.585237

Graziano, M. S., & Kastner, S. (2011b). Human consciousness and its relationship to social neuroscience: A novel hypothesis. *Cognitive Neuroscience, 2*(2), 98-113. doi: 10.1080/17588928.2011.565121

Grüsser, O. J., Pause, M., & Schreiter, U. (1990a). Localization and responses of neurones in the parieto-insular vestibular cortex of awake monkeys (Macaca fascicularis). *The Journal of Physiology, 430*, 537-557.

Grüsser, O. J., Pause, M., & Schreiter, U. (1990b). Vestibular neurones in the parieto-insular cortex of monkeys (Macaca fascicularis): visual and neck receptor responses. *The Journal of Physiology, 430*, 559-583.

Gu, Y., Angelaki, D. E., & Deangelis, G. C. (2008). Neural correlates of multisensory cue integration in macaque MSTd. *Nature Neuroscience, 11*(10), 1201-1210. doi: 10.1038/nn.2191

Gu, Y., DeAngelis, G. C., & Angelaki, D. E. (2007). A functional link between area MSTd and heading perception based on vestibular signals. *Nature Neuroscience, 10*(8), 1038-1047. doi: 10.1038/nn1935

Guldin, W. O., Akbarian, S., & Grüsser, O. J. (1992). Cortico-cortical connections and cytoarchitectonics of the primate vestibular cortex: a study in squirrel monkeys (Saimiri sciureus). *The Journal of Comparative Neurology, 326*(3), 375-401. doi: 10.1002/cne.903260306

Guldin, W. O., & Grüsser, O. J. (1998). Is there a vestibular cortex? *Trends in Neurosciences, 21*(6), 254-259.

Hamilton, A. F., Brindley, R., & Frith, U. (2009). Visual perspective taking impairment in children with autistic spectrum disorder. *Cognition, 113*(1), 37-44. doi: 10.1016/j.cognition.2009.07.007

Heidegger, M. (1962). *Being and time*. New York: Harper and Row.

Howard, I. P., & Templeton, W. B. (1966). *Human spatial orientation*. New York: Wiley.

Husserl, E. (1950). *Cartesianische Meditationen und Pariser Vorträge*. The Hague: Martinus Nijhoff Publishers.

Indovina, I., Maffei, V., Pauwels, K., Macaluso, E., Orban, G. A., & Lacquaniti, F. (2013). Simulated self-motion in a visual gravity field: sensitivity to vertical and horizontal heading in the human brain. *Neuroimage, 71*, 114-124. doi: 10.1016/j.neuroimage.2013.01.005

Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., . . . Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron, 70*(2), 363-374. doi: 10.1016/j.neuron.2011.03.009

James, W. (1890). *The principles of psychology*: Macmillan.

Jeannerod, M. (2003). The mechanism of self-recognition in humans. *Behavioural Brain Research, 142*(1-2), 1-15.

Kant, I. (1924). *Kritik der reinen Vernunft*. Berlin: Tillgner.

Karnath, H. O. (1994). Subjective body orientation in neglect and the interactive contribution of neck muscle proprioception and vestibular stimulation. *Brain, 117 (Pt 5)*, 1001-1012.

Kerkhoff, G., Hildebrandt, H., Reinhart, S., Kardinal, M., Dimova, V., & Utz, K. S. (2011). A long-lasting improvement of tactile extinction after galvanic vestibular stimulation: two Sham-stimulation controlled case studies. *Neuropsychologia, 49*(2), 186-195. doi: 10.1016/j.neuropsychologia.2010.11.014

Kovacs, G., Raabe, M., & Greenlee, M. W. (2008). Neural correlates of visually induced self-motion illusion in depth. *Cerebral Cortex, 18*(8), 1779-1787. doi: 10.1093/cercor/bhm203

Kravitz, D. J., Saleem, K. S., Baker, C. I., & Mishkin, M. (2011). A new neural framework for visuospatial processing. *Nature Reviews Neuroscience, 12*(4), 217-230. doi: 10.1038/nrn3008

Lackner, J. R., & DiZio, P. (2005). Vestibular, proprioceptive, and haptic contributions to spatial orientation. *Annual Review of Psychology, 56*, 115-147. doi: 10.1146/annurev.psych.55.090902.142023

Lackner, J. R., & DiZio, P. A. (2000). Aspects of body self-calibration. *Trends in Cognitive Sciences, 4*(7), 279-288.

Laurens, J., & Angelaki, D. E. (2011). The functional significance of velocity storage and its dependence on gravity. *Experimental Brain Research, 210*(3-4), 407-422. doi: 10.1007/s00221-011-2568-4

Leichnetz, G. R. (1989). Inferior frontal eye field projections to the pursuit-related dorsolateral pontine nucleus and middle temporal area (MT) in the monkey. *Visual Neuroscience, 3*(2), 171-180.

Lenggenhager, B., Halje, P., & Blanke, O. (2011). Alpha band oscillations correlate with illusory self-location induced by virtual reality. *The European Journal of Neuroscience, 33*(10), 1935-1943. doi: 10.1111/j.1460-9568.2011.07647.x

Lenggenhager, B., & Lopez, C. (2015). Vestibular contributions to the sense of body, self, and others. In T. Metzinger & J. M. Windt (Eds.), *Open MIND*. Frankfurt: MIND-Group.

Lenggenhager, B., Mouthon, M., & Blanke, O. (2009). Spatial aspects of bodily self-consciousness. *Consciousness and Cognition, 18*(1), 110-117. doi: 10.1016/j.concog.2008.11.003

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: manipulating bodily self-consciousness. *Science, 317*(5841), 1096-1099. doi: 10.1126/science.1143439

Lewald, J., & Karnath, H. O. (2000). Vestibular influence on human auditory space perception. *Journal of Neurophysiology, 84*(2), 1107-1111.

Limanowski, J., & Hecht, H. (2011). Where do we stand on locating the self? *Psychology, 2*(4), 312-317.

Limanowski, J., Lutti, A., & Blankenburg, F. (2014). The extrastriate body area is involved in illusory limb ownership. *Neuroimage, 86*, 514-524. doi: 10.1016/j.neuroimage.2013.10.035

Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences, 107*(26), 11727-11732. doi: 10.1073/pnas.1003483107

Longo, M. R., Schuur, F., Kammers, M. P., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition, 107*(3), 978-998. doi: 10.1016/j.cognition.2007.12.004

Lopez, C., & Blanke, O. (2011). The thalamocortical vestibular system in animals and humans. *Brain Research Reviews, 67*(1-2), 119-146. doi: 10.1016/j.brainresrev.2010.12.002

Lopez, C., Blanke, O., & Mast, F. W. (2012). The human vestibular cortex revealed by coordinate-based activation likelihood estimation meta-analysis. *Neuroscience, 212*, 159-179. doi: 10.1016/j.neuroscience.2012.03.028

Lopez, C., Halje, P., & Blanke, O. (2008). Body ownership and embodiment: vestibular and multisensory mechanisms. *Clinical Neurophysiology, 38*(3), 149-161. doi: 10.1016/j.neucli.2007.12.006

Lopez, C., Lenggenhager, B., & Blanke, O. (2010). How vestibular stimulation interacts with illusory hand ownership. *Consciousness and Cognition, 19*(1), 33-47. doi: 10.1016/j.concog.2009.12.003

Lopez, C., Schreyer, H.-M., Preuss, N., & Mast, F. W. (2012). Vestibular stimulation modifies the body schema. *Neuropsychologia, 50*(8), 1830-1837. doi: 10.1016/j.neuropsychologia.2012.04.008

Macauda, G., Bertolini, G., Palla, A., Straumann, D., Brugger, P., & Lenggenhager, B. (2014). Binding body and self in visuo-vestibular conflicts. *The European Journal of Neuroscience*. doi: 10.1111/ejn.12809

MacNeilage, P. R., Turner, A. H., & Angelaki, D. E. (2010). Canal-otolith interactions and detection thresholds of linear and angular components during curved-path self-motion. *Journal of Neurophysiology, 104*(2), 765-773. doi: 10.1152/jn.01067.2009

Margulies, D. S., Vincent, J. L., Kelly, C., Lohmann, G., Uddin, L. Q., Biswal, B. B., . . . Petrides, M. (2009). Precuneus shares intrinsic functional architecture in humans and monkeys. *Proceedings of the National Academy of Sciences, 106*(47), 20069-20074. doi: 10.1073/pnas.0905314106

McGeoch, P. D., & Ramachandran, V. S. (2008). Vestibular stimulation can relieve central pain of spinal origin. *Spinal Cord, 46*(11), 756-757. doi: 10.1038/sc.2008.47

McGeoch, P. D., Williams, L. E., Lee, R. R., & Ramachandran, V. S. (2008). Behavioural evidence for vestibular stimulation as a treatment for central post-stroke pain. *Journal of Neurology, Neurosurgery, and Psychiatry, 79*(11), 1298-1301. doi: 10.1136/jnnp.2008.146738

McIntyre, J., Zago, M., Berthoz, A., & Lacquaniti, F. (2001). Does the brain model Newton's laws? *Nature Neuroscience, 4*(7), 693-694. doi: 10.1038/89477

Metzinger, T. (2003). *Being no one*. Boston: MIT Press.

Metzinger, T. (2009). Why are out-of-body experiences interesting for philosophers? The theoretical relevance of OBE research. *Cortex, 45*(2), 256-258. doi: 10.1016/j.cortex.2008.09.004

Metzinger, T. (2013). Why are dreams interesting for philosophers? The example of minimal phenomenal selfhood, plus an agenda for future research. *Frontiers in Psychology, 4*, 746. doi: 10.3389/fpsyg.2013.00746

Mian, O. S., Li, Y., Antunes, A., Glover, P. M., & Day, B. L. (2013). On the vertigo due to static magnetic fields. *Plos One, 8*(10), e78748. doi: 10.1371/journal.pone.0078748

Mitson, L., Ono, H., & Barbeito, R. (1976). Three methods of measuring the location of the egocentre: their reliability, comparative locations and intercorrelations. *Canadian Journal of Psychology, 30*(1), 1-8.

Mittelstaedt, Horst. (1991). The role of the otoliths in perception of the orientation of self and world to the vertical. *Yearbooks Zoological Department of Zoology and Physiology of Animals, 95*, 418-425.

Mizumoto, M., & Ishikawa, M. (2005). Immunity to error through misidentification and the bodily illusion. *Journal of Consciousness Studies, 12*, 3-19.

Moseley, G. L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., & Spence, C. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proceedings of the National Academy of Sciences, 105*(35), 13169-13173. doi: 10.1073/pnas.0803768105

Neisser, U. (1988). Five kinds of self-knowledge. *Philosophical Psychology, 1*(1).

Newen, A., & Vogeley, K. (2003). Self-representation: searching for a neural signature of self-consciousness. *Consciousness and Cognition, 12*(4), 529-543.

Odkvist, L. M., Schwarz, D. W., Fredrickson, J. M., & Hassler, R. (1974). Projection of the vestibular nerve to the area 3a arm field in the squirrel monkey (saimiri sciureus). *Experimental Brain Research, 21*(1), 97-105.

Palluel, E., Aspell, J. E., & Blanke, O. (2011). Leg muscle vibration modulates bodily self-consciousness: integration of proprioceptive, visual, and tactile signals. *Journal of neurophysiology, 105*(5), 2239-2247. doi: 10.1152/jn.00744.2010

Perachio, A. A., Bush, G. A., & Angelaki, D. E. (1992). A model of responses of horizontal-canal-related vestibular nuclei neurons that respond to linear head acceleration. *Annals of the New York Academy of Sciences, 656*, 795-801.

Petkova, V. I., Bjornsdotter, M., Gentile, G., Jonsson, T., Li, T. Q., & Ehrsson, H. H. (2011). From part- to whole-body ownership in the multisensory brain. *Current Biology, 21*(13), 1118-1122. doi: 10.1016/j.cub.2011.05.022

Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: perceptual illusion of body swapping. *Plos One, 3*(12), e3832. doi: 10.1371/journal.pone.0003832

Petkova, V. I., Khoshnevis, M., & Ehrsson, H. H. (2011). The perspective matters! Multisensory integration in ego-centric reference frames determines full-body ownership. *Frontiers in Psychology, 2*, 35. doi: 10.3389/fpsyg.2011.00035

Pfeiffer, C. (2015). Multisensory spatial mechanisms of the bodily self and social cognition-A commentary on Vittorio Gallese and Valentina Cuccio. In T. Metzinger & J. M. Windt (Eds.), *Open MIND*. Frankfurt: MIND-Group.

Pfeiffer, C., Serino, A., & Blanke, O. (2014). The vestibular system: A spatial reference for bodily self-conciousness. *Frontiers in Integrative Neuroscience*. doi: 10.3389/fnint.2014.00031

Roberts, D. C., Marcelli, V., Gillen, J. S., Carey, J. P., Della Santina, C. C., & Zee, D. S. (2011). MRI magnetic field stimulates rotational sensors of the brain. *Current Biology, 21*(19), 1635-1640. doi: 10.1016/j.cub.2011.08.029

Rohde, M., Di Luca, M., & Ernst, M. O. (2011). The Rubber Hand Illusion: feeling of ownership and proprioceptive drift do not go hand in hand. *Plos One, 6*(6), e21659. doi: 10.1371/journal.pone.0021659

Rosenberg, A., & Angelaki, D. E. (2014). Gravity influences the visual representation of object tilt in parietal cortex. *The Journal of Neuroscience, 34*(43), 14170-14180. doi: 10.1523/JNEUROSCI.2030-14.2014

Samad, M., Chung, A. J., & Shams, L. (2015). Perception of body ownership is driven by bayesian sensory inference. *Plos One, 10*(2), e0117178. doi: 10.1371/journal.pone.0117178

Schlack, A., Sterbing-D'Angelo, S. J., Hartung, K., Hoffmann, K. P., & Bremmer, F. (2005). Multisensory space representations in the macaque ventral intraparietal area. *The Journal of Neuroscience, 25*(18), 4616-4625. doi: 10.1523/JNEUROSCI.0455-05.2005

Sciutti, A., Demougeot, L., Berret, B., Toma, S., Sandini, G., Papaxanthis, C., & Pozzo, T. (2012). Visual gravity influences arm movement planning. *Journal of Neurophysiology, 107*(12), 3433-3445. doi: 10.1152/jn.00420.2011

Serino, A., Alsmith, A., Costantini, M., Mandrigin, A., Tajadura-Jimenez, A., & Lopez, C. (2013). Bodily ownership and self-location: Components of bodily self-consciousness. *Consciousness and Cognition, 22*(4), 1239-1252. doi: 10.1016/j.concog.2013.08.013

Sinha, N., Zaher, N., Shaikh, A. G., Lasker, A. G., Zee, D. S., & Tarnutzer, A. A. (2008). Perception of self motion during and after passive rotation of the body around an earth-vertical axis. *Progress in Brain Research, 171*, 277-281. doi: 10.1016/S0079-6123(08)00639-0

Slater, M., Spanlang, B., Sanchez-Vives, M. V., & Blanke, O. (2010). First person experience of body transfer in virtual reality. *Plos One, 5*(5), e10564. doi: 10.1371/journal.pone.0010564

Stratton, G. M. (1899). The spatial harmony of touch and sight. *Mind, 8*(492-505).

Tiliket, C., Ventre-Dominey, J., Vighetto, A., & Grochowicki, M. (1996). Room tilt illusion. A central otolith dysfunction. *Archives of Neurology, 53*(12), 1259-1264.

Tononi, G. (2008). Consciousness as integrated information: a provisional manifesto. *The Biological Bulletin, 215*(3), 216-242.

Tononi, G. (2012). Integrated information theory of consciousness: an updated account. *Archieves Italiennes de Biologie, 150*(2-3), 56-90. doi: 10.4449/aib.v149i5.1388

Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology, 31*(1), 80-91. doi: 10.1037/0096-1523.31.1.80

Tsakiris, M., Hesse, M. D., Boy, C., Haggard, P., & Fink, G. R. (2007). Neural signatures of body ownership: a sensory network for bodily self-consciousness. *Cerebral Cortex, 17*(10), 2235-2244. doi: 10.1093/cercor/bhl131

Vallar, G., Sterzi, R., Bottini, G., Cappa, S., & Rusconi, M. L. (1990). Temporary remission of left hemianesthesia after vestibular stimulation. A sensory neglect phenomenon. *Cortex, 26*(1), 123-131.

van Elk, M., & Blanke, O. (2013). Imagined own-body transformations during passive self-motion. *Psychological Research*. doi: 10.1007/s00426-013-0486-8

Vogeley, K., & Fink, G. R. (2003). Neural correlates of the first-person-perspective. *Trends in Cognitive Sciences, 7*(1), 38-42.

Vogeley, K., May, M., Ritzl, A., Falkai, P., Zilles, K., & Fink, G. R. (2004). Neural correlates of first-person perspective as one constituent of human self-consciousness. *Journal of Cognitive Neuroscience, 16*(5), 817-827. doi: 10.1162/089892904970799

Wenzel, R., Bartenstein, P., Dieterich, M., Danek, A., Weindl, A., Minoshima, S., . . . Brandt, T. (1996). Deactivation of human visual cortex during involuntary ocular oscillations. A PET activation study. *Brain, 119 (Pt 1)*, 101-110.

Windt, J. M. (2010). The immersive spatiotemporal hallucination model of dreaming. *Phenomenology and the Cognitive Sciences, 9*, 295-316. doi: 10.1007/s11097-010-9163-1

Witkin, H. A., & Asch, S. E. (1948). Studies in space orientation; further experiments on perception of the upright with displaced visual fields. *Journal of Experimental Psychology, 38*(6), 762-782.

Zago, M., & Lacquaniti, F. (2005). Visual perception and interception of falling objects: a review of evidence for an internal model of gravity. *Journal of Neural Engineering, 2*(3), S198-208. doi: 10.1088/1741-2560/2/3/S04

Zago, M., McIntyre, J., Senot, P., & Lacquaniti, F. (2008). Internal models and prediction of visual gravitational motion. *Vision Research, 48*(14), 1532-1538. doi: 10.1016/j.visres.2008.04.005

zu Eulenburg, P., Caspers, S., Roski, C., & Eickhoff, S. B. (2012). Meta-analytical definition and functional connectivity of the human vestibular cortex. *Neuroimage, 60*(1), 162-169. doi: 10.1016/j.neuroimage.2011.12.032

Appendix

Appendix 1

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Appendix 1

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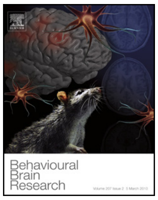

Research report

Illusory self-identification with an avatar reduces arousal responses to painful stimuli

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HIGHLIGHTS

- We experimentally induced the full body illusion through a robotic device.
- We collected SCRs and ratings following acute pain stimulation during bodily illusion.
- Reduced arousal responses were detectable under illusory states of self-consciousness.
- Reduced SCR was related to the degree of ownership experienced for the virtual body.
- Virtual body must be in anatomical configuration to be effective.

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ABSTRACT

Looking at one's own body has been shown to induce analgesia. In the present work we investigated whether illusory self-identification with an avatar, as induced experimentally through visuo-tactile stimulation, modulates the response to painful stimuli.

In 30 healthy volunteers, a robotic device was used to stroke the participants' back, while they viewed either the body of an avatar, a non-body object (control object), or a body avatar with scrambled body parts (control body). All were visually stimulated in either congruent or incongruent fashion with the participant's body. We collected physiological responses (skin conductance response: SCR) to painful stimuli delivered to the participant's hand and responses to a questionnaire inquiring about self-identification with the avatar. We expected reduced physiological responses to pain during the observation of a body avatar only during synchronous visuo-tactile stroking and no reduction for the control object and the control body.

Results showed a reduced SCR to painful stimuli when participants observed the normal body avatar being stroked synchronously that was also associated with largest self-identification ratings recordable already during the pain anticipation. Moreover, a negative correlation between self-identification and SCR was observed, suggesting that a greater degree of self-identification with the avatar was associated with larger decreases in SCR. These results suggest that during states of illusory self-identification with the avatar, the vision of an alien body (anatomically compatible for the vision and congruently stroked for the touch) is effective in modulating physiological responses to painful stimuli.

1. Introduction

Bodily self-consciousness is not considered anymore a unitary inviolable concept. Recent experimental evidences suggest that it is rather a result of multisensory bodily signal integration in the brain. Bodily self-consciousness has been proposed to comprise self-identification (the experience that 'I' identify with a body), self-location (the experience of where 'I' am located), and a first-person perspective (from where 'I' experience the world), but also relating to the sense of agency (the experience that 'I' am the agent causing 'my' actions) [1–3]. Since the first experimental induction of changes in limb-ownership and location in the rubber-hand illusion [4], further studies have demonstrated that it is possible to extend one's own body representation to different external objects such as a prosthetic hand [4] or different fake body parts [5–8] but

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also to entire bodies [9,10]. In the rubber hand illusion (RHI), the visuo-tactile congruent stimulation of one's own hidden hand and a visible anatomical compatible fake hand induces the sensation that the prosthetic limb belongs to oneself [4,11]. Similarly, the full body illusion (FBI) can be induced; thus, congruent visuo-tactile stimulation at the trunk can induce self-identification and self-location changes with respect to a virtual or fake body [12,13,9,14].

Multisensory body representation has been proposed to be crucial for self-identification with the body and for other aspects of bodily self-consciousness [4,15,9,16,17,11]; however, it has also been shown to be critical for any sensory perception including pain.

Recent studies from cognitive neuroscience show that although pain is highly subjective, it is affected by certain bodily states and experimentally modulated multisensory signals [18–20]. Thus, although nociceptive stimuli are processed through specific sensory pathways [18,21], similar to non painful stimuli, pain can be critically modulated by vision.

Previous work has shown that looking at one's own body but not to an object or at another person's body, while receiving a painful stimulus, produces analgesic effects [22,20]. Starting from this observation, we aimed at investigating the relationship between pain processing and body ownership; here, we sought for evidence that reduced responses to nociceptive stimuli can be obtained not only by looking at one's own body [20] but also when looking at another person's body or avatar, especially under conditions of self-identification with the virtual body. Thus, we asked whether changes in illusory self-identification following the induction of an FBI would be associated with a reduction of pain responses.

In two experiments, we combined robotic stimulation and virtual reality technology in order to induce the FBI [23–25]. We then investigated the response to acute noxious stimuli delivered to the participant's hand, through the recording of the SCR, corresponding to the activation of the autonomic nervous system (ANS) [26–28]. Since the response to a noxious stimulus starts before skin contact, as a consequence of anticipatory evaluation of the sensory consequence to the approaching stimulus [29], we also studied the modulation of such an anticipatory response to pain following FBI. We induced the FBI by manipulating the congruency of visuo-tactile stroking between the virtual body and participants' own body (stroking factor) and we manipulated whether the participants saw a virtual body or a control object on their head-mounted display (visual feedback configuration factor).

2. Experiment 1

2.1. Materials and methods

2.1.1. Participants

Fourteen right-handed healthy volunteers took part in Experiment 1 (mean age ±standard deviation: 24.87±2.82 years; 3 females). All participants had normal vision and were naive to the purpose of the experiment. All participants gave their written informed consent before the inclusion in the study. The study was approved by the local ethics committee,La Commission d'Ethique de la Recherche Clinique de la Faculté et de Medicine de l'Université de Lausanne,and was conducted in accordance with the ethical standards of the Declaration of Helsinki [30].

2.1.2. Experimental setup

The experiment was conducted in a light-shielded room where a robotic device for tactile stroking was installed [23]. The robotic device had 200 cm × 90 cm × 10 cm dimensions and a soft foam cover that permitted participants to lie comfortably on their back. Stroking units were integrated in the robotic device that allowed to separately stroke the left and right upper back of participants. A stroking unit consisted of an ultrasonic motor (Shinsei, USR60-E3 N, Japan, http://www.shinsei-motor.com) that actuated via a pinion-hole mechanism movable end parts on which a spring blade and a plastic sphere were mounted. Plastic spheres reached through gaps in the foam cover of the robotic device to touch the upper back of a participant and via the spring blades adapted to the curvature of participants' back during stroking.

Visual stimuli were presented on a head-mounted display (Virtual Realities, Virtual Viewer 3D, Houston, Texas, www.vrealities.com/virtualviewer3d.html) with 800 × 600 pixel resolution and 35 degrees of visual angle. On headphones white noise was presented to participants in order to prevent them from hearing acoustic cues from the robotic stroking.

A serial keypad (Targus Numeric Keypad AKP10US, Anaheim, CA, www.targus.com) was used to record participants' button press responses, which were given with participant's right hand.

In-house software (ExpyVR, Lausanne, Switzerland, http://lnco.epfl.ch/expyvr) was used for visual and acoustic stimulus presentation and recording of responses and LABview software (National Instruments Corporation, version 2010b, Austin Texas, www.ni.com/labview) was used for robotic device control.

2.1.3. Stimuli

Tactile stroking by the robotic device was specified by pre-programmed stroking sequences. A total of four random sequences were created before the experiment with Matlab software (MathWorks, version R13, Massachusetts US, http://www.mathworks.ch). These sequences specified the position of a stroking unit at 100 Hz sampling rate, within 0–20 cm distance range, and 2–12 cm/s velocity range. Within these limits, the four sequences had respectively random direction, timing, relative position, and speed.

The head-mounted display showed an image of a human body (male or female, according to participant's gender) wearing a white t-shirt and blue jeans against a gray background (virtual body, Fig. 1a) or a white rectangle, as a control condition (virtual object, Fig. 1b). The virtual body held a prone posture and was seen in bird's eye view [25].

2.1.4. SCR device

The BioSemi ActiveTwo system (ActiveTwo, BioSemi B.V., Amsterdam, Netherlands) was used as signal amplifier with specific GSR sensors consisting of 2 passive Nihon Kohden electrodes to induce an oscillator signal synchronized with the sample-rate. The sensors were applied on the distal phalanx of the index and middle finger of the left hand, while the two references electrodes were applied to the left forearm. A saline conductive paste was applied to the electrodes, in order to improve the signal-to-noise ratio.

Data were digitalized on a dedicated computer through optic connection with a sample rate of 2048 Hz and then data were re-sampled offline at 200 Hz.

2.1.5. Procedure

An experimental run consisted of an FBI-induction phase, followed by a pain-stimulation phase, questionnaire ratings, and a resting period (Fig. 1d)

The FBI-induction phase consisted of 50 s visuo-tactile stroking in synchronous or asynchronous fashion (stroking factor) seen on an avatar or object (visual feedback factor).

A total of 8 trials were presented during the pain-stimulation phase. A trial began with visually presenting a needle that moved toward the body/object eventually contacting the target ("virtual puncture") during 5 s and was followed by a fixed interstimulus interval of 5 s after which the next trial was presented. During the pain-stimulation phase, visuo-tactile stroking was continuously presented. The picture of a big static needle was displayed

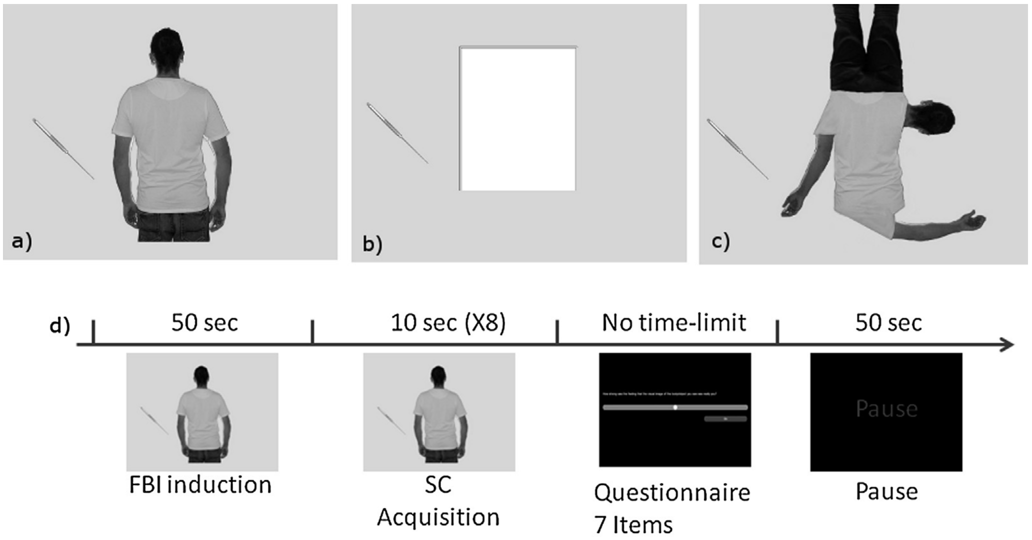

Fig. 1. Visual stimuli and procedure. (a) A human body image stimulus seen from the back was used in both experiments. (b) A control object stimulus was a white rectangle and used in Experiment 1, and (c) a scrambled body stimulus was used as a control for the body stimulus in Experiment 2. (d) Sequence of events for an experimental run of the full-body illusion, starting with visuo-tactile stroking for 50 s, followed by 8 painful stimuli with SCR acquisition for 80 s, followed by questionnaire ratings and a resting period of 50 s.

on the left side of the virtual body/object during either the induction phase and the stimulation phase (Fig. 1). For half of the trials a "real contact" condition was presented. The biologic left hand of the participant was hit with a real needle synchronously with the contact of the virtual needle with the visual target. The real needle had a blunt end with 1 mm diameter and the contacting the skin was not invasive. The real contact stimulation was administered always by the same trained experimenter who was blind to the actual stroking condition. In the other half of trials, a "simulated contact" condition was presented. Participants did not receive any stimulation during the vision of the virtual pinprick. This condition was used to assess the presence of any SCR response to the vision of the noxious stimulus hitting the target in the absence of any somatosensory painful stimulation [27].

This procedure resulted in 8 different conditions: body congruent real, body congruent simulated, body incongruent real, body incongruent simulated, object congruent real, object congruent simulated, object incongruent real, and object incongruent simulated. After the pain-stimulation phase, the questionnaire was administered; 50 s of rest separated the different condition runs.

2.1.6. *Measures*

2.1.6.1. Questionnaire ratings. During each condition run and immediately after the pain-stimulation phase, participants were asked to complete a questionnaire comprising items adapted from previous studies on bodily illusions [4,9] and pain [20] (Table 1). Responses were given through a 7 points visual analogue scale (VAS) and were automatically coded by the experimental software with a score ranging from −3 to +3.

Participants were asked to move the cursor along horizontal axes by pressing buttons with the index and ring fingers (left/right movement) with their right hand, while they confirmed their choice pressing the button in the center with the middle finger. The random sequences of either experimental conditions and questionnaire items were under computer control.

The data from each question underwent an intra-subject standardization by means of an ipsatization procedure in order to neutralize the effect in responses set [31,32]. Specifically, each rating was subtracted by the mean rating of the subject responses in all questions and conditions and then divided by the standard deviation of subject's responses in all questions and conditions.

2.1.6.2. Skin conductance response. The skin conductance level was recorded at DC level. An off-line digital high pass filter set at 0.05 Hz was applied to obtain phasic skin conductance responses [33]. This filter is effective to get back at level 0 the SCR after 1–3 s post-peak and highlights the event related responses in the skin conductance signal. The maximum amplitude of the SCR was used as measure of autonomous nervous system responses. For each trial, the maximum amplitude recorded in the time window of 7 s starting with the initial movement of the needle was extracted. The measures were intra-subject normalized [34–36] in order to obtain comparable measures among the participants, given the well known large inter-subject variability of SCR [37,38]. In addition, the mean skin conductance level (SCL) during each condition was calculated to evaluate the basal sympathetic tone [39].

2.1.7. *Data analysis*

Data were analyzed with STATISTICA 6.0 (StatSoft, Italy, http://www.statsoft.it).

A repeated measure ANOVA was run on SCR data in a 2 × 2 × 2 within subject design. The main factors were: visual feedback configuration (body/object); stroking (congruent/incongruent) and

Table 1
Questionnaire items from Q1 to Q4 are questions inquiring about bodily illusory sensations and Q6 and Q7 are questions asking for explicit pain experience while Q5 is a control question. Questions sequence were fully randomized and under computer control.

	Question
Q1	How strong was the feeling that the visual image of the body/object you saw was really you? (self identification)
Q2	How strong was the feeling that you were drifting downwards or upwards? (self location).
Q3	How Strong was the feeling that you could control the movement of the body you saw? (agency over the visual object)
Q4	How strong was the feeling that you cannot move your own body? (loss of agency)
Q5	How strong was the feeling that you had more than two bodies? (control question)
Q6	How much intense was the pain inflicted by the needle? (pain intensity)
Q7	How much unpleasant was the needle stimulation? (pain unpleasantness)

stimulus contact (real/simulated). When a significant effect was found, the η^2 effect size and power were computed.

Ipsatization transformed questionnaire ratings in Z-scores with a normal distribution allowing a proper use of parametric tests on questionnaire data [31,32]. Separated repeated measures ANOVAs were conducted for each different question on ipsatized values and on SCL measures. Each one of these ANOVAs resulted in a 2×2 within subject design factoring visual feedback configuration (body/object) and stroking (congruent/incongruent).

Significant level was set at $p < .05$, when a significant interaction was detected; post-hoc analysis were conducted with Fisher LSD test.

In addition, the Pearson's r correlation was calculated between questionnaire responses and SCR.

2.2. Results

2.2.1. Skin conductance

The ANOVA on SCR data showed a main effect of contact ($F(1,13) = 20.589$; $p < .001$, $\eta^2 = .613$; power = .987) and an interaction between visual feedback and stroking ($F(1,13) = 6.111$; $p < .05$; $\eta^2 = .320$; power = .942). The other main factors (visual feedback: $F(1,13) = 2.221$; $p = .16$; stroking: $F(1,13) = .561$; $p = .47$) and interactions were not significant (visual feedback × contact: $F(1,13) = .232$; $p = .64$; congruency × contact: $F(1,13) = 4.133$; $p = .063$; visual feedbackcongruency × contact: $F(1,13) = .084$; $p = .77$). Fisher's post-hoc tests showed that the real contact ($Z = .3 \pm .08$) induced a greater SCR than the simulated contact ($Z = -.4 \pm .08$). The interaction between visual feedback and stroking notably showed that, during the visual feedback of the body, the SCR was lower for congruent versus incongruent stroking while for the object visual feedback the trend was in the opposite direction. Post-hoc testing revealed that the body congruent condition ($Z = -.28 \pm .05$) had different responses from body incongruent ($Z = .03 \pm .09$; $p = .026$) and object congruent conditions ($Z = .08 \pm .13$; $p = .013$). At the same time the other three conditions did not show statistically significant differences in any direct comparison (Fig. 2a)

The ANOVA on SCL did not show any significant effect nor for the main effects (visual feedback: $F(1,13) = 1.288$; $p = .277$; stroking: $F(1,13) = 3.049$; $p = .104$), neither for the interaction ($F(1,13) = 1.765$; $p = .207$).

2.2.2. Questionnaire

The analysis of self-identification ratings (Q1) showed the main effect of visual feedback ($F(1,13) = 15.81$; $p \leq .001$, $\eta^2 = .549$; power = .956) but no main effect of stroking and no visual feedback x stroking interaction. Thus, self-identification was rated significantly higher in the body ($Z = .91 \pm .26$) conditions than in the object conditions ($Z = -.22 \pm .23$).

The ANOVA for self-location ratings (Q2) showed a visual feedback x stroking interaction ($F(1,13) = 5.29$; $p < .05$; $\eta^2 = .29$; power = .904). Post hoc comparisons showed that values were lower in the object incongruent condition ($Z = -1.79 \pm .39$) than in the other three conditions (body congruent = $-1.28 \pm .54$; body incongruent = $-1.28 \pm .49$; object congruent = $-.86 \pm .51$), which were at the same level (all $p \leq .05$). There was no main effect of visual feedback and no main effect of stroking for self-location ratings (Q2).

Questions about agency (Q3 and Q4), the control question (Q5), and questions about pain experience (Q6 and Q7) revealed no significant main effects and no interactions. The absence of significant differences for the questions about pain experience (Q6 and Q7) suggests that our experimental manipulation did not result in consciously reportable effects on pain experience (Fig. 2b).

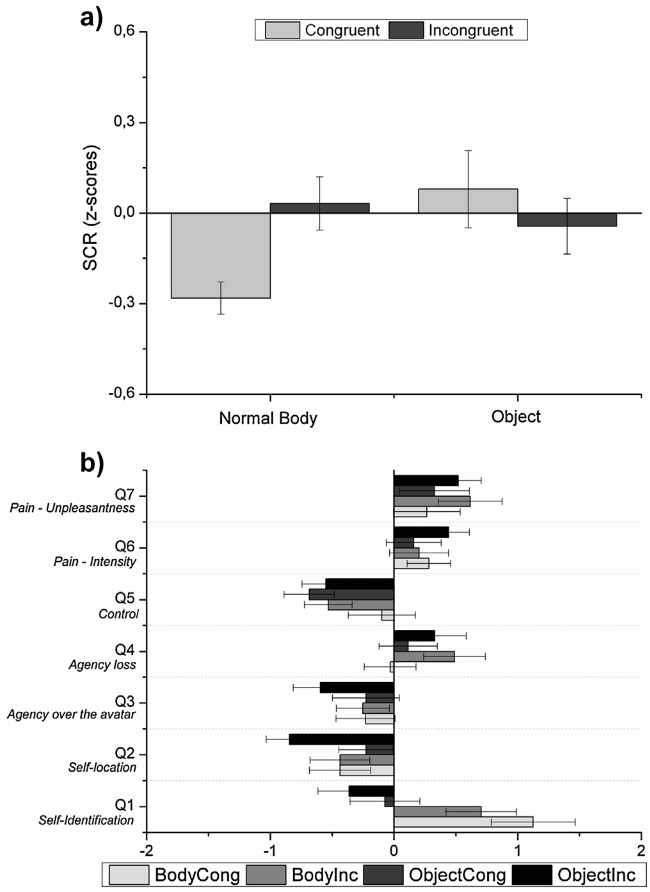

Fig. 2. Experiment 1 results. (a) Columns represent the mean SCR response for the significant interaction between visual feedback (body/object) and stroking (congruent/incongruent). The SCR has been transformed in z-scores. The panel (b) shows mean questionnaire ratings. The thin bars indicate standard errors.

2.2.3. Correlation analysis

Correlation analysis showed a significant negative correlation between self-identification ratings (Q1) and real contact SCR ($r = -.27$; $p < .05$), that is, a high degree of self-identification was associated with low SCR. None of the other questions showed significant correlations with the implicit measures.

3. Experiment 2

3.1. Materials and methods

3.1.1. Participants

Sixteen right-handed healthy volunteers participated (Age±SD: 23.56±2.50 years, 4 females), who had not participated in Experiment 1 and were thus naïve to the purpose of the experiment. All participants had normal vision and gave their written informed consent before the inclusion in the study. The study was approved by the local ethics committee, La Commission d'Ethique de la Recherche Clinique de la Faculté et de Medicine de l'Université de Lausanne, and was conducted in accordance with the ethical standards of the Declaration of Helsinki [30].

3.1.2. Materials, methods, and procedures

The materials, methods, procedures, and analysis were the same as in Experiment 1, except for the following differences.

In Experiment 2, we investigated whether any visual effect of self-identification on SCR needed the visual observation of a realistic and anatomically intact body. For this purpose, we presented participants with either a virtual human body (similar to Experiment 1), or with a scrambled version of the same body, shaped with anatomically impossible limb configuration (Fig. 1c). More precisely, the trunk of the virtual body was presented at the center of the image and similarly to the original image, and the other body segments were presented at incongruent positions (Fig. 1c). The scrambled body image was created with GIMP software (GIMP 2.6.10; www.gimp.org) and was a modification of the avatar image in such a way that we provided a unitary picture that could be processed also as a whole and not just as a fragmented summation of smaller figures. We named this condition "scrambled body". The experimental design resulted in a 2 × 2 × 2 within subjects design factoring: visual body configuration (anatomical/scrambled body), stroking (congruent/incongruent) and stimulus contact (real/simulated) for the SCR analysis, and a series of 2 × 2 within subjects design factoring: visual body configuration (anatomical/scrambled body), stroking (congruent/incongruent) for questionnaire and SCL analysis.

3.2. Results

3.2.1. Skin conductance

The ANOVA on SCR data showed a main effect of contact ($F(1,15) = 68.148$; $p < .001$, $\eta^2 = .819$; power > .999) and a main effect of visual feedback ($F(1,15) = 34.909$, $p < .001$; $\eta^2 = .699$ power > .999) moreover the interaction between visual feedback and stroking factors was significant ($F(1,15) = 6.46$; $p < .05$; $\eta^2 = .301$; power = .95) as well as the interaction between visual feedback and contact ($F(1,15) = 11.221$; $p < .01$, $\eta^2 = .428$; power = .997). The main factor stroking ($F(1,15) = .417$; $p = .528$) and the other interactions were not significant (stroking × contact: $F(1,15) = .056$; $p = .817$; visual feedback × stroking × contact: ($F(1,15) = .024$; $p = .879$).

The real contact ($Z = .37 \pm .04$) induced a greater SCR than the simulated contact ($Z = -.38 \pm .04$). The visual feedback main effect showed that independently from the stroking main effect, seeing a virtual body in anatomical configuration ($Z = -.19 \pm .03$) induced lower SCR to painful stimuli than seeing a scrambled body ($Z = .18 \pm .03$). The interaction between visual feedback and stroking factors, congruently with Experiment 1 and our prediction, showed that, using the anatomical configuration as a visual feedback, the SCR was lower for congruent than for incongruent stroking while for the scrambled body there was an opposite trend. Post hoc comparisons showed that the body congruent condition ($Z = -.33 \pm .05$) differed significantly from scrambled congruent condition ($Z = .31 \pm .09$; $p < .001$) and scrambled incongruent ($Z = .05 \pm .09$; $p < .05$), moreover a difference close to significance was found between anatomical body congruent and anatomical body incongruent ($Z = -.05 \pm .06$; $p = .08$) contrast (Fig. 3a).

The post hoc analysis for the visual body configuration by contact interaction showed that the main effect of visual body configuration was driven by differences in the real contact conditions as the real touch during anatomical body conditions ($Z = .06 \pm .07$) differed significantly from the real touch during scrambled body configurations ($Z = .68 \pm .08$; $p < .001$). Moreover, both were stronger than the simulated contact conditions (all $p < .001$), which did not show significant difference for the two visual body configurations (simulated anatomical body $= -.45 \pm .05$, simulated scrambled body $= -.31 \pm .06$; $p = .178$).

Consistently with Experiment 1, the ANOVA on SCL did not show significant results nor for the main effects (visual feedback: $F(1,15) = .647$; $p = .434$; stroking: $F(1,15) = .067$; $p = .798$), neither for the interaction ($F(1,15) = .096$; $p = .761$).

3.2.2. Questionnaire data

The ANOVA for self-identification ratings (Q1) showed significant main effects of visual body configuration ($F(1,13) = 5.99$; $p < .05$; $\eta^2 = .285$; power = .629) and stroking ($F(1,13) = 5.04$; $p < .05$; $\eta^2 = .251$; power = .556). There was no visual body configuration by stroking interaction. The anatomical body ($Z = .55 \pm .18$) conditions induced higher self-identification ratings than the scrambled body conditions ($Z = -.11 \pm .26$). Moreover, the congruent stroking ($Z = .56 \pm .24$) induced higher ratings compared to the incongruent ($Z = -.12 \pm .22$) suggesting an additive but not interactive effect which identified the anatomical body congruent stroking condition as the one with the stronger effect of self-identification with the human picture.

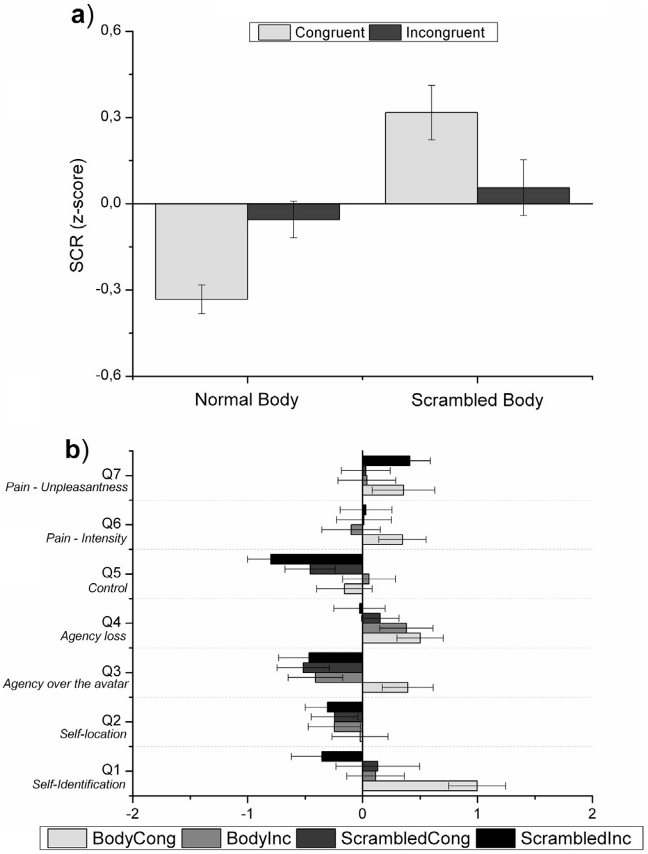

Fig. 3. Experiment 2 results. (a) Columns represent the mean SCR response for the significant interaction between visual feedback (body/object) and stroking (congruent/incongruent). The SCR has been transformed in z-scores. The panel (b) shows mean questionnaire ratings. The thin bars indicate standard errors.

Questions about self-location (Q2) and agency (Q3 and Q4) did not reveal any significant main effect and no interaction.

The control question (Q5) showed a significant main effect of the visual feedback ($F(1,13) = 10.23$; $p < .01$; $\eta^2 = .406$; power = .997; body $= -.05 \pm .19$; scrambled $= -.63 \pm .18$). Consistent with Experiment 1, none of the questions about pain experience (Q6 and Q7) showed significant main effects or interactions.

3.2.3. Correlation

Correlation analysis showed a significant negative correlation between self-identification ratings (Q1) and real contact SCR ($r = -.31$; $p < .05$). No other questionnaire items showed a significant correlation with the SCR.

4. Discussion

In the present study, we found that changes in self-identification with a virtual body modulate arousal responses to acute painful stimulations, as reflected by a decreased SCR. Although, external stimuli that evoke nociceptive afferent signals are the main contributor to pain experience, other internal factors contribute to the genesis and the modulation of the pain experience, such as generically defined cognitive or affective components. Among these factors, it has been possible to differentiate affective-motivational components, such as emotions or meditation-induced states [40,34], from more cognitive factors, such as attention and expectations related to incoming stimuli features [41,42,29]. Moreover, perceptual factors, such as proprioception [43] and the visual size of a body part play a role [44].

Looking at one's own body but not looking at a neutral object or at another person's body has been reported to induce analgesia for acute painful stimulation [22,20]. Here, we sought for a similar modulation of pain responses induced by the vision of a virtual body that also depended upon the level of illusory self-identification with that body during a full-body illusion [9] induced by controlled robotic stimulations [23–25].

In the first experiment, we compared automatic responses to acute painful stimulations, while a virtual body was shown in back-view on an HMD. These responses were compared with those obtained when seeing a control neutral object [26,45,46,9,8]. Our results revealed that the SCR to painful stimuli decreased for real and simulated noxious stimuli, specifically under congruent visuo-tactile stimulation and when the body, but not the object, was seen.

This result was further qualified by the second experiment, where another control condition was added, consisting of a scrambled human figure, typically used in studies testing body and face perception [47–49]. The specific aim of Experiment 2 was to assess the importance of a realistic body configuration [48] for inducing the FBI and the reduction in the SCR to painful stimuli. The arousal responses to the applied pinpricks, both real and simulated, showed, consistently with Experiment 1, a selectively decreased SCR, only when the body was shown in the anatomical configuration and under congruent visuo-tactile stimulation. Moreover, negative results from SCL analysis suggested that the changes in arousal responses that we observed were related more to the transient event related response than to a modification of an altered basal sympathetic tone [39].

The present results add to previous findings on the modulation of pain experience by vision. Vision of noxious stimuli seen as approaching another person's body induces arousal responses in healthy humans [27]. It has been argued that such responses are mainly based on the cognitive evaluation of the approaching stimulus which would produce an automatic anticipatory response [29,50] that has been hypothesized to be mediated by emphatic sharing of the affective component of pain [51,52]. Furthermore, previous works reported that the vision of one's own stimulated body parts can modulate pain thresholds [20,44] or the rating of pain intensity [22], suggesting an analgesic effect when looking at one's own body. The present study goes beyond such previous results by linking the visual response to an incoming threat directed towards another person's body, to illusory self-identification experienced towards an observed virtual body.

We hypothesized that the increased self-identification, when seeing the virtual body stroked in a congruent fashion, would be reflected in changes in the processing of painful stimuli akin to those described during the direct observation of one's own body typically consisting of a reduced response to painful stimuli [22,20,44]. Questionnaire data showed that higher self-identification was recorded with the avatar only when presented with an anatomically correct body configuration and when stroked congruently, according to the literature [4,53,28,9,8].

Investigating the relationship between the self-identification and reduced SCR further, we found that the overall correlation between the magnitude of illusory self-identification and the magnitude of SCR was significant. The correlation was negative in both experiments, sustaining that the more self-identification with the avatar our participants reported, the stronger was the reduction of the SCR for painful stimuli. Although, in the correlation analysis all conditions were considered together with the potential risk of an autocorrelation bias, it is noteworthy that illusory self-identification was the only item from a total of 7 items that showed the same negative correlation with SCR in experiments 1 and 2.

Our findings of a reduced arousal response are in line with earlier studies reporting elevated pain thresholds when seeing a body part or when self-identifying with a virtual body [45,20], but also extend these data on visual analgesia described earlier. In particular, we show here that such decreased arousal response to painful stimuli is tuned by bodily self-consciousness and also modulates anticipatory levels of painful stimuli processing and thus is not strictly dependant on the somatosensory nociceptive input. However whereas these pain thresholds data have recently been extended with explicit ratings of pain experience [22], we did not observe similar effects in explicit pain ratings in experiment 1 and 2. Consistently with our results, a recent study (conducted in two different laboratories) showed that explicit pain ratings for stimuli delivered to the biological hand did not change during the RHI [54]. It is worth noting that we assessed pain ratings only once for each condition during the questionnaire phase, and not on a trial by trial basis after each stimulation, in order to reduce possible interference with the induced illusory state and skin conductance recording. However, this procedure of measuring pain ratings only once might weaken the confidence with pain ratings as several external confounding effects, like memory or other post-perceptual processes, might have interfered with the judgment of stimulations which was delayed.

It has also been proposed that the body is processed as a whole, as suggested by the reported advantage for a global processing of body pictures shown in an upright posture as compared to upside-down or non-anatomical postures [55,48]. In the current study, we showed that in order to induce the FBI, the picture of the avatar needs to be presented in its correct anatomical configuration. Although, modulation of pain experience for an isolated body part was found when looking at the body part [20,44], the present data, comparing the observed effects for the full normal versus scrambled body, suggest that global bodily processing of a seen human body impacts self-identification and arousal responses to painful stimuli. Interestingly, although we presented avatars that matched the gender of our participants, the avatars appearances were different with respect to the specific hair style, or the skin colour of participants. However, our results indicate that primarily the anatomical configuration of the avatar defined the possibility to increase the self-identification with it, and not its actual similarity with participant's body, congruently with the finding that even an opposite gender avatar could induce embodiment effects [56,57].

In conclusion, we found that it is possible to reduce the implicit arousal response to acute painful stimuli throughout the full body illusion. This effect is already available during the anticipatory response to the incoming expected painful stimulation; it is related to the degree of self-identification with the stroked picture and would be achieved only for pictures of human bodies presented with a normal anatomical configuration. However, this implicit arousal reduced response is not transferred in an aware reduced experience of pain. Our data suggests that pain processing shares functional mechanism with self-identification and extends previous research towards a fundamental understanding of self-consciousness.

References

[1] Blanke O, Metzinger T. Full-body illusions and minimal phenomenal selfhood. Trends Cogn Sci 2009;13(1):7–13.

[2] Blanke O. Multisensory brain mechanisms of bodily self-consciousness. Nat Rev Neurosci 2012:556–71.
[3] Ferri F, Frassinetti F, Ardizzi M, Costantini M, Gallese V. A sensorimotor network for the bodily self. J Cogn Neurosci 2012:1584–95.
[4] Botvinick M, Cohen J. Rubber hands feel touch that eyes see. Nature 1998;391(6669):756.
[5] Costantini M, Haggard P. The rubber hand illusion: sensitivity and reference frame for body ownership. Conscious Cogn 2007;16(2):229–40.
[6] Lloyd DM. Spatial limits on referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. Brain Cogn 2007;64(1):104–9.
[7] Perez-Marcos D, Slater M, Sanchez-Vives MV. Inducing a virtual hand ownership illusion through a brain–computer interface. NeuroReport 2009;20(6):589–94.
[8] Tsakiris M, Carpenter L, James D, Fotopoulou A. Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects? Exp Brain Res 2010;204(3):343–52.
[9] Lenggenhager B, Tadi T, Metzinger T, Blanke O. Video ergo sum: manipulating bodily self-consciousness. Science 2007;317(5841):1095–9.
[10] van der Hoort B, Guterstam A, Ehrsson HH. Being Barbie: the size of one's own body determines the perceived size of the world. PloS one 2011;6(5):e20195.
[11] Tsakiris M. My body in the brain: a neurocognitive model of body-ownership. Neuropsychologia 2010;48(3):703–12.
[12] Aspell JE, Lenggenhager B, Blanke O. Keeping in touch with one's self: multisensory mechanisms of self-consciousness. PloS one 2009;4(8):e6488.
[13] Ehrsson HH. The experimental induction of out-of-body experiences. Science 2007;317(5841):1048.
[14] Petkova VI, Björnsdotter M, Gentile G, Jonsson T, Li T-Q, Ehrsson HH. From part- to whole-body ownership in the multisensory brain. Current Biol 2011;21(13):1118–22.
[15] Ehrsson HH, Holmes NP, Passingham RE. Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. J Neurosci 2005;25(45):10564–73.
[16] Salomon R, van Elk M, Aspell JE, Blanke O. I feel who I see: visual body identity affects visual-tactile integration in peripersonal space. Conscious Cogn 2012;21(3):1355–64.
[17] Tsakiris M, Hesse MD, Boy C, Haggard P, Fink GR. Neural signatures of body ownership: a sensory network for bodily self-consciousness. Cerebral Cortex 2007;17(10):2235–44.
[18] Haggard P, Iannetti GD, Longo MR. Spatial sensory organization and body representation in pain perception. Current Biol 2013;23(4):R164–76.
[19] Iannetti GD, Mouraux A. From the neuromatrix to the pain matrix (and back). Exp Brain Res 2010;205:1–12.
[20] Longo MR, Betti V, Aglioti SM, Haggard P. Visually induced analgesia: seeing the body reduces pain. J Neurosci 2009;29(39):12125–30.
[21] Lenz FA, Casey KL, Jones EG, Willis WD. Organization of the central pain pathways. In: The human pain system. Cambridge: Cambridge University Press; 2010. p. 64–195.
[22] Longo MR, Iannetti GD, Mancini F, Driver J, Haggard P. Linking pain and the body: neural correlates of visually induced analgesia. J Neurosci 2012;32(8):2601–7.
[23] Duenas J, Chapuis D, Pfeiffer C, Martuzzi R, Ionta S, Blanke O, Gassert R. Neuroscience robotics to investigate multisensory integration and bodily awareness. IEEE Eng Med Biol Soc Conf 2011;2011:8348–52.
[24] Ionta S, Heydrich L, Lenggenhager B, Mouthon M, Fornari E, Chapuis D, et al. Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. Neuron 2011;70(2):363–74.
[25] Pfeiffer C, Lopez C, Schmutz V, Duena JA, Martuzzi R, Blanke O. Multisensory origin of the subjective first-person perspective: visual, tactile, and vestibular mechanisms. PloS One 2013;8(4):e61751.
[26] Armel KC, Ramachandran VS. Projecting sensations to external objects: evidence from skin conductance response. Proc R Soc B: Biol Sci 2003;270(1523):1499–506.
[27] Forgiarini M, Gallucci M, Maravita A. Racism and the empathy for pain on our skin. Front Psychol 2011;2:108.
[28] Guterstam A, Petkova VI, Ehrsson HH. The illusion of owning a third arm. PloS One 2011;6(2):e17208.
[29] Clark JA, Brown CA, Jones AKP, El-Deredy W. Dissociating nociceptive modulation by the duration of pain anticipation from unpredictability in the timing of pain. Clin Neurophysiol 2008;119(12):2870–8.
[30] World Medical Organization. Declaration of Helsinki. Br Med J 1996;313(7070):1448–9.
[31] Broughton R, Wasel N. A text-stimuli presentation manager for the IBM PC with ipsatization correction for response sets and reaction times. Behav Res Meth Ins C 1990;22(4):421–3.
[32] Cattell RB. Psychologicalmeasurement: ipsative, normative and interactive. Psychol Rev 1944;51:292–303.
[33] Andreassi JL. Psychophysiology: human behavior & physiological response. 5th edn. Mahwah: Lawrence Erlbaum Associates; 2000.
[34] Rhudy JL, Bartley EJ, Williams AE. Habituation, sensitization, and emotional valence modulation of pain responses. Pain 2010;148(2):320–7.
[35] Rhudy JL, Williams AE, McCabe KM, Russell JL, Maynard LJ. Emotional control of nociceptive reactions (ECON): do affective valence and arousal play a role? Pain 2008;136(3):250–61.
[36] Williams AE, Rhudy JL. Emotional modulation of autonomic responses to painful trigeminal stimulation. Int J Psychophysiol 2009;71(3):242–7.
[37] Fowles DC, Christie MJ, Edelberg R, Grings WW, Lykken DT, Venables PH. Publication recomandations for electrodermal measurements. Psychophysiology 1981;18(3):232–9.
[38] Lykken DT, Venables PH. Direct measurement of skin conductance: a proposal for standardization. Psychophysiology 1971;8(5):656–72.
[39] Nagai Y, Critchley HD, Featherstone E, Trimble MR, Dolan RJ. Activity in ventromedial prefrontal cortex covaries with sympathetic skin conductance level: a physiological account of a default mode of brain function. NeuroImage 2004;22(1):243–51.
[40] Brown CA, Jones AKP. Meditation experience predicts less negative appraisal of pain: electrophysiological evidence for the involvement of anticipatory neural responses. Pain 2010;150(3):428–38.
[41] Brown CA, Jones AKP. A role for midcingulate cortex in the interruptive effects of pain anticipation on attention. Clin Neurophysiol 2008;119(10):2370–9.
[42] Brown CA, Seymour B, Boyle Y, El-Deredy W, Jones AKP. Modulation of pain ratings by expectation and uncertainty: behavioral characteristics and anticipatory neural correlates. Pain 2008;135(3):240–50.
[43] Gallace A, Torta DME, Moseley GL, Iannetti GD. The analgesic effect of crossing the arms. Pain 2011;152(6):1418–23.
[44] Mancini F, Longo MR, Kammers MPM, Haggard P. Visual distortion of body size modulates pain perception. Psychol Sci 2011;22:325–30.
[45] Hänsel A, Lenggenhager B, von Känel R, Curatolo M, Blanke O. Seeing and identifying with a virtual body decreases pain perception. Eur J Pain 2011;15:874–9.
[46] Hohwy J, Paton B. Explaining away the body: experiences of supernaturally caused touch and touch on non-hand objects within the rubber hand illusion. PloS one 2010;5(2):e9416.
[47] Hershler O, Hochstein S. At first sight: a high-level pop out effect for faces. Vision Res 2005;45(13):1707–24.
[48] Reed CL, Stone VE, Bozova S, Tanaka J. The body-inversion effect. Psychol Sci 2003;14(4):302–8.
[49] Reed CL, Stone VE, Grubb JD, McGoldrick JE. Turning configural processing upside down: part and whole body postures. J Exp Psychol: Hum Percept Perform 2006;32(1):73–87.
[50] Ploghaus A. Dissociating pain from its anticipation in the human brain. Science 1999;284(5422):1979–81.
[51] Hein G, Singer T. I feel how you feel but not always: the empathic brain and its modulation. Curr Opin Neurobiol 2008;18(2):153–8.
[52] Singer T, Seymour B, O'Doherty J, Kaube H, Dolan RJ, Frith CD. Empathy for pain involves the affective but not sensory components of pain. Science 2004;303(5661):1157–62.
[53] Ehrsson HH, Spence C, Passingham RE. That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. Science 2004;305:875–7.
[54] Mohan R, Jensen KB, Petkova VI, Dey A, Barnsley N, Ingvar M, McAuley JH, Moseley LG, Ehrsson HH. No pain relief with the rubber hand illusion. PloS One 2012;7(12):e52400.
[55] Bosbach S, Knoblich G, Reed CL, Cole J, Prinz W. Body inversion effect without body sense: insights from deafferentation. Neuropsychologia 2006;44(14):2950–8.
[56] Petkova VI, Ehrsson HH. If I were you: perceptual illusion of body swapping. PloS One 2008;3(12):e3832.
[57] Slater M, Spanlang B, Sanchez-Vives MV, Blanke O. First person experience of body transfer in virtual reality. PloS One 2010;5(5):e10564.

Appendix 2

Salomon R, Lim M, Pfeiffer C, Gassert R, and Blanke O. (2013) Full body illusion is associated with widespread skin temperature reduction. Frontiers in Behavioral Neuroscience. 7:65.

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Full body illusion is associated with widespread skin temperature reduction

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A central feature of our consciousness is the experience of the self as a unified entity residing in a physical body, termed bodily self-consciousness. This phenomenon includes aspects such as the sense of owning a body (also known as body ownership) and has been suggested to arise from the integration of sensory signals from the body. Several studies have shown that temporally synchronous tactile stimulation of the real body and visual stimulation of a fake or virtual body can induce changes in bodily self-consciousness, typically resulting in a sense of illusory ownership over the fake body. The present study assessed the effect of anatomical congruency of visuo-tactile stimulation on bodily self-consciousness. A virtual body was presented and temporally synchronous visuo-tactile stroking was applied simultaneously to the participants' body and to the virtual body. We manipulated the anatomical locations of the visuo-tactile stroking (i.e., on the back, on the leg), resulting in congruent stroking (stroking was felt and seen on the back or the leg) or incongruent stroking (i.e., stroking was felt on the leg and seen on the back). We measured self-identification with the virtual body and self-location as well as skin temperature. Illusory self-identification with the avatar as well as changes in self-location were experienced in the congruent stroking conditions. Participants showed a decrease in skin temperature across several body locations during congruent stimulation. These data establish that the full-body illusion (FBI) alters bodily self-consciousness and instigates widespread physiological changes in the participant's body.

Keywords: bodily self-consciousness, body representation, body illusion, self-representation, body-ownership, neuroscience robotics

INTRODUCTION

Since William James's characterization of self-consciousness in the 19th century (James, 1890/1950), the psychological "self" has been the subject of much intrigue in the world of psychology, philosophy, and more recently, neuroscience. It has been proposed that the processing and integration of body-related information is important to develop a comprehensive neurobiological model of self-consciousness (Damasio, 2000; Jeannerod, 2006; Craig, 2009; Blanke, 2012). Recent advances in virtual reality (VR) technologies have enabled the investigation of bodily self-consciousness by providing subjects with ambiguous multisensory information about the location and appearance of their own body (Serino et al., 2008; Salomon et al., 2009, 2012). This has made it possible to study three important aspects of bodily self-consciousness and how they relate to the processing of bodily signals: self-identification with the body (the experience of owning a body), self-location (the experience of where I am in space), and first-person perspective (the experience of from where I perceive) (Blanke, 2012; Pfeiffer et al., 2013).

Although the sense of owning a body is often taken for granted, there are many cases of impaired sense of body ownership. For example, neurological patients with damage in the parietal lobe or insula will often neglect or deny ownership for body parts, one side of the body, or the entire body (e.g., Karnath et al., 2005; Vallar and Ronchi, 2009; Heydrich et al., 2010). Recent research has shown that hand ownership can also be manipulated in healthy individuals. Botvinick and Cohen's discovery of the rubber hand illusion (RHI) revealed that an illusory ownership for a rubber hand arises when synchronous visuo-tactile stimulation is administered to a person's occluded hand and that of a viewed rubber hand. This illusion is abolished when the tactile stimulation on the person's real hand is asynchronous to the stimulation seen on the rubber hand (Botvinick and Cohen, 1998) and can also be induced using VR technology (e.g., Slater et al., 2008; Evans and Blanke, 2013). As in other multisensory illusions, where specific combinations of multisensory information give rise to an erroneous subjective perception (e.g., McGurk and Macdonald, 1976), bodily illusions indicate states in which people report strong sensations of erroneous bodily self-consciousness due to an experimental manipulation of multisensory conflict between visual, proprioceptive, and tactile cues. The multisensory conflict between the visuo-tactile stimulation induces bodily illusions, reflecting alterations of bodily self-consciousness (Ehrsson, 2007; Blanke, 2012).

The RHI allows to investigate the integration of visual, tactile and proprioceptive signals and its importance for central body representation. However, more recent studies have shown that visuo-tactile mismatch may modify not only ownership of a body part, but may also induce ownership for a fake or virtual body (self-identification with a filmed or virtual body; Ehrsson, 2007; Petkova and Ehrsson, 2008), changes in self-location (Lenggenhager et al., 2007; Aspell et al., 2009), and changes in subjective first-person perspective (Ionta et al., 2011; Pfeiffer et al., 2013). The latter paradigm (i.e., full-body illusion, FBI) consists of participants viewing a video image on a head mounted display (HMD) that was linked to a video camera (placed 2 m behind the person) filming the participant's back from behind. Participants thus viewed the video image of their body while an experimenter stroked their back with a stick (the stroking was perceived by the participants on their back and also seen on the back of the virtual body). The HMD displayed the stroking of the virtual body either in real time or not (using an online video-delay or offline pre-recorded data), generating synchronous and asynchronous visuo-tactile stimulation.

The RHI and the FBI are most often quantified based on participants' responses to questionnaires and responses in different behavioral tasks. Several studies have shown that illusion conditions can elicit a change in the perceived location of the body or hand (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005; Lenggenhager et al., 2007), as well as changes in tactile processing (Pavani et al., 2000; Aspell et al., 2009; Zopf et al., 2010). Likewise, physiological measures have been employed and revealed heightened skin conductance responses (SCR) in reaction to threats to an illusorily embodied rubber hand (Armel and Ramachandran, 2003) or body (e.g., Ehrsson, 2007; Petkova and Ehrsson, 2008; Slater et al., 2008). The FBI has also been shown to affect pain perception by increasing pain thresholds (Hänsel et al., 2011). Additionally, differences in histamine reactivity (Barnsley et al., 2011) and the cooling of the participant's hand during the RHI (Moseley et al., 2008) have been found to accompany changes in illusory hand ownership. In summary, both the RHI and the FBI have been associated with physiological, behavioral, and tactile perceptual changes, whereas only the RHI has been linked to physiological changes in temperature and immune regulatory processes. These physiological changes have been suggested to reflect parasympathetic changes related to the modulations in body ownership. Such changes of temperature regulation can be found in several clinical conditions associated with disturbances in body ownership such as complex regional pain syndrome (Jänig and Baron, 2003; Moseley, 2005), anorexia (Lautenbacher et al., 1991), self-injurious behavior (Symons et al., 2001) as well as others (for more details of such clinical conditions see Table S1 in Moseley et al., 2008). It has been proposed that these modulations of temperature related to body ownership may be mediated though the insular cortex which has been shown to be involved in illusions of body ownership (e.g., Tsakiris, 2010; Blanke, 2012; Heydrich and Blanke, 2013) as well as coding of introspective information (Craig et al., 2000; Damasio et al., 2000; Craig, 2009).

While the FBI and the RHI are both induced by temporally synchronous visuo-tactile stroking of a seen body or hand with the participant's body or hand, the induced state of bodily self-consciousness differs in several aspects. For example, the RHI shows high sensitivity to both postural and anatomical congruence (Tsakiris and Haggard, 2005; Costantini and Haggard, 2007) as well as to the spatial distance between the seen and the touched hand. Thus, one study tested the effects of varying distance between the viewed rubber hand and the real hand and found that the illusion was strongest when the hands were near to each other and decayed rapidly when they were moved apart (Lloyd, 2007). Differently, FBIs can be induced when seeing a virtual body from a body-centered viewpoint (Petkova et al., 2011), but also from a distance (Ehrsson, 2007; Lenggenhager et al., 2007). Furthermore, classical FBI and RHI paradigms compare conditions in which a temporal conflict (and hence an anatomical conflict) exists (asynchronous visuo-tactile condition) to those with neither temporal nor anatomical conflicts (synchronous visuo-tactile conditions). However, to the best of our knowledge no experiment has compared the effects of an anatomical mismatch without any temporal conflict in the FBI.

Another difference between FBI and RHI relates to the anatomical specificity of the illusion. Studies have shown that during the RHI the proprioceptive drift may be constrained to the specific being finger stroked (Tsakiris and Haggard, 2005). However, the FBI, in which participants are typically stroked on their back, induces a change in self-location relating to the full body and its position in space rather than only the stroked region (Lenggenhager et al., 2007; Ionta et al., 2011). Recent findings from skin temperature measurements in the RHI have also shown a certain degree of specificity with decreased temperature in the illusion condition only in the stroked hand, but not for the contralateral hand nor for other non-stroked control sites [i.e., the ipsilateral ankle; (Moseley et al., 2008)]. This provides additional, physiological evidence that the RHI illusion induces a local and anatomically specific change in embodiment. The FBI, however, may induce a more widespread change in the body representation (at the trunk and potentially beyond), although no direct physiological evidence of such widespread changes has been provided.

Here, a novel robotic device for tactile stimulation (Duenas et al., 2011) is combined with VR to perform precise and reproducible visuo-tactile manipulations of the FBI. The robotic device was capable of independently stroking both the back (as in previous FBI studies) but also the legs, allowing us to explore if the FBI can be evoked by stroking of the legs. We investigated the following questions: Is anatomically congruent visuo-tactile stimulation necessary for the induction of the FBI (as has been shown previously for the RHI, but not yet tested for the FBI)? Would the induction of the FBI be accompanied with skin temperature reduction and will the temperature reduction be widespread or locally confined to the location of congruent visuo-tactile stroking as has been shown for the RHI (Moseley et al., 2008)? Participants were stroked by the robotic device on their back or leg while seeing anatomically congruent or incongruent visual feedback. Skin temperature, self-identification, self-location and tactile perception were measured. We hypothesized that (1) self-identification will be stronger during spatially-congruent versus incongruent conditions, and that (2) these illusion-inducing conditions will be associated with a reduction of skin temperature, which unlike in the RHI (Moseley et al., 2008) will not be specific to the location of visual tactile stimulation but rather widespread throughout all four recording sites. Following the results of Moseley et al. (2008) we expected that (3) response times (RTs) in the speeded tactile reaction would be longer in the congruent stroking conditions. Finally in line with previous experiments (e.g., Lenggenhager et al., 2009) we expected (4) a modulation of the RTs in the mental ball drop task as a function of visual-tactile stroking congruency.

METHODS

PARTICIPANTS

Twenty-two volunteers (14 male, 8 female, mean age = 22.1 years, *SD* = 2.3) participated in the study. Participants had normal or corrected to normal vision and gave written informed consent. All participants were right handed. The study was performed in accordance to the ethical standards of the Declaration of Helsinki. The experimental protocol was approved by the local ethics committee: La Commission d'ethique de la recherche Clinique de la Faculte de Biologie et de Medecine—at the University of Lausanne, Switzerland.

MATERIALS AND STIMULI

We used a robotic stroking device, which allows for the precise application of tactile stimuli to ensure reproducibility and consistency across the experimental conditions and participants. The device used in this study is detailed in Duenas et al. (2011). In brief, the stroking mechanism consists of four individual stimulation modules—two at the back and two at the legs—driven by four ultrasonic motors (Shinsei Corp., Japan) over a rack and pinion gear. The stimulation modules move a polymer sphere that contacts the body, held by a polymer spring blade which ensures constant contact pressure (**Figure 1C**). Stroking movement is position controlled with a sampling rate of 200 Hz and can be controlled at velocities of 2–12 cm/s. The four stroking modules followed a sawtooth trajectory with a range of 20 cm for back-stroking modules and 16 cm for leg-stroking modules (left and right) at 0.4 Hz. LabVIEW software (National Instruments Corporation, version 2010b, www.ni.com/labview) was used to control the robotic stroking device.

EXpyVR (Custom in house software, http://lnco.epfl.ch/expyvr) was used for the programming and executing of the experiment, and recording of RTs. Responses were collected using a keypad (Targus Numeric Keypad AKP10US, www.targus.com).

Participants wore a V-Real Viewer 3D SVGA HMD (800 × 600 resolution, 35° field of view, www.vrealities.com/virtualviewer3d.html). On the HMD, participants viewed the virtual avatar from behind, with an overlay of the position and range of stroking

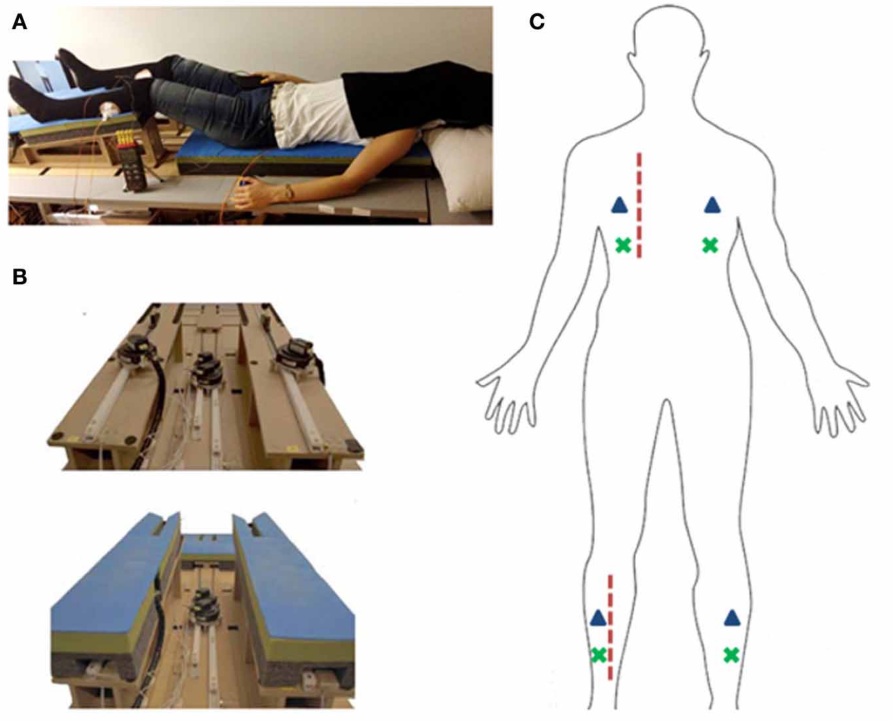

FIGURE 1 | Experimental setup. (A) Picture of experimental setup. Participant lying on robotic stroking device. **(B)** Robotic stoking device shown from feet perspective. Top: padding removed for motor view. Bottom: robot with padding as used in the experiment. **(C)** Schematic representation of stroking regions (dashed red line), tactile vibrators (blue triangles), and thermocouple placement (green x).

corresponding to that of the robotic stroking modules (Duenas et al., 2011; Ionta et al., 2011).

The participants were outfitted with four tactile vibrators at the left back, right back, left leg, right leg. Each vibrator consisted of a small vibrating motor (Precision MicroDrives shaftless vibration motors, model 312).

Participants' skin temperature was measured with a HH309A Data Logger Thermometer (Omega, Stamford, USA) with four type K thermocouples and a real-time clock. The skin temperature of participants were measured at four locations, 4 cm below the tactile vibrators on the left back, right back, left leg, and right leg. The temperature at each location was recorded every 2 s over the entire course of each experimental block, with the start of the experiment coinciding with the beginning of the temperature recording. We tested the variance of the thermometer in seven participants using the same locations and durations as used in the experiment. The participants were lying in a relaxed supine position without and visual or tactile stimulation. The mean variance of skin temperature change was 0.0005°C.

EXPERIMENTAL DESIGN

We used full-factorial design with a 2 (Visual Stroking: back, leg) ×2 (Tactile Stroking: back, leg) within-participant manipulation.

PROCEDURE

At the start of the experiment, participants were briefed about the stimuli they were going to experience and observe, and instructed on the different tasks they were to perform. All participants wore a white t-shirt and black socks which allowed for the placement of tactile vibrators and thermocouples on the skin. Participants were placed in a supine position on the robotic stroking device and wore a HMD covered by a black cloth to occlude peripheral vision. Participants held a ball (12 cm diameter) in their left hand and a response button device in their right hand.

A training session was carried out before the experiment, where participants saw a moving red dot against a black background and experienced the stroking first on their left back (15 s). This was followed by an auditory cue for a Mental Ball Dropping (MBD) Task (adapted from Lenggenhager et al., 2009; Ionta et al., 2011). The MBD task was used to measure self-location, by measuring the modulation of the experimental conditions on the judged time for an imaginary ball dropping from the participants' hand to reach the floor. First, participants pressed a button to indicate that they imagined releasing the ball from their hand (which was positioned close to the body at level with participants lying on the back). Secondly, participants held the button depressed during imagined ball dropping, and released the button to indicate that they imagined the ball hitting the floor. Button press duration (i.e., RT) were shown to be a sensitive measure of participants self-location in previous work (Lenggenhager et al., 2009).

Participants then performed a Speeded Tactile Reaction task. Tactile processing at different locations of the body was measured by a novel approach modified from the Temporal Order Judgments (TOJ) task, which showed that the RHI slowed tactile processing (Moseley et al., 2008). For the task in this experiment, participants' reaction times to vibration stimuli on four locations (left and right back and left and right leg) were tested. Each tactile vibrator was placed 5 cm laterally from the midpoint of the robot's stroking range. Participants felt four tactile vibrations (100 ms duration) at four different locations in random order during each trial, with random inter-stimulus intervals (0.5, 1, and 1.5 s) between vibrations. Participants were told to respond immediately each time they felt a vibration. Their RTs at the different locations were compared to a baseline measured in 40 practice trials (10 times at each location) before the actual experiment to correct for differences in tactile processing at different regions of the body. This procedure was repeated twice during the training session, with participants experiencing the stroking on their left leg during the second trial. Participants indicated their understanding of the tasks after the training session before proceeding on to the main experiment.

In each trial, participants were subjected to 40 s of stroking by the robotic device and observed a synchronous stroking pattern on a virtual body through the HMD. The stroking was applied on either their left back or left leg in each trial and participants were presented a synchronous movement of a red dot on either the left back or left leg of the virtual body (**Figure 1**). They were immediately prompted by an audio cue for a mental ball-drop and given 5 s to respond, followed by a Speeded Tactile Reaction task lasting 7 s. Each of the four experimental conditions (observed congruent back and leg stroking, observed incongruent back, and leg stroking) was presented five times in a single block, over two blocks (**Figure 2**).

The four conditions presented were spatially congruent back-stroking, spatially congruent leg-stroking, spatially incongruent back-stroking and spatially incongruent leg-stroking. The order of conditions was randomized for every block.

After having completed the experiment on the robotic device participants completed a questionnaire at the end of the experiment on a visual analogue scale (VAS) with scores ranging from −3 (absolutely NOT applicable) to +3 (absolutely applicable) pertaining to the two conditions, congruent, and incongruent stroking. All participants were aware of the difference between the two conditions. Questions were modified from (Lenggenhager et al., 2009; Ionta et al., 2011) and inquired about illusory touch, self-identification, and also contained control items (**Figure 3**).

Finally, participants were asked to give free verbal responses related to their sensations during the experiment. For each response they gave they were then prompted by the experimenter to reveal if this sensation was different for the congruent and incongruent conditions and if it differed for the locations of visuo-tactile stroking during the congruent condition (i.e., back-back vs. leg-leg). Responses were written down by the experimenter.

ANALYSIS

Self-identification questionnaire ratings were analyzed with 2×2 repeated measures ANOVA with Congruence (congruent/incongruent) and Question (Q1–5) as factors. Fisher's Least Significant Difference (LSD) analysis with threshold at $p < 0.05$ was used for all *post-hoc* comparisons. For presentation purposes the scale was then transformed into positive units resulting in a

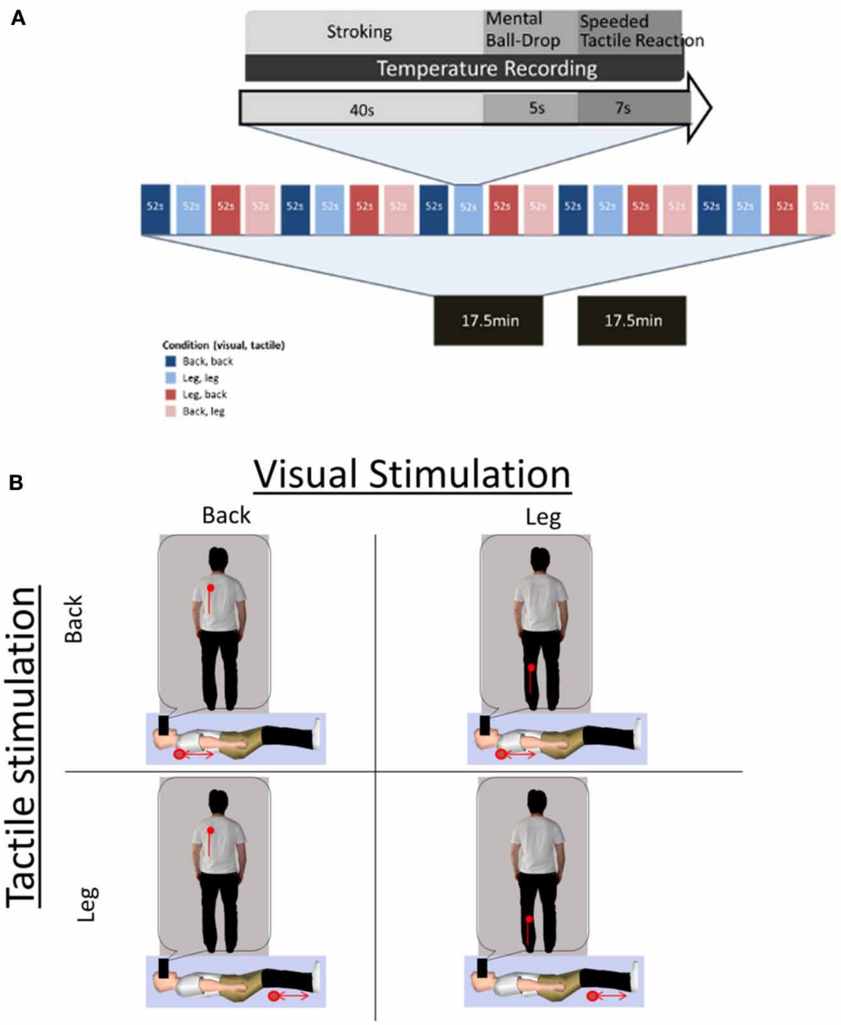

FIGURE 2 | Experimental paradigm and factorial design. (A) Experimental procedure of each trial (top), each block (20 trials-middle), and full experiment (two blocks-bottom). **(B)** Factorial design of the experiment: The four panels show different visuo-tactile stroking conditions. Participants lay supine and received tactile stroking on the back or leg (red dot and arrow represent tactile stroking range). Participants observed a virtual body (vertical body) and viewed visual stroking on the back or the leg as a movement of a red dot (vertical line marks the extent of visual stimulation and was not presented to participants). Note that the viewed virtual body was aligned in the same plane as the participants' body and is rotated for presentation purposes only.

scale of 1–7 corresponding to the −3 (absolutely NOT applicable) to +3 (absolutely applicable) originally measured.

Processing of RTs from the MBD task included removing dataset outlier values exceeding two standard deviations from the participant's mean for each individual. Condition average RTs for four experimental conditions were calculated and statistically analyzed with a 2 × 2 repeated measures ANOVA with factors Visual stimulation location (back/leg) and Stroking location (back/leg).

Processing of RTs for the Speeded Tactile Reaction Task consisted of removing for each individual dataset outlier values exceeding two standard deviations from the participant's mean. These were analyzed with 2 × 2 × 4 repeated measures ANOVA with factors tactile stimulation location (left and right back, left and right leg), Visual stimulation location (back/leg), Stroking location (back/leg).

Temperature data during the 40 s (20 time points) of stroking were analyzed by means of independent repeated measures 2 × 2 × 4 ANOVA for each time point (1-20), with Visual stimulation location (back/leg), Stroking location (back/leg), and Thermometer location (left and right back, left and right leg) as factors. Changes in temperature (ΔT) were calculated by subtracting the skin temperature at the start of stroking (time point 1) from all subsequent time points (time point 2–20) for each trial. Bonferroni correction for multiple comparisons was used for statistical analysis of temperature.

Overall changes in temperature were analyzed using a repeated measures 2 × 2 ANOVA with Visual stimulation location (back/leg) and Stroking location (back/leg) as factors. This was done once for the time period corresponding to the onset of the illusion as well as for the overall experimental epoch.

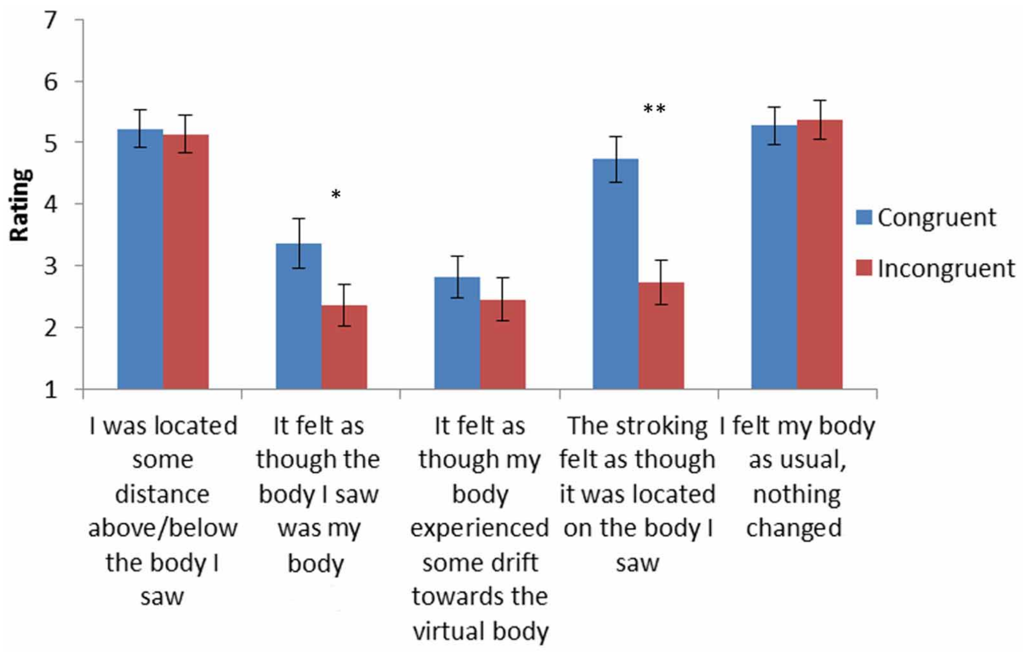

FIGURE 3 | Questionnaire ratings for Q1-5 (mean ± standard error). $N = 22$. *Indicates $p < 0.002$, and **indicates $p < 0.0001$.

For the analysis of temperature data, five participants were excluded from the analysis due to movements during the experiment which displaced the thermocouples. For the MBD task, outliers were discarded (total loss, 1.4% of trials, out of which 1 participant, whose mean reaction times were over 3 s, was excluded from analysis). For the analysis of RTs for the Speeded Tactile Reaction Task Trials outliers were removed (total loss, <1% of trials).

RESULTS

SELF-IDENTIFICATION

Subjective responses are shown in **Figure 3** and revealed stronger self-identification with the virtual body for congruent versus incongruent conditions [Q2: It felt as though the body I saw was as if it were my body; congruent trials $M = 3.36$, $SE = 0.39$; than incongruent trials: $M = 2.36$, $SE = 0.33$; $F_{(1,\ 21)} = 7.21$, $p = 0.013$]. There was also a significant congruence effect for Q4 (The stroking felt as though it was located on the body I saw) [$F_{(1,\ 21)} = 34.22$, $p < 0.001$], indicating illusory touch for the viewed body for the congruent condition ($M = 4.7$, $SE = 0.36$) that was larger than in the case of the incongruent condition ($M = 2.7$, $SE = 0.35$). The questions related to changes in self-location (Q1 and Q3) as well as the control question (Q5) showed no differences between the conditions.

SELF-LOCATION

Statistical analysis of RTs from the MBD task showed a trend for an interaction between visual and tactile input locations on participants' perception of self-location [$F_{(1,\ 20)} = 3.65$, $p = 0.07$]. *Post-hoc* comparisons revealed that participants had shorter RTs during the congruent condition ($M = 872$ ms, $SE = 5$ ms) than in the incongruent condition ($M = 884$ ms, $SE = 5$ ms, $p = 0.03$). When examining all visual and tactile stroking locations the back-congruent condition ($M = 860$ ms, $SE = 5$ ms) showed faster reaction times as compared to the incongruent leg-stroking condition ($M = 890$ ms, $SE = 5$ ms) ($p < 0.01$). This result indicates a change in self-location between congruent and incongruent conditions. No other effect was found for visual and tactile interaction (all $p > 0.2$).

TEMPERATURE CHANGES

No significant differences in temperature were found for the different measurement locations (left/right leg, left/right back $p = 0.8$ n.s.). There were no significant interactions between temperature measurement location and the other factors (all $p > 0.25$) at any of the 20 time points. This indicated that the cooling effect (see below) was not linked to any specific location of measurement. Hence, the measurements from all four locations were averaged.

Analysis of the temperature changes showed a strong effect of visual-tactile congruency on skin temperature [$F_{(1,\ 18)} = 70.115$, $p < 0.001$] with lower skin temperature in the congruent condition ($M = -0.0066$, $SE = 0.00064$) than in the incongruent condition ($M = -0.00007$, $SE = 0.0002$). The effect of location of stroking showed a trend [$F_{(1,\ 18)} = 3.7881$, $p = 0.06$] with lower temperature when the back was stroked ($M = -0.0037$, $SE = 0.0004$) than when the leg was stroked ($M = -0.0029$, $SE = 0.0002$). Finally the interaction between congruency and stroking location was also significant [$F_{(1,\ 18)} = 55.268$, $p < 0.001$]. *Post-hoc* Bonferroni tests indicated that this interaction was driven primarily by a large temperature difference between the back

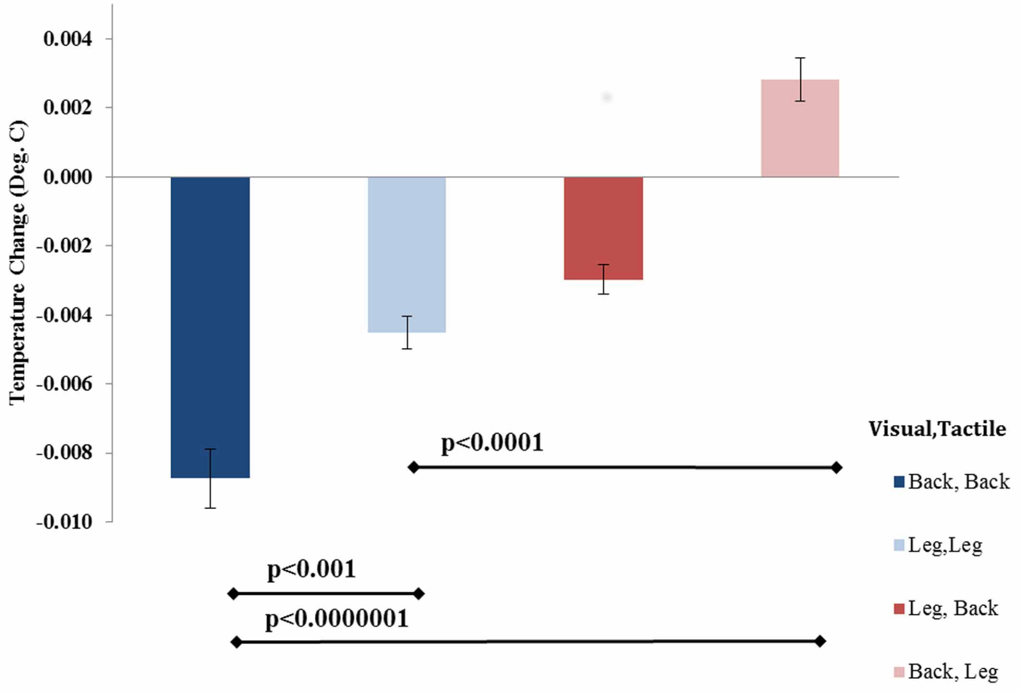

FIGURE 4 | Temperature data in all conditions. Temperature changes across four locations and across all time points (mean ± standard error). $N = 17$.

congruent (back-back) and back incongruent (back-leg) conditions (see **Figure 4**).

We then analyzed the evolution of the temperature changes over time. A separate ANOVA was conducted for each of the measured time points of the temperature data (see methods), hence removing any autocorrelations between timepoints. This revealed a significant effect of the interaction for visual and tactile stimulation location (e.g., back-back) starting from the 12th time point to the 20th time point (24–40 s of stroking) on the temperature [$F_{(1,\ 16)} = 4.89, p = 0.042$] (**Figure 5** and Table S2A, for individual statistics at each time point). *Post-hoc* tests indicated that this interaction was driven by a significant reduction of skin temperature in congruent versus incongruent conditions for all measurement locations [$F_{(1,\ 16)} = 70.11$, $p < 0.001$]. We performed a permutation test on a binary vector containing 12 zeros and 8 ones (see Methods) to determine the probability of obtaining 8 consecutive significant time points within a 20 time point set. Within the simulated distribution of 1,000,000 permutations, only 94 occurrences of 8 consecutive time points occurred by chance, suggesting a p-value of 0.000094. There was no main effect of visual stimulation location, nor tactile stimulation location or skin temperature measurement location on changes in temperature throughout the 20 time points [$F_{(1,\ 16)} = 0.26$, $p = 0.84$] (see Table S2B, for individual statistics at each time point).

As the time course analysis indicated that the temperature change evolved over time we repeated the analysis for the overall temperature change and restricted it to the later epoch (24–40 s) of the trial. The results for the temperature change during this epoch showed larger differences and can be viewed in Figure S1.

SPEEDED TACTILE REACTION TASK

Results from the speeded tactile reaction task revealed no effects or interactions for visual stimulation, stroking, and location of vibration stimuli (left and right back, left and right leg) (all $p > 0.1$).

FREE RESPONSES

Free responses from subjects who reported bodily sensations (12/22) were collected and revealed that the congruent back stimulation was more pleasant than the congruent leg stimulation.

DISCUSSION

The present data revealed a continuous widespread decrease in skin temperature during the time course of the FBI. We found that the temperature decrease was not specific to the site of measurement, showing similar effects in all locations despite the considerable distance between the measurement locations. Furthermore, the present results show that anatomically congruent and temporally synchronous stimulation of the legs can induce a FBI. Additionally, we show that temporal synchrony between the visual and the tactile cue is not sufficient for inducing the FBI but an anatomical congruence of the visual and tactile stimulations is also required.

Subjective responses recorded via questionnaires and free responses are in accord with previous works using temporal synchrony manipulation (Lenggenhager et al., 2009; Ionta et al., 2011). These revealed that illusory self-identification with the visual virtual body (Q2) and illusory touch of the visuo-tactile event (Q4) were stronger in the congruent conditions. In their

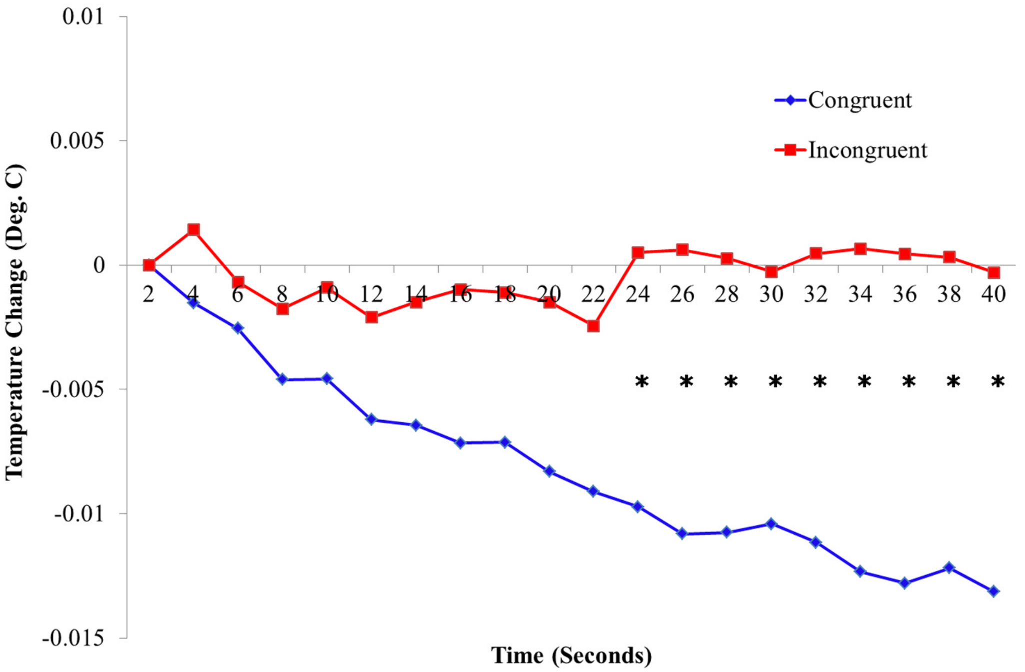

FIGURE 5 | Temperature time course data. Temperature changes across four locations during 40 s of stroking for all conditions. Blue and Red lines represent temperature changes between congruent and both incongruent conditions, respectively. *indicate locations of significant differences between congruent and incongruent conditions (individual ANOVA, $p < 0.05$, Bonferoni corrected). $N = 17$.

free responses most participants reported a stronger effect of illusory self-identification during congruent back-stroking trials as compared to congruent leg-stroking trials. Some responses include: "Back stroking led to a more effective way of thinking of the virtual body as a real body" and "Back-congruent condition was more pleasant and the feeling of my body being the virtual body was stronger for the back stroking than for leg stroking."

Previous findings of participant's subjective feeling of ownership for a rubber hand or virtual body (as determined from responses to questionnaires) have shown differences between synchronous and asynchronous visual-tactile stimulations. These typically show stronger ownership for the fake body or body part in temporally synchronous conditions than temporally asynchronous conditions. However, it has been argued that these effects may be driven by a strong sensation of disownership for the body in the asynchronous condition. For instance, a study with 131 participants showed an ownership rating at +0.4 for synchronous conditions, but a larger negative magnitude of −1.2 for asynchronous conditions (Longo et al., 2008). As such, de Vignemont (2010), posits that the sense of ownership experienced by participants during synchronous stroking could possibly reflect participants' confidence in their judgment instead, with participants being more certain that the rubber hand did not belong to them in the asynchronous condition. The current study carefully controlled the synchrony of stroking—by means of a robotic system combined with VR—ensuring visual and tactile synchrony throughout all conditions and across different distant stimulation sites; hence the effects shown here are not related to a sense of disownership caused by temporally asynchronous stimulation. This extends the previous findings to suggest that anatomical congruence even in the absence of temporal conflicts is an important factor for illusory self-identification (as tested here), and potentially also for hand ownership as tested in the RHI.

Objective physiological measurements of participants' skin temperature indicated a cooling of the skin which was significant after 24 s of congruent visuo-tactile stimulation. Importantly, these changes (illusory self-identification, and cooling) were absent or weaker during incongruent stimulation. The present findings extend previous findings of cooling of skin temperature during illusory hand ownership (Moseley et al., 2008; Kammers et al., 2011). It has been suggested that the cooling of skin temperature during bodily illusions relates to a modulation of homeostatic activity due to a change in body representation. The alteration of the normal body representation by the illusion has been suggested to induce a "disownership" of the true body part, leading to a modulation of skin temperature, tactile processing (Moseley et al., 2008), pain thresholds (Hänsel et al., 2011), and even histamine reactivity (Barnsley et al., 2011). However, these previous studies have shown anatomically specific changes in line with the localized effects of the RHI. In the current study, and contrary to previous results the induction of the FBI resulted in a widespread temperature change in all four measured locations (legs and back). This is in accord with previous findings showing that despite localized visuo-tactile stimulation (on the back), the induced self-identification and self-location effects indicate changes encompassing the full body. The FBI has also demonstrated more flexible parameters than the RHI for self-identification with a false body. For instance, both male and female participants experience the same degree of illusion with the use of a male virtual avatar (Ionta et al., 2011) or male mannequin (Petkova and Ehrsson, 2008); furthermore the FBI can be induced for different viewpoints and different spatial distances between stroked and seen body (Ionta et al., 2011; Petkova et al., 2011). The RHI has been shown to be more restricted to specific spatial configurations (Costantini and Haggard, 2007; Lloyd, 2007). Our results build on these findings to suggest that the body representation is malleable enough to experience an illusion of the whole body, even when stroking is applied to the back or to the legs. While not measured in the current experiment, we speculate that this difference may be related to the difference in the size (or somatosensory receptor density) of the tactile receptive fields on the back/leg versus the hand (Gardner, 1988; Nakamura et al., 1998; Kurth et al., 2000). The larger receptive fields on the back and leg regions allow only a much coarser somatosensory resolution which may in turn lead to a less spatially specific and hence more global illusion resolution.

While not tested in this experiment, a possible mechanism for the effects of illusory self-identification on body temperature, brought about by visuo-tactile manipulation, could involve the insula, which is known to be one of the centers of activation during cross-modal visual and somatosensory activation (Bottini et al., 1995; Hadjikhani and Roland, 1998). The insula has also been found to be the main cortical substrate involved in discriminating innocuous thermal sensation (Craig et al., 2000), thermal regulation (Maihöfner et al., 2002) and is also found to play a critical role in the sense of limb ownership (Baier and Karnath, 2008; Karnath and Baier, 2010). It has thus been postulated to be the key neural substrate that mediates the influence of temperature on interoceptive processes (Kang et al., 2011).

It is noteworthy to mention that changes in body temperature found in the present study were highly significant, but very small (i.e., in the range of 0.006–0.014°C); those reported in the original experiment by Moseley [and as measured by a hand-held thermometer device (Rayek)] were larger and around 0.24°C (Moseley et al., 2008 Exp. 1–3). There are several methodological differences between both experiments which may account for the discrepancies. First, the experiment by Moseley used the RHI as opposed to a FBI which may be associated with different temperature effects. In the previous RHI experiment the cooling effects were found for the hand which may have different thermal variation than the back and thigh that were measured in the present experiment. Also, in Moseley's experiment, temperature was recorded by means of a hand-held thermometer with readings every 30 s for 7–8 min, giving five readings for each location (stimulated hand, unstimulated hand, and ipsilateral ankle) in each trial. Here, we used a 4-channel thermometer with thermocouples as temperature sensors to record temperature every 2 s for 40 s, giving 20 readings for each location in each trial. The constant recording of temperature throughout the experiment allowed for the collection of a more continuous and well-controlled dataset, enabling a rigorous analysis of the temperature changes induced by the illusion. Finally, the shorter trial durations may also have affected the magnitude of the temperature change, as the trials in our experiment were considerably shorter than those used by Moseley et al. (40 s vs. 7–8 min). In Moseley et al. (2008) the temperature changes after 24 s (**Figure 1B**) are of a similar magnitude to those reported here, and the peak temperature change is found after about 4 min of stroking. Thus, the temperature change observed in our experiment may not have reached its asymptote in our shorter trails.

With a continuous temperature measurement at a high sampling rate, this study offers novel evidence, based on objective measurements, of the onset of physiological changes associated with illusory self-identification with a virtual body. Differences in skin temperature during the four conditions occurred from the start of stroking, with the gradual temperature change of the skin during both congruent trials, and minor fluctuations of temperature during incongruent trials. However, the differences among the conditions only became significant after 24 s of stroking. Previous research has shown that bodily illusions require time for their induction [i.e., ~11 s for the RHI (Ehrsson et al., 2004; Kammers et al., 2009)]. Therefore, we predicted that the temperature change would show similar dynamics and would require some time for induction. This is also in line with the findings of the Moseley et al. (2008) paper showing that the temperature change evolved over several minutes in the RHI (Moseley et al., 2008) (**Figure 1B**). These findings suggest that the psychological feeling of illusory self-identification during the FBI may be linked to the increasing magnitude of a widespread cooling of the body (at least with respect to those body parts sampled in the present study). We have argued earlier (Blanke, 2012) that differences in bodily self-consciousness between RHI and FBI might be related to the relevance of the stroked body regions for a global representation of the bodily self. Specifically, peripheral body regions might be less crucial than trunk regions for global aspects of the bodily self.

The measurement of self-location using the MBD task showed that participants had shorter RTs during congruent visuo-tactile stroking conditions. This result indicates a change in perceived self-location between the same conditions that were associated with changes in body temperature and self-identification with the virtual body. Neuroimaging experiments directly comparing visuo-tactile conflicts with and without temporal mismatch are necessary to investigate how changes in self-location map to changes in illusory self-identification and temperature change (Lenggenhager et al., 2009; Ionta et al., 2011).

CONCLUSIONS

The findings of the current study have important implications for the understanding of bodily self-consciousness. They demonstrate for the first time that changes in full body self-consciousness induced by synchronous visuo-tactile stimulation relate to systematic and successive changes in skin temperature. Contrary to results from the RHI, these temperature changes are widespread and involve a cooling which spreads to both sides of the body as well as to regions anatomically distant from the stimulated region. These findings are compatible with the thesis that the FBI alters more global aspects of bodily self-consciousness as compared to the more local and limb-specific changes induced by the RHI (Blanke and Metzinger, 2009). This extends previous findings regarding differences in the behavioral and neural mechanisms of the FBI and RHI (Ehrsson et al., 2004; Ionta et al., 2011) suggesting that the sense of ownership over a limb and the full body may be quite different. Additionally, our results show that temporally synchronous stimulation between a seen body part and a different, touched body part is not sufficient for the induction of illusory self-identification with a virtual body and cooling of one's own body; temporally synchronous stimulation needs to be applied with an anatomical congruency. Our results highlight that the sense of ownership is a spatially multifaceted experience affecting both explicit as well as implicit bodily measures.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/Behavioral_Neuroscience/10.3389/fnbeh.2013.00065/abstract

REFERENCES

Armel, K. C., and Ramachandran, V. S. (2003). Projecting sensations to external objects: evidence from skin conductance response. *Proc. Biol. Sci.* 270, 1499–1506. doi: 10.1098/rspb.2003.2364

Aspell, J., Lenggenhager, B., and Blanke, O. (2009). Keeping in touch with one's self: multisensory mechanisms of self-consciousness. *PLoS ONE* 4:e6488. doi: 10.1371/journal.pone.0006488

Baier, B., and Karnath, H. O. (2008). Tight link between our sense of limb ownership and self-awareness of actions. *Stroke* 39, 486–488. doi: 10.1161/STROKEAHA.107.495606

Barnsley, N., McAuley, J., Mohan, R., Dey, A., Thomas, P., and Moseley, G. (2011). The rubber hand illusion increases histamine reactivity in the real arm. *Curr. Biol.* 21, R945–R946. doi: 10.1016/j.cub.2011.10.039

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nat. Rev. Neurosci.* 13, 556–571. doi: 10.1038/nrn3292

Blanke, O., and Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends Cogn. Sci.* 13, 7–13. doi: 10.1016/j.tics.2008.10.003

Bottini, G., Paulesu, E., Sterzi, R., Warburton, E., Wise, R., Vallar, G., et al. (1995). Modulation of conscious experience by peripheral sensory stimuli. *Nature* 376, 778–781. doi: 10.1038/376778a0

Botvinick, M., and Cohen, J. (1998). Rubber hands 'feel'touch that eyes see. *Nature* 391, 756. doi: 10.1038/35784

Costantini, M., and Haggard, P. (2007). The rubber hand illusion: sensitivity and reference frame for body ownership. *Conscious. Cogn.* 16, 229–240. doi: 10.1016/j.concog.2007.01.001

Craig, A. (2009). How do you feel–now? The anterior insula and human awareness. *Nat. Rev. Neurosci.* 10, 59. doi: 10.1038/nrn2555

Craig, A. D., Chen, K., Bandy, D., and Reiman, E. M. (2000). Thermosensory activation of insular cortex. *Nat. Neurosci.* 3, 184–190. doi: 10.1038/72131

Damasio, A. (2000). *The Feeling of What Happens: Body and Emotion in the Making of Consciousness*, (Vintage: Harvest Books), 213–215.

Damasio, A. R., Grabowski, T. J., Bechara, A., Damasio, H., Ponto, L. L., Parvizi, J., et al. (2000). Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nat. Neurosci.* 3, 1049–1056. doi: 10.1038/79871

De Vignemont, F. (2010). Body schema and body image—Pros and cons. *Neuropsychologia* 48, 669–680. doi: 10.1016/j.neuropsychologia.2009.09.022

Duenas, J., Chapuis, D., Pfeiffer, C., Martuzzi, R., Ionta, S., Blanke, O., et al. (2011). Neuroscience robotics to investigate multisensory integration and bodily awareness. *Conf. Proc. IEEE Eng. Med. Biol. Soc.* 8348–8352. doi: 10.1109/IEMBS.2011.6092059.

Ehrsson, H., Spence, C., and Passingham, R. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science* 305, 875. doi: 10.1126/science.1097011

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science* 317, 1048. doi: 10.1126/science.1142175

Evans, N., and Blanke, O. (2013). Shared electrophysiology mechanisms of body ownership and motor imagery. *Neuroimage* 64, 216–228. doi: 10.1016/j.neuroimage.2012.09.027

Gardner, E. P. (1988). Somatosensory cortical mechanisms of feature detection in tactile and kinesthetic discrimination. *Can. J. Physiol. Pharmacol.* 66, 439–454. doi: 10.1139/y88-074

Hadjikhani, N., and Roland, P. E. (1998). Cross-modal transfer of information between the tactile and the visual representations in the human brain: a positron emission tomographic study. *J. Neurosci.* 18, 1072–1084.

Hänsel, A., Lenggenhagerl, B., Känell, R., Curatolol, M., and Blankel, O. (2011). Seeing and identifying with a virtual body decreases pain perception. *Eur. J. Pain* 15, 874–879. doi: 10.1016/j.ejpain.2011.03.013

Heydrich, L., and Blanke, O. (2013). Distinct illusory own-body perceptions caused by damage to posterior insula and extrastriate cortex. *Brain* 136, 790–803. doi: 10.1093/brain/aws364

Heydrich, L., Dieguez, S., Grunwald, T., Seeck, M., and Blanke, O. (2010). Illusory own body perceptions: case reports and relevance for bodily self-consciousness. *Conscious. Cogn.* 19, 702–710. doi: 10.1016/j.concog.2010.04.010

Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., et al. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron* 70, 363–374. doi: 10.1016/j.neuron.2011.03.009

James, W. (1890/1950). *The Principles of Psychology*. New York, NY: Dover Publications.

Jänig, W., and Baron, R. (2003). Complex regional pain syndrome: mystery explained? *Lancet Neurol.* 2, 687–697. doi: 10.1016/S1474-4422(03)00557-X

Jeannerod, M. (2006). *Motor Cognition: what Actions Tell the Self*. Oxford: Oxford University Press.

Kammers, M., De Vignemont, F., Verhagen, L., and Dijkerman, H. C. (2009). The rubber hand illusion in action. *Neuropsychologia* 47, 204–211. doi: 10.1016/j.neuropsychologia.2008.07.028

Kammers, M. P. M., Rose, K., and Haggard, P. (2011). Feeling numb: temperature, but not thermal pain, modulates feeling of body ownership. *Neuropsychologia* 49, 1316–1321. doi: 10.1016/j.neuropsychologia.2011.02.039

Kang, Y., Williams, L. E., Clark, M. S., Gray, J. R., and Bargh, J. A. (2011). Physical temperature effects on trust behavior: the role of insula. *Soc. Cogn. Affect. Neurosci.* 6, 507–515. doi: 10.1093/scan/nsq077

Karnath, H. O., and Baier, B. (2010). "Anosognosia for hemiparesis and hemiplegia: disturbed sense of agency and body ownership," in *The Study of Anosognosia*, ed G. P. Prigatano (Oxford: Oxford university Press), 39–62.

Karnath, H. O., Baier, B., and Nägele, T. (2005). Awareness of the functioning of one's own limbs mediated by the insular cortex? *J. Neurosci.* 25, 7134–7138. doi: 10.1523/JNEUROSCI.1590-05.2005

Kurth, R., Villringer, K., Curio, G., Wolf, K. J., Krause, T., Repenthin, J., et al. (2000). fMRI shows multiple somatotopic digit representations in human primary somatosensory cortex. *Neuroreport* 11, 1487–1491.

doi: 10.1097/00001756-200005150-00025

Lautenbacher, S., Pauls, A. M., Strian, F., Pirke, K.-M., and Krieg, J.-C. (1991). Pain sensitivity in anorexia nervosa and bulimia nervosa. *Biol. Psychiatry* 29, 1073–1078. doi: 10.1016/0006-3223(91)90249-L

Lenggenhager, B., Mouthon, M., and Blanke, O. (2009). Spatial aspects of bodily self-consciousness. *Conscious. Cogn.* 18, 110–117. doi: 10.1016/j.concog.2008.11.003

Lenggenhager, B., Tadi, T., Metzinger, T., and Blanke, O. (2007). Video ergo sum: manipulating bodily self-consciousness. *Science* 317, 1096. doi: 10.1126/science.1143439

Lloyd, D. M. (2007). Spatial limits on referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. *Brain Cogn.* 64, 104–109. doi: 10.1016/j.bandc.2006.09.013

Longo, M. R., Cardozo, S., and Haggard, P. (2008). Visual enhancement of touch and the bodily self. *Conscious. Cogn.* 17, 1181–1191. doi: 10.1016/j.concog.2008.01.001

Maihöfner, C., Kaltenhäuser, M., Neundörfer, B., and Lang, E. (2002). Temporo-spatial analysis of cortical activation by phasic innocuous and noxious cold stimuli–a magnetoencephalographic study. *Pain* 100, 281. doi: 10.1016/S0304-3959(02)00276-2

McGurk, H., and Macdonald, J. (1976). Hearing lips and seeing voices. *Nature* 264, 746–748.

Moseley, G. L. (2005). Distorted body image in complex regional pain syndrome. *Neurology* 65, 773. doi: 10.1212/01.wnl.0000174515.07205.11

Moseley, G. L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., et al. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proc. Natl. Acad. Sci. U.S.A.* 105, 13169–13173. doi: 10.1073/pnas.0803768105

Nakamura, A., Yamada, T., Goto, A., Kato, T., Ito, K., Abe, Y., et al. (1998). Somatosensory homunculus as drawn by MEG. *Neuroimage* 7, 377–386. doi: 10.1006/nimg.1998.0332

Pavani, F., Spence, C., and Driver, J. (2000). Visual capture of touch: out-of-the-body experiences with rubber gloves. *Psychol. Sci.* 11, 353. doi: 10.1111/1467-9280.00270

Petkova, V. I., and Ehrsson, H. H. (2008). If I were you: perceptual illusion of body swapping. *PLoS ONE* 3:e3832. doi: 10.1371/journal.pone.0003832

Petkova, V. I., Khoshnevis, M., and Ehrsson, H. H. (2011). The perspective matters! Multisensory integration in ego-centric reference frames determines full-body ownership. *Front. Psychol.* 2:35. doi: 10.3389/fpsyg.2011.00035

Pfeiffer, C., Lopez, C., Schmutz, V., Duenas, J. A., Martuzzi, R., and Blanke, O. (2013). Multisensory origin of the subjective first-person perspective: visual, tactile, and vestibular mechanisms. *PLoS ONE* 8:e61751. doi: 10.1371/journal.pone.0061751

Salomon, R., Malach, R., and Lamy, D. (2009). Involvement of the intrinsic/default system in movement-related self recognition. *PLoS ONE* 4:e7527. doi: 10.1371/journal.pone.0007527

Salomon, R., Van Elk, M., Aspell, J. E., and Blanke, O. (2012). I feel who I see: visual body identity affects visual–tactile integration in peripersonal space. *Conscious. Cogn.* 21, 1355–1364. doi: 10.1016/j.concog.2012.06.012

Serino, A., Pizzoferrato, F., and Ladavas, E. (2008). Viewing a face (especially one's own face) being touched enhances tactile perception on the face. *Psychol. Sci.* 19, 434. doi: 10.1111/j.1467-9280.2008.02105.x

Slater, M., Perez-Marcos, D., Ehrsson, H. H., and Sanchez-Vives, M. V. (2008). Towards a digital body: the virtual arm illusion. *Front. Hum. Neurosci.* 2:6. doi: 10.3389/neuro.09.006.2008

Symons, F. J., Sutton, K. A., and Bodfish, J. W. (2001). Preliminary study of altered skin temperature at body sites associated with self-injurious behavior in adults who have developmental disabilities. *Am. J. Ment. Retard.* 106, 336–343. doi: 10.1352/0895-8017(2001)106<0336:PSOAST>2.0.CO;2

Tsakiris, M. (2010). My body in the brain: a neurocognitive model of body-ownership. *Neuropsychologia* 48, 703–712. doi: 10.1016/j.neuropsychologia.2009.09.034

Tsakiris, M., and Haggard, P. (2005). The rubber hand illusion revisited: visuotactile integration and self-attribution. *J. Exp. Psychol. Hum. Percept. Perform.* 31, 80. doi: 10.1037/0096-1523.31.1.80

Vallar, G., and Ronchi, R. (2009). Somatoparaphrenia: a body delusion. A review of the neuropsychological literature. *Exp. Brain Res.* 192, 533–551. doi: 10.1007/s00221-008-1562-y

Zopf, R., Savage, G., and Williams, M. A. (2010). Crossmodal congruency measures of lateral distance effects on the rubber hand illusion. *Neuropsychologia* 48, 713–725. doi: 10.1016/j.neuropsychologia.2009.10.028

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Appendix 3

Noel J-P, Pfeiffer C, Blanke O, and Serino A. (under review) Peripersonal space as the space of the bodily self. Under review at Cognition.

Peripersonal Space as the space of the Bodily Self

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Abstract

Bodily self-consciousness (BSC) refers to experience of our self as located within an owned body (self-identification) and as occupying a specific location in space (self-location). BSC can be altered through multisensory stimulation, as in the Full Body Illusion (FBI). If participants view a virtual body from a distance being stroked, while receiving synchronous tactile stroking on their physical body, they feel such as the virtual body were their own and their perceived self location shifts towards the virtual body. Here we hypothesized that - while normally the experience of the body in space depends on the integration of multisensory body-related signals within a limited space surrounding the body (i.e. peripersonal space, PPS) - during the FBI the boundaries of PPS would shift towards the virtual body, that is towards the position of self-location. To test this hypothesis, we used synchronous visuo-tactile stroking to induce the FBI, as contrasted with a control condition of asynchronous stroking. Concurrently, we applied an audio-tactile interaction paradigm to estimate the boundaries of PPS. PPS was measured in front of and behind the participants' body as the distance where tactile information interacted with auditory stimuli looming in space toward the participant's physical body. We found that during synchronous stroking, i.e. when participants experienced the FBI, PPS boundaries extended in the front-space, towards the avatar, and concurrently shrunk in the back-space, as compared to the asynchronous stroking control condition, where no FBI was induced. These findings support the view that during the FBI, PPS boundaries translate toward the virtual body, such that the PPS representation shifts from being centered at the location of the physical body to being now centered at the subjectively experienced location of the self.

Keywords: Peripersonal Space, Full Body Illusion, Self-Location, Self, Multisensory Integration.

1. Introduction

A fundamental aspect of our sense of self as subject of conscious experience is the experience of the bodily self, that is, the feeling of being located within a body we own and control (Blanke & Metzinger, 2009; Gallagher, 2005; Jeannerod, 2006). Empirical data demonstrate that the feeling of owning a body (self-identification), as well as the sense of being located within the boundaries of that body (self-location), are fundamentally rooted in the congruent and cohesive integration of multiple sensory modalities within the spatio-temporal dimensions of the physical body (Blanke, 2012). In fact, manipulating the spatio-temporal congruency of different sensory modalities can induce different bodily illusions, such as the Rubber Hand Illusion (RHI: Botvinick & Cohen, 1998) and the Full Body Illusion (FBI: Lenggenhager, Tadi, Metzinger, & Blanke, 2007) and out-of-body illusions (Ehrsson, 2007). During the FBI subjects see a virtual body (avatar), placed 2 meters in front them, being stroked, while synchronously receiving a congruent tactile stimulation on their physical body. Under such circumstances participants report to identify with the virtual body (change in self-identification), and feel displaced toward the virtual body (change in self-location). These effects are absent, or reduced, when tactile and visual stimulation are asynchronously administered. Bodily illusions such as the RHI and the FBI reveal that both body-part and full-body representations are malleable in that a sense of ownership can be induced for physical or virtual replacements of our body and that the spatial limits of self-experience can go beyond those of our physical body.

While similar findings have been repetitively reported for different multisensory manipulations (see Blanke, 2012; Ehrsson, 2012; Serino et al., 2013 for reviews), the brain mechanisms underlying these effects are not yet known. It has been proposed that, during the FBI, synchronous tactile stimulation on the participants' body and visual stimulation from the avatar seen at an extracorporeal location might enlarge the visual and/or auditory receptive fields of neurons coding for peripersonal space (PPS) (Blanke, 2012; Makin, Holmes, & Ehrsson, 2008). Normally, multisensory PPS neurons integrate tactile, visual, and auditory stimuli when presented at a limited distance from the body (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997; Graziano & Cooke, 2006; Bremmer at al, 2002; Makin et al., 2007; Gentile et al., 2011), but not when further away. This limit defines the boundary of PPS, that have also been reported to be plastic in that the space where multisensory stimuli are integrated extends when individuals interact with far locations, for instance, by using tools (Maravita & Iriki, 2004; Làdavas & Serino, 2008). It is possible that feeling touch on one's own body, while viewing tactile stimulation administered on a virtual body at a distance may also alter the boundaries of the PPS representation. Accordingly, previous studies have shown that the spatial constraints of multisensory integration between vision and touch vary during the FBI (Aspell, Lenggenhager, & Blanke, 2009) or the RHI (Pavani, Spence, & Driver, 2000; Zopf, Savage, & Williams, 2010). Here we describe how the boundaries of PPS shape during the FBI. In particular, we test the hypothesis that, while normally the PPS representation is bound to the physical body, during the FBI PPS becomes referenced at the illusory perceived self-location.

To test that hypothesis, we induced the FBI (Lenggenhager et al., 2007), while we concurrently measured the spatial extent of PPS representation by means of a dynamic audio-tactile interaction task (Canzoneri et al., 2012). We administered tactile stimulation on the participant's physical body and synchronous spatially conflicting visual stimulation of a virtual body to experimentally induce a change in BSC, as reported by participants through a questionnaire. In a control condition, tactile and visual stimulation were administered asynchronously. Concurrently, in order to define the boundary of PPS representation, participants were asked to respond as fast as possible to vibro-tactile stimuli administered on their trunk, while task-irrelevant sounds loomed toward their trunk. Based on previous findings (Canzoneri et al., 2012; 2013a; 2013b; Teneggi et al., 2013), we predicted that reaction times to tactile stimuli would decrease once the sound overcame a particular distance from the body, which can be taken as a proxy for the boundary of PPS. In Experiment 1, dynamic sounds were presented in the participants' front space. In this way, we tested whether during synchronous visuo-tactile stroking inducing the FBI, the PPS boundary extends in the front, toward the virtual body, as compared to the asynchronous control condition. In Experiment 2, moving sounds were presented in the participants' back-space, to test whether the extension of PPS toward the virtual body in the front-space (as predicted in Experiment 1) was associated with a concurrent shrinkage of PPS in the back-space (or whether it was rather associated with no change). Such findings would indicate a shift of PPS representation from the physical body to the illusory perceived location of the self. We predicted no changes in PPS boundaries (either in the front or in the back) during the asynchronous stroking condition, where no FBI was induced.

2. Material and Methods

2.1 Participants

Nineteen and fifteen students from the Ecole Polytechnique Federale de Lausanne participated in Experiment 1 (9 females, mean age = 23.0 years, range 18-29) and in Experiment 2 (4 females, mean age 24.2 years, range 19 – 31), respectively. All participants were right-handed, had normal or corrected-to-normal eyesight, normal hearing, and no history of neurological or psychiatric disease. The study was approved by Brain Mind Institute Ethics Committee for Human Behavioral Research of the EPFL and conducted in line with the Declaration of Helsinki. All participants gave informed consent prior to participation and were remunerated with 20 Swiss Francs for their time.

2.2. Stimuli and Apparatus

Figure 1A shows the experimental setup. In order to measure the boundaries of PPS representation, participants stood in the middle of two arrays of 8 speakers each, placed besides their chest, one on the right and one on the left, at 50 cm distance from their midline. Four speakers on each side were placed in the participant's front space, and were utilized in Experiment 1 to map the front PPS, and 4 speakers on each side were placed in the participant's backspace and were utilized in Experiment 2 to map their back space PPS. The loudspeakers extended from 100 cm in front of the subjects to 100 cm in the back. In addition, participants were outfitted with a vibro-tactile device (Precision MicroDrives shaftless vibration motors, model 312–101), which was placed on the participant's chest in Experiment 1 and on his/her back in Experiment 2, at stern level. Participants were handed a wireless gamepad (XBOX 360 controller, Microsoft, Redmond, WA), which they held in their right hand and used to respond to vibro-tactile stimulation.

In order to induce the FBI, two video cameras (Logitech HD Webcam C270, 1280x720 pixels, Logitech Fluid Crystal Technology) recorded the participant from a distance of 200 cm (in the back), and this signal was relayed stereoscopically to a Head Mounted Display (HMD, Oculus Rift SDK, Oculus VR, 100° field of view, 60Hz) worn by the subject. Synchronous visuo-tactile stroking was achieved by direct real-time (<50 ms delay) display of visual signals from the cameras to the HMD. During asynchronous visuo-tactile stimulation the camera signal was delayed by 500 ms before feeding it to the HMD.

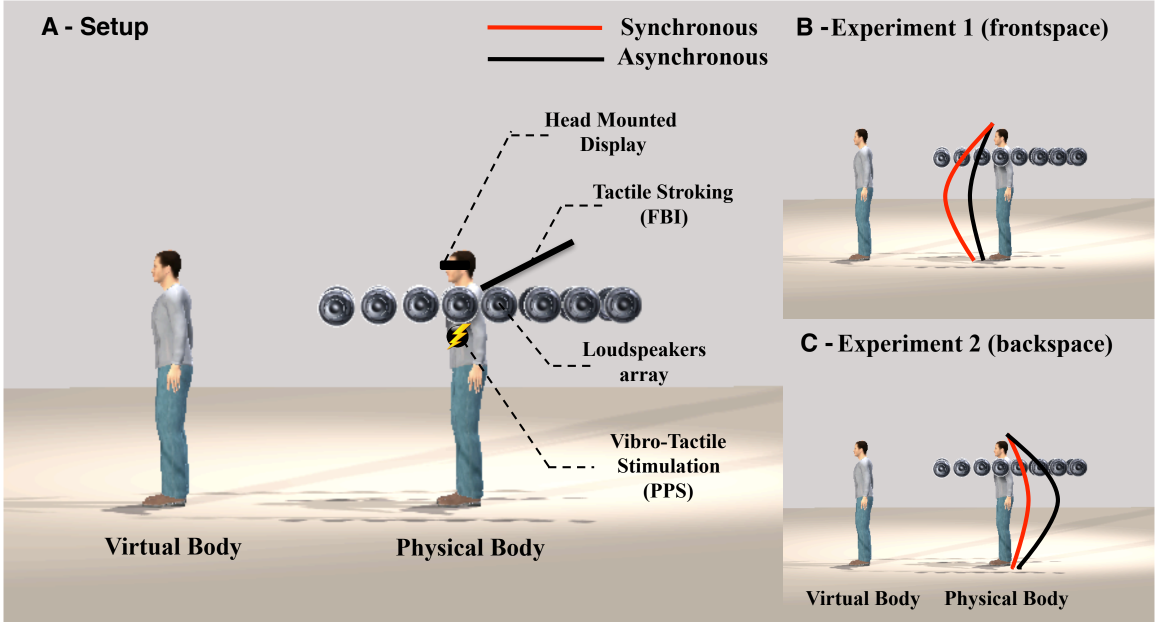

Figure 1. *Experimental Setup and hypothesis.* (A). In order to induce the Full Body Illusion (FBI), the participant viewed on a head-mounted display a virtual body in front. Tactile stroking was administered to the participant's back while synchronous or asynchronous visual stroking was seen on the back of the virtual body. Peripersonal Space (PPS) representation was measured by recording response times to vibrotactile stimuli applied to the participant's chest while concurrent task-irrelevant looming sounds were administered from a loudspeaker array placed beside the participant. We hypothesized that during synchronous stroking, i.e., when the FBI is induced, PPS representation extends toward the virtual body in the front-space (B, red line), and concurrently shrinks in the back-space (C, red line), as compared to the asynchronous stroking control condition (B and C, black lines).

2.3 Experimental Manipulations and Outcome Measures

2. 3. 1 Full Body Illusion Manipulations.

For each experiment, two conditions of synchronous and asynchronous visuo-tactile stroking were presented in separate blocks, whose order was counterbalanced between participants. These conditions differed in the temporal synchronicity between felt and seen touch (synchronous: <50 ms delay; asynchronous: 500 ms delay, where tactile stimulus preceded the visual stimulus). Participants stood straight and, through a video feed relayed to the HMD, passively watched a virtual body, i.e. a video recording of their own body from 200 cm behind their actual location. The experimenter randomly stroked the participants' upper back at approximately 2Hz. At the end of each condition, the FBI questionnaire (adapted from Lenggenhager et al., 2007)) was administered to quantify the subjective experience associated with the FBI. Questions were: Q1. It seemed as if I was feeling the touch of the stick in the location where I saw the virtual body being touched. Q2. It seemed as if the touch I felt was caused by the stick touching the virtual body. Q3. I felt as if the virtual body was my body Q4. I felt as if my body was drifting towards the virtual body Q5. It seemed as if I might have more than one body. Q6. It seemed as if the touch I was feeling came from somewhere between my own body and the virtual body. Q7. It appeared (visually) as if the virtual body was drifting backwards (towards my body). Q8. It seemed as if I was in two places at the same time. Questions were computerized and presented in random order. Participants responded on a visual horizontal 11-point scale ranging from 0 (lowest) to 10 (highest).

2. 3. 2 Peripersonal Space Measurement.

In order to measure changes in PPS during the FBI, visuo-tactile stimulation was intermingled with audio-tactile trials. In those PPS trials, a looming sound approached the participant (in the front, for Experiment 1, and in the back, for Experiment 2) at a velocity of 75 cm/sec. On each trial, after one out of six possible delays from sound onset (SOA; T1 = 190 ms to T6 = 1.14 seconds in increments of 190 ms), a tactile vibration (100 ms duration) was delivered. Participants were instructed to respond by button press as fast as possible upon perceiving the vibro-tactile stimulus on their chest (for Experiment 1) or back (for Experiment 2) and their reaction times (RT) were measured. As sounds loomed from far to close, the sooner a tactile vibration was given (e.g. at T1), the further away was the sound located in space (e.g. D6) when participants received tactile stimulation. We define, hence, T1 through T6 as corresponding in the spatial dimension to D6 (far from the participant) through D1 (close to the participant). In addition to experimental trials, baseline and catch trials were included. Baseline trials were unimodal tactile trials in which participants responded to touch (at the temporal equivalent to either D1 or D6), but no auditory stimulus was delivered. Catch trials were unimodal auditory trials in which participants had to withhold response (as there was no tactile stimuli).

2. 4 Procedure.

After an initial 60 second visuo-tactile stroking induction-phase to the FBI, three trials of the PPS task were administered. Interstimulus interval between these consecutive PPS trials was set to 0.5 seconds. Then, 10 seconds of merely FBI inducement followed, before the next round of three PPS trials. The FBI stroking continued throughout the experiment, and this pattern (three PPS trials followed by 10 seconds of solely FBI stroking) was repeated until the end of the block. Each block (and therefore, each stroking condition) consisted of 72 PPS experimental trials (12 repetitions X 6 Sound Distances), 24 baseline trials (12 repetitions X 2 baseline Sound Distances, D1 and D6), and 12 catch trials.

3. Results

3. 1 Experiment 1 (front-space)

3. 1.1 Full Body Illusion: Questionnaire

In order to confirm that visuo-tactile stroking in the synchronous condition induced the FBI, we compared participants' rating to Experimental questions, assessing changes in BSC (averaging responses to questions 1, 2, 3, and 6), and Control questions (averaging responses to questions 4, 5, 7, 8, 9, 10, and 11), collected after the Synchronous and Asynchronous conditions (see Palluel, Aspell, & Blanke, 2011, for a similar approach). A 2 (Question Type; Experimental vs. Control) X 2 (Condition: Synchronous vs. Asynchronous) within-subjects ANOVA performed on those questionnaire scores showed a significant Question Type X Condition interaction ($F(1, 18) = 6.066$, $p < 0.05$, $\eta^2 = 0.355$). Subsequent Paired-Samples t-test showed that participants rated higher Experimental questions after the Synchronous as compared to the Asynchronous visuo-tacle condition ($t(18) = 2.980$, $p < 0.05$), whereas no difference was found for the Control questions ($t(18) = 1.580$, $p = 0.20$; see Fig. 2A).

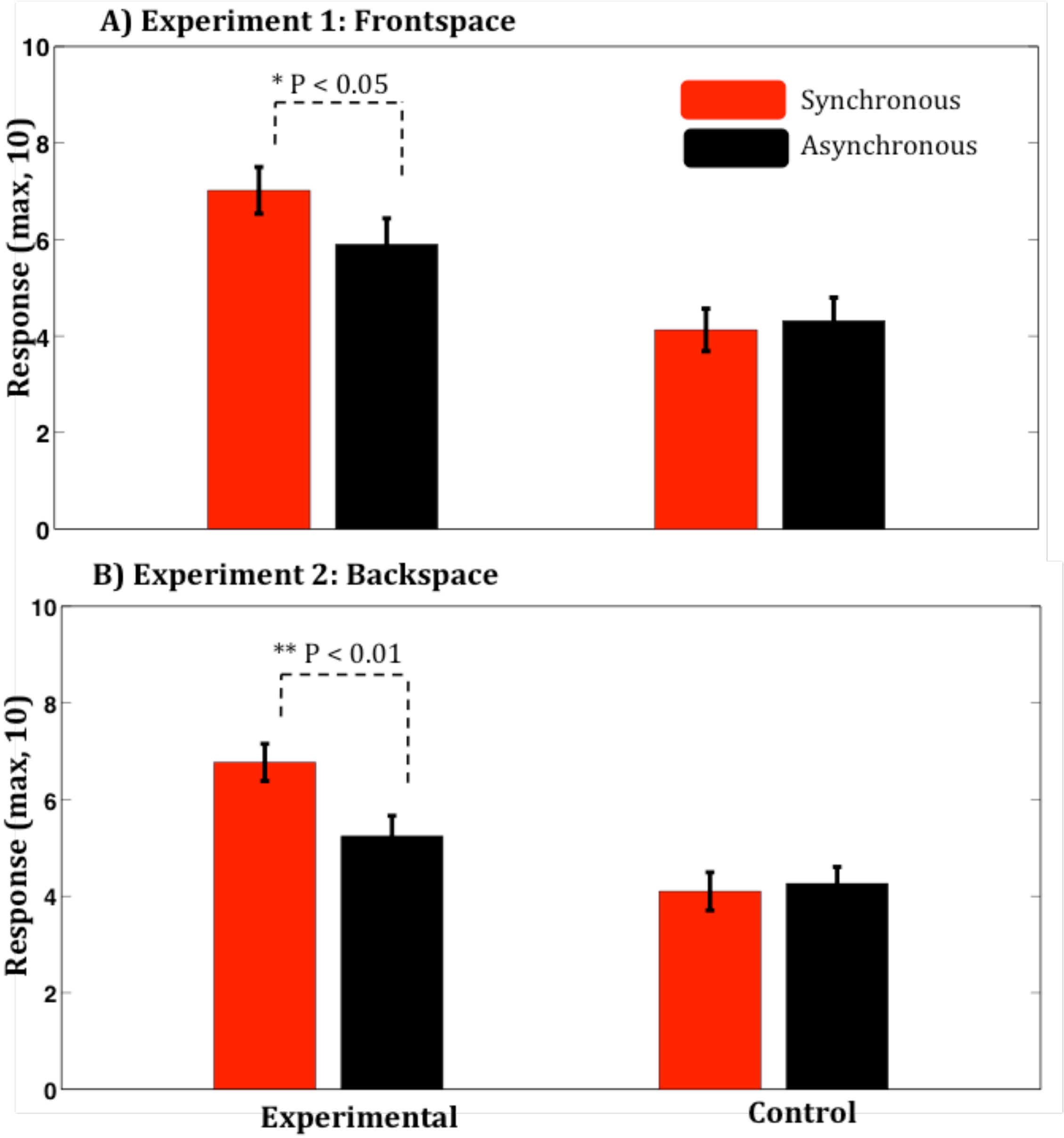

Figure 2*. Body Illusion questionnaire results from Experiment 1 (A) and Experiment 2 (B).* Results for Experimental questions, assessing changes in BSC (averaging responses to questions 1, 2, 3, and 6) are shown on the left side and results for Control questions (averaging responses to questions 4, 5, 7, 8, 9, 10, and 11) on the right side. Average responses (Error bars represent S.E.M.) are plotted as a function of visuo-tactile stroking condition (synchronous in red; asynchronous in black).

3.1.2 Peripersonal Space: audio-tactile interaction task.

Subsequently we analyzed whether the visuo-tactile synchrony manipulation, inducing the FBI, also altered audio-tactile interaction in PPS. A Paired-Samples *t*-test ran on the catch trials showed that both when participants received Synchronous (M = 98.2%, S.E.M = 3%) and Asynchronous (M = 97.2%, S.E.M = 4%) stroking conditions they were very accurate at the task at hand ($t(18) = .741$, $p > 0.05$).

Mean reaction times (RT) to tactile stimuli at the different sound distances were computed, after trimming responses exceeding 2.5 the RT standard deviation (< 3% of total trials). A 2 (Condition: Synchronous vs. Asynchronous) x 6 (Sound Distance: D1 through D6) within-subjects ANOVA was performed on participants' RT to vibro-tactile stimulation. Results, shown in Figure 3, highlighted a significant main effect both for Synchronicity ($F(1, 18) = 12.24$, $p < 0.01$, $\eta^2 = 0.40$) and for Sound Distance ($F(5, 90) = 22.88$, $p < 0.001$, $\eta^2 = .56$). More interestingly for the purpose of the present study, the two-way Condition X Sound Distance interaction was also significant ($F(5, 90) = 2.51$, $p < 0.05$, $\eta^2 = 0.12$). To study the source of the significant two-way interaction, we ran two separate ANOVAs, one per synchronicity condition, with Sound Distance as main factor. The aim of these analyses was to identify, for the Synchronous and the Asynchronous conditions, the critical distance at which looming sounds speeded up tactile RT, which can be considered as a proxy of the boundary of PPS, and to test whether this distance varied between the two conditions. The main effect of distance in the Synchronous condition was significant (*F*(5, 90) = 21.65, *p* < 0.001, η^2 = .54) and post-hoc comparisons showed that RT at D1 through D5 were equivalent to each other, and significantly faster than RT at D6 (p < 0.05, Bonferroni-corrected). In the case of the Asynchronous condition the main effect of Sound Distance (*F*(5, 90) = 12.68, *p* < 0.001, η^2 = .41) was also significant; however as expected and differently to the Synchronous condition, results revealed that now only D1 through D4 exhibited similar reaction times, while these were significantly different from D5 and D6 (p < 0.05, Bonferroni-corrected). These results imply that the PPS boundary under Asynchronous visuo-tactile stimulation was placed between D4 and D5, whereas it enlarged to be placed between D5 and D6, i.e. at a farther location of space, toward the virtual body, under Synchronous visuo-tactile stimulation. Indeed, multiple comparisons at each sound distance between Synchronous and Asynchronous conditions showed that RT was statistically significant only at D5 (t(18) = -3.64, p < 0.01, Bonferroni-corrected), with faster RTs in the Synchronous (M = 343 ms; S.E.M= 12 ms) than in the Asynchronous condition (M = 387 ms; S.E.M =16 ms).

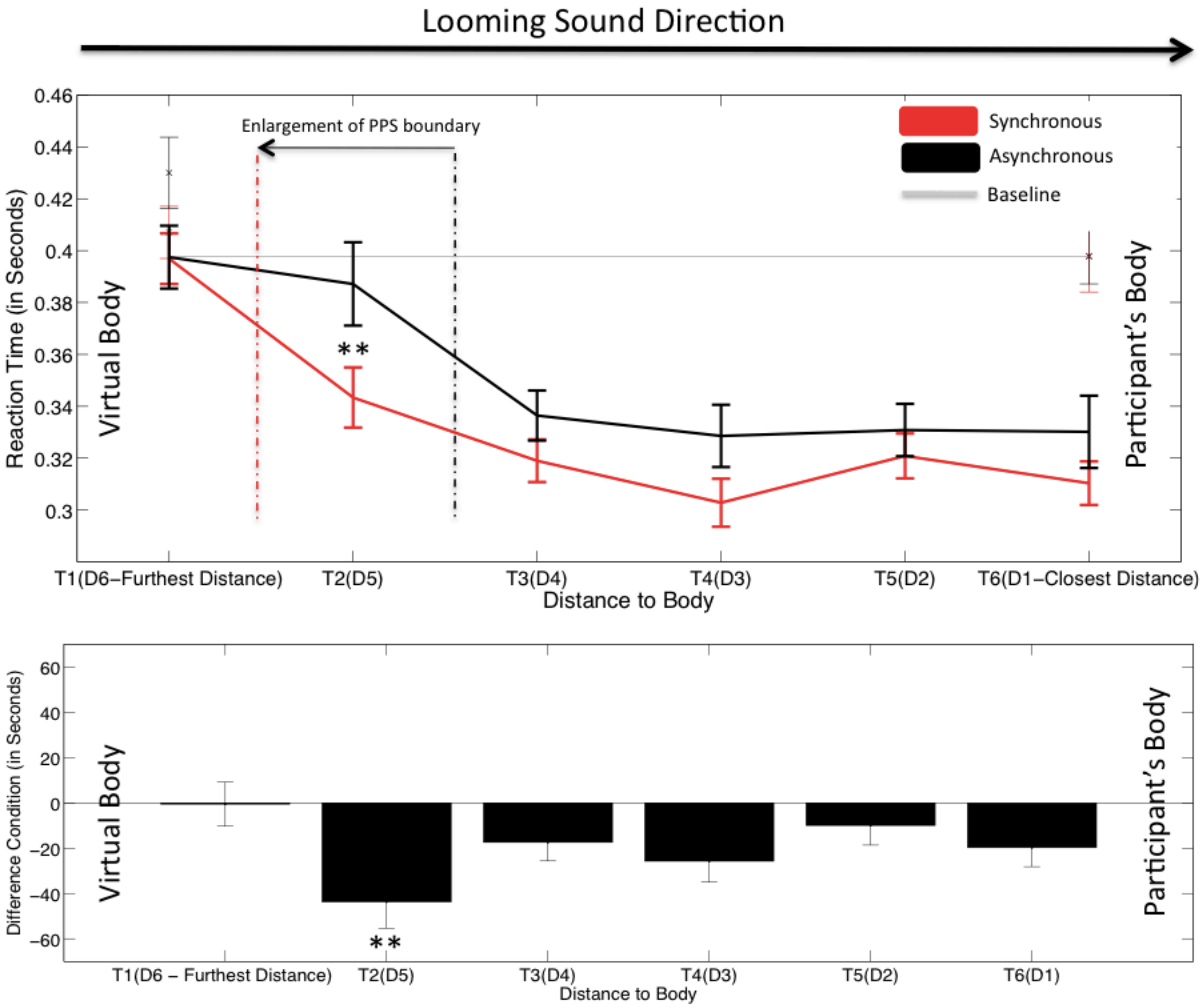

***Figure 3**. PPS representation in the front-space (Experiment 1) for the synchronous and the asynchronous Stroking condition. Upper Panel: Reaction times (RT) to the tactile stimulus on the chest are plotted as a function of Stroking condition and the distance between the auditory stimuli and the tactile stimulation. Error bars represent S.E.M and ** indicate difference between Synchronous and Asynchronous condition, $p < 0.01$ (Bonferroni-corrected): The grey horizontal line indicates RT in baseline, unimodal tactile trials. Lower Panel: Difference between Synchronous and Asynchronous conditions is plotted as a function of Sound Distance to the body. Error bars represent S.E.M and ** indicate difference between Synchronous and Asynchronous condition $p < 0.01$ (Bonferroni-corrected).*

Finally, in order to assure that the aforementioned results were due to a facilitation of tactile processing due to multisensory integration of audio-tactile signals, we compared tactile RT when the looming sound was perceived at the different distances with RT in unimodal tactile baseline trials, when no sounds were administered. Faster RT in audio-tactile conditions as compared to unimodal tactile conditions can be considered a facilitation effect due to multisensory integration within the PPS. To this aim. we compared RT to audio-tactile trials for each Sound Distance with the average of the fastest RT at the baseline. Comparison to baseline demonstrated that in the case of the Synchronous stroking stimulation, RT at D1 through D5 were significantly faster from baseline ($p < 0.05$, corrected), but not RT at D6 ($p=0.63$). For the Asynchronous condition, only RT at D1 through D4 were significantly faster from baseline ($p < 0.05$, Bonferroni corrected), but not RT and D5 and D6 (both p-values > 0.41). These comparisons confirm that the limit of audio-tactile interaction, i.e. the PPS boundary, was located between D4 and D5 in the Asynchronous stroking condition, and between D5 and D6, i.e. further away from the physical body and closer to the avatar, during the Synchronous condition.

3. 2 Experiment 2 (back-space)

3. 2.1 Full Body Illusion: Questionnaire

As for Experiment 1, a 2 (Question Type; Experimental vs. Control) X 2 (Condition: Synchronous vs. Asynchronous) within-subjects ANOVA performed on the scores at the questionnaire revealed a significant Question Type X Condition interaction ($F(1,14) = 7.494$, $p < 0.05$, $\eta^2 = .349$). This interaction was driven by significantly higher scores in the Synchronous as compared to the Asynchronous condition for Experimental questions ($t(14) = 3.036$, $p < 0.01$, $\eta^2 = 0.534$), but not for Control questions ($t(14) = 0.182$, $p = 0.858$). These results replicated those from Experiment 1 and are reported in Figure 2B..

3.2.2 Peripersonal Space: audio-tactile interaction task.

A Paired-Samples *t*-test ran on the auditory unimodal trials revealed that, as for Experiment 1, participants were generally very accurate at withholding response when it was demanded from them (Synchronous condition: M = 96.4%, S.E.M = 1.5%; Asynchronous condition: M = 93.5%, S.E.M = 2.6%), and this did not differ between stroking conditions ($t(14) < 1$, ns).

Mean RT to vibro-tactile stimulation (trimmed for 2.5 standard deviations, < 2% total trials) was entered into a 2 (Condition) x 6 (Sound Distance) within-subjects ANOVA. Results, shown in Figure 3, demonstrated a significant main effect of Sound Distance ($F(5,70) = 12.54$, $p < 0.001$, $\eta^2 = 0.47$), as well as a Sound Distance X Condition interaction ($F(5, 70) = 5.97$, $p < 0.001$, $\eta^2 = 0.29$). In order to interpret the source of the two-way interaction, we ran two separate ANOVAs, one per synchronicity condition. The main effect of Sound Distance in the Synchronous condition was significant ($F(5, 70) = 9.57$, $p < 0.001$, $\eta^2 = .40$) and post-hoc comparisons showed that RT at D1 through D4 were equivalent to each other, and significantly faster than RT at D5 and D6 ($p < 0.05$, Bonferroni-corrected). In the case of the Asynchronous condition the main effect of Sound Distance ($F(5, 70) = 11.82$, $p < 0.001$, $\eta^2 = .45$) was again significant; however, post-hoc comparisons revealed that D1 through D5 exhibited similar reaction times, while these were significantly different from D6 ($p < 0.05$, Bonferroni-corrected). These results imply that the PPS boundary under Asynchronous visuo-tactile stimulation was placed between D5 and D6, whereas it shrank to be placed between D4 and D5, i.e. at a closer location of space, under Synchronous visuo-tactile stimulation.

Multiple comparisons at each sound distance revealed that only the comparison between Synchronous and Asynchronous conditions at D5 was statistically significant ($t(14) = 4.12$, $p < 0.01$, Bonferroni-corrected), with slower RTs in the Synchronous condition (Mean RT= 352 ms; S.E.M =15 ms) than in the Asynchronous condition (Mean RT = 310 ms; S.E.M= 17ms). Note that the location at which audio-tactile RT differed in space (namely, D5) was the same as in Experiment 1, however, the direction of the effect is inversed here. While in Experiment 1, at D5 participants were faster in the Synchronous condition, now they are faster in the Asynchronous condition.

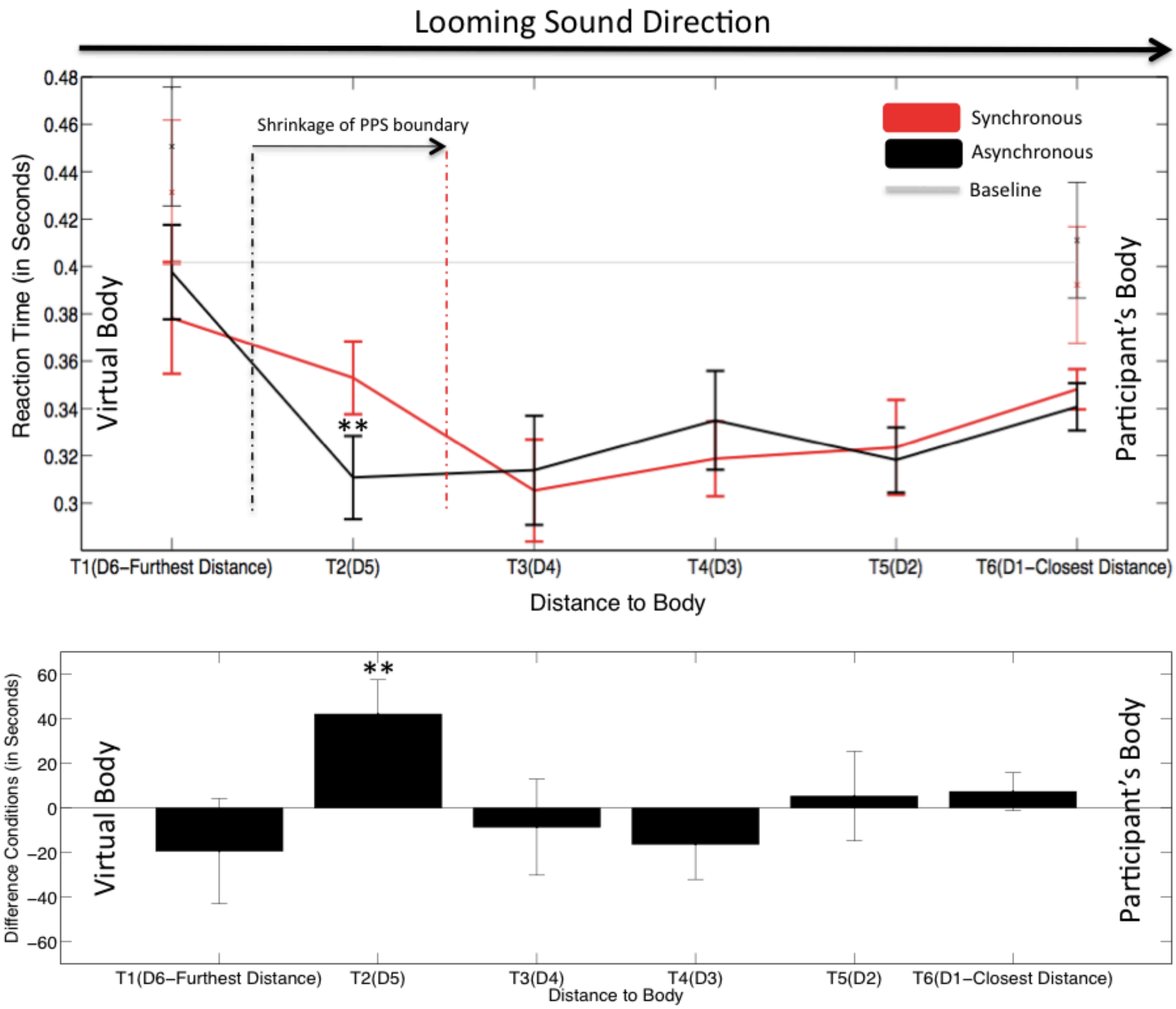

***Figure 3**. PPS representation in the back-space (Experiment 2) during Synchronous and Asynchronous stroking. Upper Panel: RT to the tactile stimulus on the back is plotted as a function of synchronicity during the Full Body Illusion and the distance between the auditory stimuli and the tactile stimulation. Error bars represent S.E.M and ** indicate difference between Synchronous and Asynchronous condition, $p < 0.01$ (Bonferroni-corrected): The grey horizontal line indicates RT in baseline, unimodal tactile trials. Lower Panel: Difference between Synchronous and Asynchronous conditions is plotted as a function of sound distance to the body. Error bars indicate +/- 1 S.E.M, and ** indicate difference between Synchronous and Asynchronous condition $p < 0.01$ (Bonferroni-corrected).*

Lastly, we compared tactile RT when the looming sounds were perceived at the different distances with RT in unimodal tactile baseline trials in order to assure that the above-mentioned distance effects were in fact a space-dependent multisensory facilitation effect. To this aim, as in experiment 1, we compared RT to audio-tactile trials for each Sound Distance with the average of the fastest RT at the baseline. Comparison to baseline demonstrated that in the case of the Synchronous stroking stimulation, RT at D1 through D4 were significantly faster from baseline ($p < 0.05$, corrected), but not RT at D5 and D6. For the Asynchronous condition RT at D1 through D5 were significantly faster from baseline ($p < 0.05$, Bonferroni corrected). These comparisons confirm that the limits of audio-tactile interaction, i.e. the PPS boundary, was located between D5 and D6 in the Asynchronous stroking condition, and between D4 and D5 in the Synchronous one.

3.3. Comparison between front-space and back-space PPS during synchronous and asynchronous visuo-tactile stroking.

In order to compare the effect of synchronous visuo-tactile stimulation, inducing the FBI, on PPS representation in the front and back space, we ran a final analysis using a mixed-model ANOVA with Condition (Synchronous or Asynchronous) and Sound Distance (D1 through D6) as within-subjects variables, and with Experiment (Exp 1, front-space; Exp 2, back-space) as the between-subjects variable. As expected from the aforementioned results, findings revealed a significant three way interaction ($F(5, 160) = 6.97$, $p < 0.001$, $\eta^2 = 17$). This results is explained by the significant enlargement of PPS in the front-space in the Synchronous condition as opposed to the Asynchronous condition (section 3.1.2), and to a significant reduction of PPS in the backspace in the Synchronous condition as opposed to the Asynchronous one (section 3.2.2). For illustration purposes, this result is displayed in Figure 4 as the absolute value of the difference between multimodal audio-tactile trials at each spatial distance (B6 corresponding to the furthest distance in the back, and F6 corresponding to the furthest distance in the front) and the fastest unimodal tactile baseline condition. Thus, positive values represent a multisensory facilitation effect induced by sounds within the PPS on tactile processing.

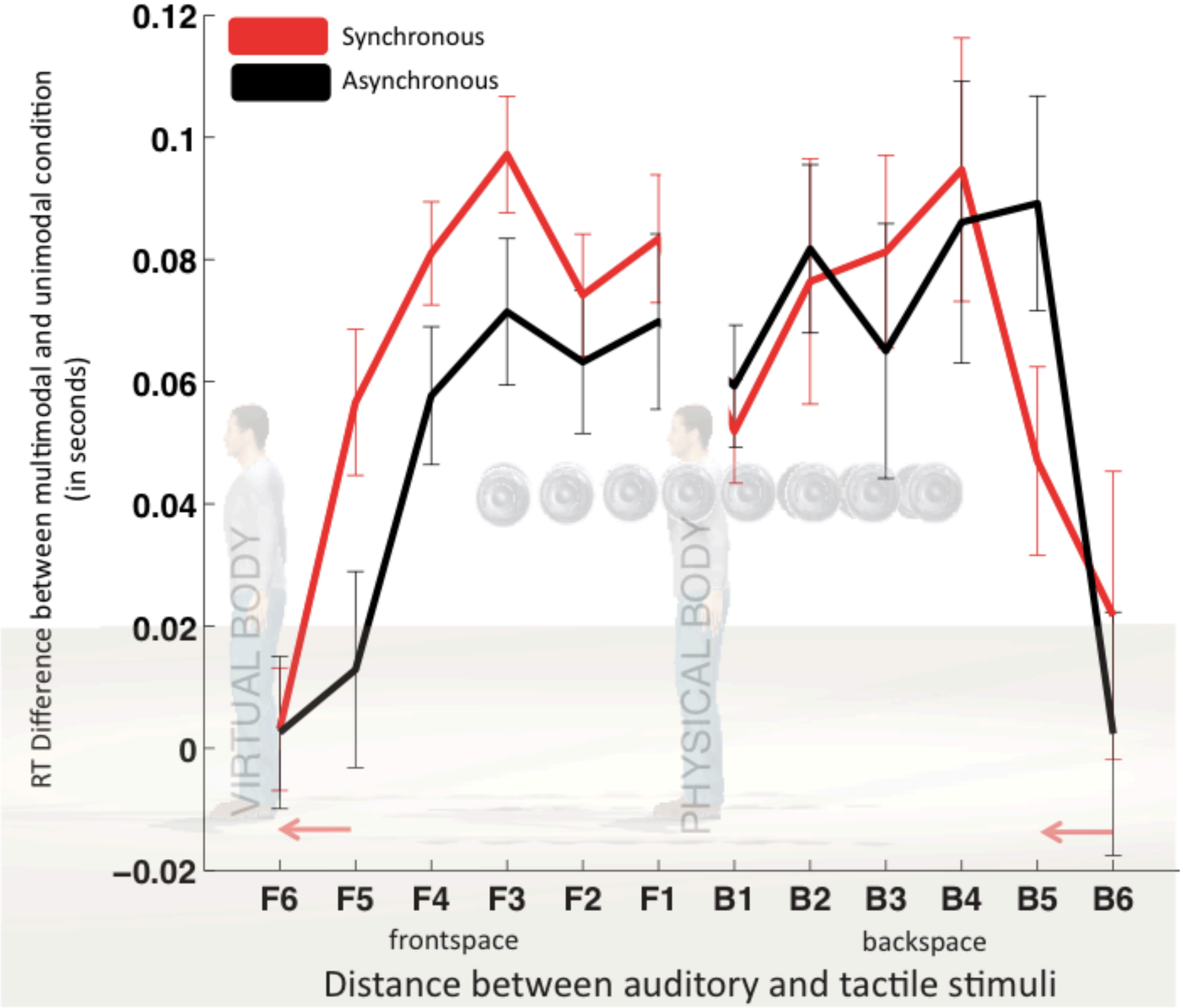

***Figure 4**. PPS representation in the front- and back-space during Synchronous and Asynchronous stroking. RT difference between unimodal tactile stimulus on the trunk and multimodal audio-tactile stimuli is plotted as a function of synchronicity of visuo-tactile stimulation during the Full Body Illusion and the distance between the auditory stimuli and the body. Error bars represent S.E.M. Higher values imply higher facilitation on tactile processing due to audio-tactile interaction.*

4. Discussion

In the present study we induced the Full-Body Illusion (FBI) in order to manipulate the experience of one's own bodily self in space. When participants received a tactile stimulation on their physical body while viewing a synchronous stimulation administered to a virtual body seen at a distance, they reported a greater feeling of being directly touched by the stimulus touching the virtual body, of feeling touch at the location of the virtual body and, and of feeling to drift forward toward the virtual body, indicating a shift in the experienced location of the self from one's own physical body towards a virtual replacement of it. In line with previous findings, these effects were more weakly induced during asynchronous visuo-tactile stimulation (see Lenggenhager et al., 2007; Blanke et al., 2012; Serino et al., 2013). The focus and main new finding from the present study is that the FBI was associated with a shift in the representation of the PPS. We used an audio-tactile interaction task to identify the point in space where a looming sound speeded up tactile processing as a proxy of the boundaries of multisensory PPS (see Canzoneri et al., 2012; Canzoneri et al., 2013a; Canzoneri et al., 2013b; Teneggi et al., 2013). In Experiment 1, when we measured the extension of PPS in the front-space, between the participant's physical body and the avatar, we found, as predicted, that the PPS boundary enlarged toward the location of the avatar in the synchronous visuo-tactile stroking condition inducing the FBI, as compared to the asynchronous control condition. In Experiment 2, mapping PPS on the participant's back, we found that the PPS boundary shrunk in the synchronous as compared to the asynchronous condition. Taken together, these two new findings support the view that during the FBI, PPS boundaries translate toward the virtual body, such that the PPS representation shifts from being centered at the location of the physical body to being now centered at the subjectively experienced location of the self.

Previous studies suggest that multisensory receptive fields of PPS neurons can react to artificial copies of the body. In patients with cross-modal extinction, Farnè and colleagues (2000) showed that visual stimuli presented close to a prosthetic hand interacted with tactile stimuli at the patient's contralesional hand as much as visual stimuli presented close to the patient's real hand did. In close analogy, in monkeys, stimuli applied to a fake arm triggered responses from PPS neurons, suggesting that PPS receptive fields can incorporate a fake limb (Graziano, Cooke, & Taylor, 2000). More recently, Brozzoli et al. (2012) showed in humans that brain areas likely representing PPS around the hand, such as the ventral premotor cortex and the posterior parietal cortex, which normally process visual stimuli presented in a limited peri-hand space, responded to visual stimuli presented close to a rubber hand after synchronous visuo-tactile stimulation of the participants' and of the rubber hand. These findings generally show that some response properties, which normally apply to one's own real hand, transfer to an artificial replacement of the hand. Similar effects have also been shown after individuals use a tool to extend the physical limits of their own body (see e.g., Iriki et al., 1996; Farne & Ladavas, 2000; Canzoneri et al., 2013a), and those findings have been advocated to suggest that tools can be included into one's own body representation (Iriki & Maravita, 2004; Maravita, Spence, Kennett, & Driver, 2002). Results from our study are different from those previous ones at least in one critical respect. Contrarily to the cases of rubber hand and tool-use, during the FBI, we did not find only an extension of PPS in the direction of the avatar's location, but also a concurrent contraction of the back PPS. The combination of these effects suggest a genuine spatial shift of PPS receptive fields, centered on the location of the physical body prior to the FBI, towards the center of self-location during the FBI. While normally integration of tactile stimuli at the body and of external stimuli in the environment (in this case sounds) is maximal around the location of the physical body, when participants experienced a shift of their perceived self location, due to the FBI, the spatial gradient of multisensory integration congruently shifted in the direction of self-location as induced by the FBI. These findings confirm that the center of the PPS representation is not bound to the physical body and shows that not only arm-related PPS representations are malleable. Importantly, we show that the PPS is centered at the experienced location of the self. Normally self-location and body location coincide, and so does PPS. However, if body location and self-location are dissociated, for instance by means of conflicting multisensory stimulation, PPS representation shapes congruently with the change in self experience. More generally, the present findings suggest that PPS can be considered as a representation of the self in space, which may mediate interactions between the individual and the environment. This proposal fits with previous results showing that the size of PPS varies across individuals not only depending on the dimension of their bodies (Lourenco & Longo, 2007), but also, more interestingly, depending on individual personality traits (e.g., claustrophobia; anxiety; Longo et al., 2011; Sambo & Iannetti, 2013). Our data also corroborate recent reports showing that PPS shapes not only during physical body-objects interactions, such as those mediated by tool-use, but also during virtual interactions with far objects, mediated by a computer mouse (Bassolino et al., 2010) or surgical robots (Rognini et al., 2013; Sengül et al., 2012), and even after social interactions with other persons, depending on the positive or negative value of those interactions (Teneggi et al., 2013).

To conclude, the present study supports a neurophysiological explanation for the effects of conflicting multisensory stimulation on BSC during the FBI: viewing a tactile simulation on a another body at a distance, while receiving synchronous tactile stimulation on one's own body, changes PPS boundaries, likely based on changes in the properties of multisensory receptive fields of PPS neurons (Blanke, 2012; Ehrsson et al., 2012; Serino et al., 2013). Such change is characterized not simply by an extension of PPS receptive fields towards the location of seen touch, but rather by a shift or translation of PPS receptive fields from the location of the physical body to the experienced location of the self.

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References

Aspell, J.E., Lenggenhager, B. & Blanke, O. (2009) Keeping in touch with one's self: multisensory mechanisms of self-consciousness. PLoS ONE 4, e6488.

Bassolino, M., Serino, A., Ubaldi, S., & Ladavas, E. Everyday use of the computer mouse extends peripersonal space representation. Neuropsychologia, 48(3), 803-811.

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature reviews. Neuroscience*, *13*(8), 556–571. doi:10.1038/nrn3292

Blanke, O. & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. Trends Cogn. Sci. 13, 7–13.

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. Nature, 391, 756.

Brozzoli, C., Gentile, G., & Ehrsson, H. H. (2012). That's Near My Hand! Parietal and Premotor Coding of Hand-Centered Space Contributes to Localization and Self-Attribution of the Hand. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *32*(42), 14573–14582. doi:10.1523/JNEUROSCI.2660-12.2012

Canzoneri, E., Magosso, E., & Serino, A. (2012). Dynamic sounds capture the boundaries of peripersonal space representation in humans. *PloS one*, *7*(9), e44306. doi:10.1371/journal.pone.0044306

Canzoneri, E., Marzolla, M., Amoresano, A., Verni, G., & Serino, A. (2013a). Amputation and prosthesis implantation shape body and peripersonal space representations. Scientific reports, 3, 2844. doi:10.1038/srep02844

Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., & Serino, A. (2013b). Tool-use reshapes the boundaries of body and peripersonal space representations.

Experimental brain research. Experimentelle Hirnforschung. Expérimentation cérébrale, 228(1), 25–42. doi:10.1007/s00221-013-3532-2

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science*, *317*(5841), 1048. doi:10.1126/science.1142175

Ehrsson, H.H. The concept of body ownership and its relation to multisensory integration. In: The New Handbook of Multisensory Processes, B.E. Stein (Ed.) (2012) pp 775-792, MA: MIT Press (Cambridge)

Farne, A., & Ladavas, E. (2000). Dynamic size-change of hand peripersonal space following tool use. Neuroreport 11, 1645 – 1649

Farnè, A, Pavani, F., Meneghello, F., & Làdavas, E. (2000). Left tactile extinction following visual stimulation of a rubber hand. *Brain : a journal of neurology*, *123 (Pt 1*, 2350–60.

Gallagher, S. (2005) How the Body Shapes the Mind. Oxford University Press

Graziano, M. S., Cooke, D. F., Taylor, S. R. (2000). Coding the Location of the Arm by Sight Coding the Location of the Arm by Sight, *Science 1782*. doi:10.1126/science.290.5497.1782

Graziano, M. S. A., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. Neuropsychologia, 44(13), 2621–2635.

Iriki, A. et al. (1996) Coding of modified body schema during tool use by macaque postcentral neurones. Neuroreport 7, 2325 – 2330

Jeannerod, M. (2006). Motor cognition: What actions tell the Self. Oxford University Press.

Làdavas, E., & Serino, A. (2008). Action-dependent plasticity in peripersonal space representations. Cognitive neuropsychology, 25(7-8), 1099–1113.

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: manipulating bodily self-consciousness. *Science (New York, N.Y.)*, *317*(5841), 1096–9. doi:10.1126/science.1143439

Longo, M. R., & Lourenco, S. F. (2007). Space perception and body morphology: extent of near space scales with arm length. Exp Brain Res, 177(2), 285-290.

Lloyd, D. M. (2007). Spatial limits on referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. Brain and Cognition, 64(1), 104–109. doi:10.1016/j.bandc.2006.09.013

Lourenco, S. F., Longo, M. R., & Pathman, T. Near space and its relation to claustrophobic fear. Cognition, 119(3), 448-453.

Makin, T. R., Holmes, N. P., & Ehrsson, H. H. (2008). On the other hand: dummy hands and peripersonal space. *Behavioural brain research*, *191*(1), 1–10. doi:10.1016/j.bbr.2008.02.041

Maravita, A., Spence, C., Kennett, S., & Driver, J. (2002).Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition* 83 (2), 25-34.

Maravita, A., & Iriki, A. (2004). Tools for the body (schema). Trends in cognitive sciences, 8(2), 79–86. doi:10.1016/j.tics.2003.12.008

Miller, J.O. (1982). Divided attention: evidence for coactivation with redundant signals. *Cogn Psychol*;13:247-279

Palluel, E., Aspell, J.E., & Blanke. O. (2011). Leg muscle vibration modulates bodily self-consciousness: integration of proprioceptive, visual, and tactile signals. *Journal of neurophysiology*, 105 (5), 2239-47.

Pavani F., Spence C., Driver J. (2000). Visual capture of touch: Out-of-the-body experiences with rubber gloves. Psychological Science 11 (5), 353-359

Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1997). The space around us. Science, 277, 190–191

Rognini, G., Sengul, A., Aspell, J. E., Salomon, R., Bleuler, H., & Blanke, O. Visuo-tactile integration and body ownership during self-generated action. Eur J Neurosci, 37(7), 1120-1129.

Sambo, C. F., & Iannetti, G. D. Better safe than sorry? The safety margin surrounding the body is increased by anxiety. J Neurosci, 33(35), 14225-14230.

Sengul, A., van Elk, M., Rognini, G., Aspell, J. E., Bleuler, H., & Blanke, O. Extending the body to virtual tools using a robotic surgical interface: evidence from the crossmodal congruency task. PLoS One, 7(12), e49473.

Serino, A., Alsmith, A., Costantini, M., Mandrigin, A., Tajadura-Jimenez, A., & Lopez, C. (2013). Bodily ownership and self-location: Components of bodily self-consciousness. Consciousness and cognition, 22(4), 1239–1252. doi:10.1016/j.concog.2013.08.013

Teneggi, C., Canzoneri, E., di Pellegrino, G., & Serino, A. (2013). Social modulation of peripersonal space boundaries. Current biology: CB, 23(5), 406–411. doi:10.1016/j.cub.2013.01.043

Zopf, R., Savage, G., & Williams, M. (2010). Crossmodal congruency measures of lateral distance effects on the rubber hand illusion. Neuropsychologia, 48, 713-725.

Appendix 4

Pfeiffer C, Serino A, and Blanke O. (2014) The vestibular system: a spatial reference for bodily self-consciousness. Frontiers in Integrative Neuroscience. 8:31.

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The vestibular system: a spatial reference for bodily self-consciousness

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Self-consciousness is the remarkable human experience of being a subject: the "I". Self-consciousness is typically bound to a body, and particularly to the spatial dimensions of the body, as well as to its location and displacement in the gravitational field. Because the vestibular system encodes head position and movement in three-dimensional space, vestibular cortical processing likely contributes to spatial aspects of bodily self-consciousness. We review here recent data showing vestibular effects on first-person perspective (the feeling from where "I" experience the world) and self-location (the feeling where "I" am located in space). We compare these findings to data showing vestibular effects on mental spatial transformation, self-motion perception, and body representation showing vestibular contributions to various spatial representations of the body with respect to the external world. Finally, we discuss the role for four posterior brain regions that process vestibular and other multisensory signals to encode spatial aspects of bodily self-consciousness: temporoparietal junction, parietoinsular vestibular cortex, ventral intraparietal region, and medial superior temporal region. We propose that vestibular processing in these cortical regions is critical in linking multisensory signals from the body (personal and peripersonal space) with external (extrapersonal) space. Therefore, the vestibular system plays a critical role for neural representations of spatial aspects of bodily self-consciousness.

Keywords: bodily self-consciousness, multisensory integration, first-person perspective, self-location, self-motion, mental spatial transformation, body representation, vestibular cortex

INTRODUCTION

Humans' experience as subject ("I", the self) is typically bound to the spatial dimensions of the physical body. This is expressed by the concept of bodily self-consciousness, which consists of several aspects including the experience that "I" am localized at a specific place and spatial volume (self-location), the experience that "I" take an experiential and visuospatial perspective of the world (first-person perspective), the experience that "I" identify with the body as a whole (self-identification) as opposed to feeling ownership for a body part, and that "I" am causing actions through the body (sense of agency) (Haggard et al., 2003; Jeannerod, 2003; Blanke and Metzinger, 2009; Blanke, 2012; Metzinger, 2013; Serino et al., 2013). This review will mainly focus on what we call spatial aspects of bodily self-consciousness, i.e., self-location and first-person perspective. These phenomenal experiences are defined by spatial parameters, such as the location and volumetric expansion of the self and the origin and direction of perspective (Blanke and Metzinger, 2009). In contrast, we will be less concerned with non-spatial aspects of bodily self-consciousness, i.e., self-identification and agency. These phenomenal experiences are invariant to changes in spatial parameters (see Metzinger, 2013 for a discussion on self-identification without a body in lucid dreams and during out-of-body experiences).

Experimental research shows that both spatial and non-spatial aspects of bodily self-consciousness emerge from pre-reflective and non-conceptual representations of bodily signals in the brain (Metzinger, 2003; Gallagher, 2005; Blanke and Metzinger, 2009; Ehrsson, 2012). Those are sensory signals from exteroception, such as visual and auditory signals (e.g., Ehrsson, 2007; Lenggenhager et al., 2007; Tajadura-Jiménez et al., 2009), from somatosensation, such as tactile and proprioceptive signals (e.g., Seizova-Cajic et al., 2007; Palluel et al., 2011; for reviews see Haggard et al., 2003; Serino and Haggard, 2010) and from interoception, such as cardiac, nociceptive, and thermal signals (Hänsel et al., 2011; Aspell et al., 2013; for an interoception-based account on consciousness see Craig, 2002, 2009). Altogether, these experimental studies imply that by integrating multisensory signals the brain generates a coherent spatial representation of body parts, the body as a whole, and the body as related to the external world.

However, much less is known about the role of the vestibular system for bodily self-consciousness. Because the vestibular system encodes the position and movement of the head in three-dimensional space, and because in the central nervous system vestibular signals are strongly integrated with motor, visual, somatosensory and proprioceptive signals (Grüsser et al., 1990a,b; Gu et al., 2007; Prsa et al., 2012), central vestibular processing may be an important contributor to the neural computations underlying spatial aspects of bodily self-consciousness. Specifically, vestibular signals might contribute in generating a spatial representation of the body as a whole with respect to the external world, i.e., in the gravitational field in particular. These vestibular signals might be critical for updating whole body representation while this one moves in external space. Accordingly, the vestibular system would encode spatial references for self-location and first-person perspective.

This review summarizes and critically discusses both direct and indirect evidence for this proposal. While topics in the fields of bodily self-consciousness and central vestibular processing have been mostly studied in isolation, with this review article we hope to motivate a converging approach from these exciting research fields.

The review is divided in three parts. In the first part, we briefly introduce the vestibular system and then summarize current knowledge about the role of vestibular processing for spatial aspects of bodily self-consciousness. We conclude the first part by several questions that remain open to experimental research. In the second part, we review experimental data about vestibular contributions to cognitive and perceptual processes that involve spatial representations of the bodily self with respect to the external world. We think that these self-related processes draw on similar functional mechanisms as spatial aspects of bodily self-consciousness, and we discuss these experimental data as indirect evidence for vestibular contributions to spatial aspects of bodily self-consciousness. The third and final part of this review is concerned with the neural correlates of vestibular processing underlying self-location and first-person perspective. We propose that self-location and first-person perspective are encoded by a posterior cortical network consisting of the temporoparietal junction (TPJ), i.e., a region that has been causally linked to bodily self-consciousness, and three vestibular cortex regions, i.e., the parietoinsular vestibular cortex (PIVC), the medial superior temporal region (MST), and the ventral intraparietal region (VIP), which together perform the necessary computation subserving a multisensory spatial reference for bodily self-consciousness. We discuss the known functional properties of these regions and their putative role in bodily self-consciousness. Together we provide an argument supporting our hypothesis and present a testable outlook for future research for the study of vestibular processing in spatial aspects of bodily self-consciousness.

PART ONE: THE VESTIBULAR SYSTEM AND BODILY SELF-CONSCIOUSNESS: CURRENT KNOWLEDGE AND OPEN QUESTIONS

THE VESTIBULAR SYSTEM

The vestibular system encodes linear and rotatory acceleration of the head. It senses constant linear acceleration by earth gravity and thus signals to the brain head movement and position with respect to a constant gravitational acceleration. The vestibular system contributes to a variety of central nervous system functions including motor control, e.g., stabilizing gaze by the vestibular-ocular reflex (Schwarz, 1976), body posture (Pozzo et al., 1990), perception, e.g., of verticality (Lopez et al., 2007), and of self-motion (Brandt et al., 1998). Moreover, it also contributes to cognition, e.g., spatial navigation and memory (Arthur et al., 2009), and bodily self-consciousness (Blanke et al., 2002; Pfeiffer et al., 2013), which is the main topic of this review.

Peripheral system

The peripheral vestibular organs are located bilaterally in the head and are part of the inner ear (**Figure 1A**). They consist of two otolith organs (utricle and saccule) that sense linear acceleration, e.g., by head motion or gravitational force, and three semicircular canals (anterior, posterior and horizontal canal) that sense rotational acceleration around three cardinal axes (yaw, roll, pitch, **Figure 1B**). Thus, the vestibular sensory organs encode head position and movement in three-dimensional space.

Experimental research on the vestibular system has mainly used two approaches in order to stimulate the vestibular system, i.e., by natural and artificial stimulation. Natural vestibular stimulation can be experimentally induced by head accelerations, e.g., by passive whole-body rotation or translation (e.g., Prsa et al., 2012; van Elk and Blanke, 2014) that are sensed by the semicircular canals or otolith organs respectively. Natural vestibular stimulation may be given under terrestrial conditions by constant gravitational forces due to the attraction exerted by the earth on mass. Because the otolith organs sense constantly the vector of constant acceleration by gravity, static body or head tilts with respect to gravity can be used to naturally stimulate the otolith organs. The effects of weightlessness on vestibular processing have been studied in spacecrafts in orbit or in aircrafts during prolonged free fall (i.e., up to several months duration) or during parabolic flight (i.e., less than a minute duration).

Artificial peripheral vestibular stimulation techniques are: monopolar or bipolar electrical stimulation at the mastoids (Galvanic Vestibular Stimulation, GVS), thermal irrigation of one or both ear canals (Caloric Vestibular Stimulation, CVS), and auditory stimulation on headphones (clicks and short-tone bursts). These stimulation techniques activate the semicircular canals, otolith organs, the vestibular nerve, or a combination of the previous. Notably, these artificial stimulations co-activate nociceptive, thermal, and auditory sensory receptors—for comparison of these techniques and cortical processing see Lopez et al. (2012b).

Vestibular cortex

The central nervous system vestibular pathway consists of: (i) vestibular nerve projections from the vestibular organs to the vestibular nucleus in the brainstem; (ii) projections from the brainstem to thalamic nuclei, cerebellum, and spinal cord; and (iii) projections from the thalamus to the cerebral cortex. The interested reader can find comprehensive reviews on the peripheral and central vestibular system in Goldberg et al. (2012) and Lopez and Blanke (2011).

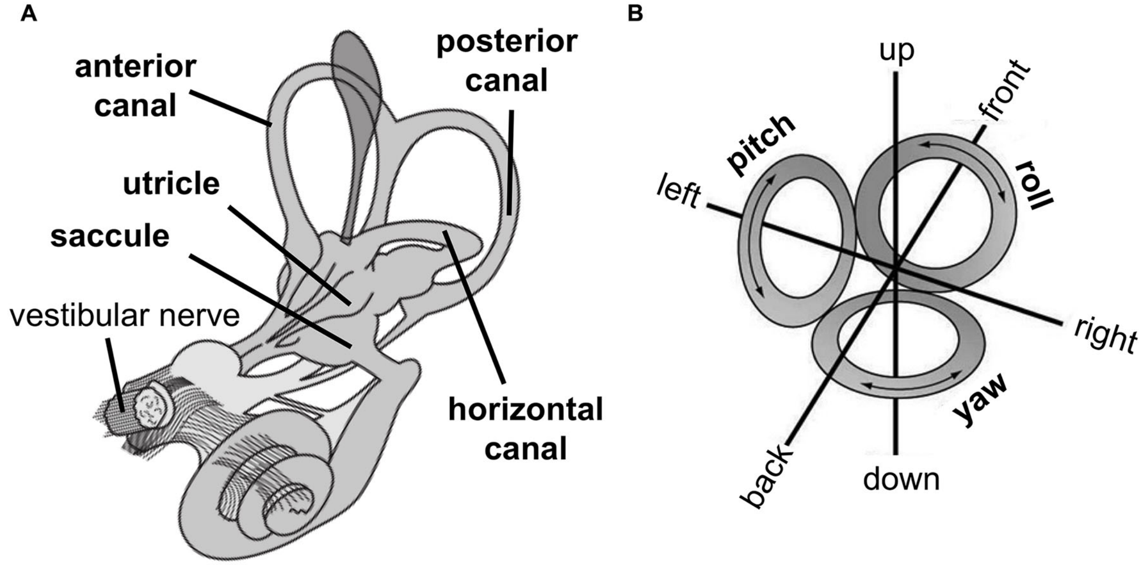

FIGURE 1 | (A) Peripheral vestibular organs in the inner ear consist of otoliths, i.e., utricle and saccule, which sense linear acceleration, and semicircular canals, i.e., anterior, posterior, and horizontal canal, which sense rotational acceleration. The vestibular nerve projects signals from otoliths and semicircular canals to the central nervous system. **(B)** The vestibular system encodes movement in three-dimensional space denoted as linear movements, i.e., in front, back, left, right, up, and down direction (by otolith organs) and rotational movements, i.e., yaw (by the horizontal canal) and pitch and roll (by both anterior and posterior canal). (Images are derivatives of works by NASA, licensed under creative commons.)

While for vision, audition, and somatosensation specific unisensory primary cortices have been identified, no such unisensory vestibular cortex seems to exist in the human brain. Rather, vestibular cortex is considered as any cortical region receiving vestibular input from the thalamus and is a distributed cortical network that overlaps with multisensory and motor representations from vision, somatosensation, proprioception, and action (Lopez and Blanke, 2011).

Electrophysiological recordings in non-human primates have identified vestibular inputs in several cortical regions including the somatosensory cortex (area 3aN, area 3aH, area 2v), PIVC, dorsal MST, medial temporal cortex, frontal cortex (frontal eye field and supplementary eye field), and cingulate cortex (Grüsser et al., 1990b; Guldin et al., 1992; Bremmer et al., 2002; Gu et al., 2007). These recordings revealed therefore thalamocortical projections to all major cortical lobes except the occipital lobe.

In order to measure human vestibular cortical processing, many studies have used functional magnetic resonance imaging (fMRI). While fMRI has the advantage of high spatial resolution and non-invasiveness, it is worth noting that studying vestibular processing in fMRI has several limitations. First, participants are required to lie supine and must avoid head movements, which differs from conditions of vestibular stimulation in natural context, typically involving different head postures and movements. Secondly, in order to stimulate the peripheral vestibular organs artificial stimulation techniques (GVS, CVS, clicks) are used. These co-activate other sensory modalities and complicate the interpretation of observed brain activation as purely vestibular Lopez et al. (2012b). Finally, the static magnetic field of the MR scanner induces a constant vestibular stimulus that, depending on participant's head position, differently activates the vestibular sensory organs and can even induce vertigo (Mian et al., 2013). Thus, there are limitations with current fMRI approaches to study central vestibular processing. It will be an important future goal to develop novel approaches allowing more natural and specific vestibular stimulation during non-invasive neuroimaging in humans.

VESTIBULAR CONTRIBUTIONS TO BODILY SELF-CONSCIOUSNESS

Theory

It has been proposed that bodily self-consciousness is based on the brain's multisensory integration of visual, vestibular, somatosensory, proprioceptive and motor signals (Haggard et al., 2003; Blanke et al., 2004; Blanke and Mohr, 2005). This theory distinguishes between personal (including also peripersonal) space, which is a volume of space occupied by the physical body and the space immediately surrounding the body, and extrapersonal space, that is the space outside of personal space. The theory proposes that the vestibular system is critically involved in integrating sensory signals from personal space (e.g., somatosensory, proprioceptive, visual, and auditory signals) with sensory signals from extrapersonal space (e.g., visual and auditory signals). It was proposed that particularly otolithic vestibular signals about constant gravitational acceleration provide a world-centered reference for the bodily self. By means of multisensory integration between personal and extrapersonal space the brain generates a spatial representation of the body as a whole, with a given location and orientation with respect to the external world, i.e., bodily self-consciousness. In line with this theory, Lopez et al. (2008) argued that vestibular otolithic signals are highly relevant for spatial aspects of bodily self-consciousness, i.e., self-location and first-person perspective, which depend on signals from both personal and extrapersonal space, and that vestibular signals may be less relevant for non-spatial aspects of bodily self-consciousness, e.g., self-identification, which depend mainly on signals from personal space and relate mostly to the body itself, rather than to the body relative to the external world (see also Blanke, 2012).

Clinical data

The strongest support for the proposal that vestibular processing contributes to bodily self-consciousness comes from observations in neurological patients suffering from out-of-body experience who show a three-way disembodiment of their bodily self-consciousness (Devinsky et al., 1989; Blanke et al., 2002, 2004; Brandt et al., 2005; De Ridder et al., 2007; Ionta et al., 2011; Pfeiffer et al., 2013). During an out-of-body experience patients typically identify with an illusory body in external space (disembodied self-identification), feel to be elevated above their physical body (disembodied self-location), and to have an elevated visuospatial perspective directed back downward to the physical body (disembodied first-person perspective).

Out-of-body experience in some neurological patients were caused by damage (Ionta et al., 2011), dysfunction (Blanke et al., 2004), or electrical stimulation (Blanke et al., 2002) at the TPJ, i.e., a brain region that receives strong vestibular inputs (Lopez et al., 2008, 2012b; zu Eulenburg et al., 2012). In addition to out-of-body experiences, electrical stimulation at TPJ also induced vestibular, visual, and kinesthetic hallucinations (Blanke et al., 2002). Vestibular processing and out-of-body experience were linked at the phenomenal level in a different study on healthy individuals. Cheyne and Girard (2009) found that humans suffering from sleep paralysis (i.e., a sleep disorder that is associated with immobility after awakening from sleep) often experienced vestibular-motor hallucinations as well as out-of-body experiences. According to self-report these experiences occurred mostly in supine posture and began mostly with vestibular-motor hallucinations that were followed by out-of-body experiences.

Out-of-body experiences most frequently occur in supine posture when otolithic vestibular signals are altered with respect to the vertical body axis (Green, 1968), suggesting that otolithic vestibular processing is critical for these changes in bodily self-consciousness (Lopez et al., 2008). Together, these reviewed data suggest that altered vestibular processing at temporoparietal cortex is associated with disturbances in bodily self-consciousness during out-of-body experiences.

Experimental data

Similar changes in bodily self-consciousness can be studied in healthy humans using different body illusions, such as the body-swap illusion (Petkova and Ehrsson, 2008), the out-of-body illusion (Ehrsson, 2007) or the full-body illusion (Lenggenhager et al., 2007). During a classic version of the full-body illusion (Lenggenhager et al., 2007) a participant views (from a third-person viewpoint) a virtual body being stroked at the back, i.e., visual stroking, and simultaneously feels stroking at his or her physical body, i.e., tactile stroking. Importantly, the visual stroking of the virtual body and the tactile stroking at participant's physical body are spatially separated. Synchronous visuotactile stroking typically increases self-identification with the virtual body and increases self-location in the direction of the virtual body, when compared with an asynchronous stroking control condition (comprehensive reviews and comparison to similar illusions in Blanke, 2012; Serino et al., 2013).

Using such a full-body illusion setup we recently showed that the subjectively experienced direction of first-person perspective, together with self-location, was altered by directional conflict between otolithic vestibular and visual gravitational signals (Ionta et al., 2011; Pfeiffer et al., 2013). **Figure 2** shows the experimental setup and results. Participants viewed a virtual body from an elevated visuospatial viewpoint, seeing visual gravity in downward direction, and simultaneously lay in supine body posture, receiving otolithic vestibular signals about their body being upward directed relative to gravity. Under these conditions individuals differed in terms of their experienced first-person perspective: up-group participants experienced an upward-directed first-person perspective and an upward-directed change in self-location during the full-body illusion. In contrast, down-group participants experienced a downward-directed first-person perspective and downward-directed change in self-location. Interestingly, individual differences in first-person perspective and self-location were reflected in changes in neural processing, as revealed by fMRI, in the bilateral TPJ, or more precisely in the posterior superior temporal gyrus (pSTG), a region close to the lesion overlap found in a group of patients with out-of-body experiences, i.e., angular gyrus (Ionta et al., 2011).

Pfeiffer et al. (2013) found at the behavioral level that individual differences in the subjective first-person perspective depended on individual differences in the way individuals weight visual and vestibular information, as assessed by subjective visual vertical judgments (Oltman, 1968). Participants oriented a visual line with respect their subjective vertical. A tilted frame around the line induced a small bias in subjective visual vertical judgments in some of the participants (visual independent group), while inducing larger subjective visual vertical biases in other subjects (visual dependent group). We found that assignment of participants to visual field dependent-independent groups, depending on their performance in the visual vertical judgment task, was predictive of their subjective first-person perspective during the full-body illusion. Specifically, participants from the visual independent group more likely experienced an up-looking first-person perspective during the full-body illusion, meaning that their subjective first-person perspective was congruent with vestibular signals. On the other hand, participants from the visual dependent group were more likely to experience a down-looking first-person perspective during the full-body illusion, meaning that their subjective first-person perspective was in line with visual signals.

Together, these studies support the hypothesis that the vestibular system contributes to whole-body spatial representation underlying bodily self-consciousness (Blanke et al., 2004; Blanke, 2012). One may wonder whether also body-part spatial representations depend on vestibular signals. Indeed, body-part representations are related to whole-body representations (Petkova et al., 2011; Ehrsson, 2012) and several studies observed vestibular effects on touch localization and shape perception of the hand

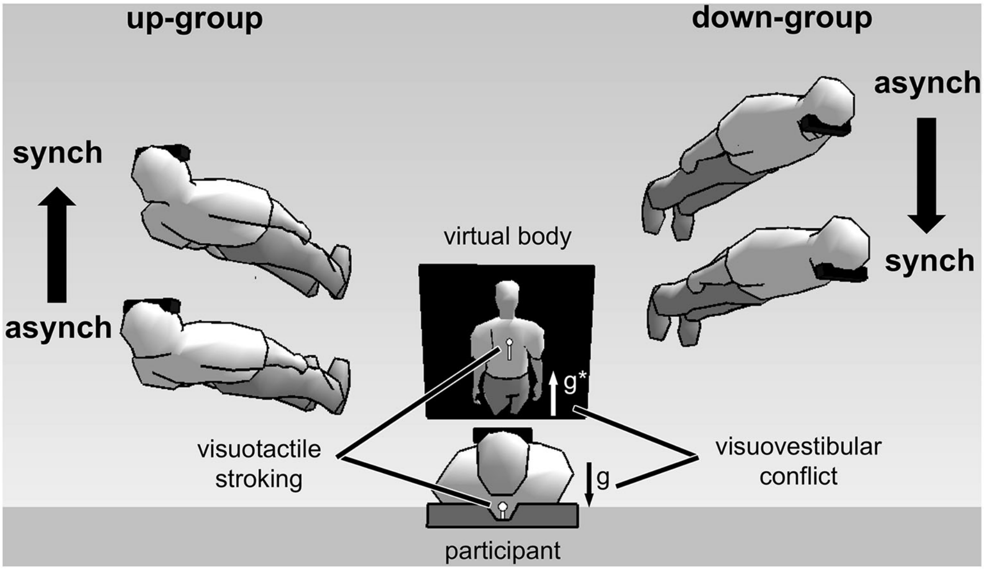

FIGURE 2 | Experimental setup and results of full-body illusion experiments using visuovestibular and visuotactile conflict (Ionta et al., 2011; Pfeiffer et al., 2013). (Image center shows) A participant in supine posture views a virtual body on a head-mounted display. Vestibular otolithic signals about gravity (g) are in opposite direction with respect to visual gravitational signals (g*)—thus in visuovestibular conflict. Results showed individual difference in first-person perspective experience. Virtual bodies at the left side of the figure represent subjective experiences made by up-group participants. These participants experienced an upward first-person perspective and showed congruent upward change in self-location during synchronous (synch) as compared to asynchronous (asynch) stroking condition. The opposite pattern was observed for down-group participants (shown at the right side of the figure).

(Lopez et al., 2010, 2012a,c; Ferre et al., 2011, 2013). However, these studies did not test whether vestibular stimulation also affected spatially integrated whole-body representations that underlie spatial aspects of bodily self-consciousness.

PART ONE: CONCLUSION AND OPEN QUESTIONS

Multisensory conflicts, i.e., between vestibular otolithic and visual gravitational signals in healthy subjects, as well as vestibular hallucinations, i.e., due to functional interference at TPJ in neurological patients, have been associated with changes in bodily self-consciousness, most consistently regarding it's spatial aspects: first-person perspective and self-location. Phenomenal experiences during these illusions included vestibular hallucinations, i.e., illusory reversals of the visuospatial first-person perspective with respect to gravity. Furthermore, ambiguous visual gravitational and vestibular otolithic signals induced changes of both first-person perspective and self-location. These observations suggest a critical role of vestibular cortical processing underlying spatial aspects of bodily self-consciousness.

Yet, very little is known about the functional and neural mechanisms underlying these effects. For instance, the vestibular peripheral system was never been directly stimulated during an out-of-body experience and a full-body illusion. It is thus not well studied how otolithic, semicircular, or both signals together affect spatial aspects of bodily self-consciousness. Furthermore, little is known about how vestibular processing contributes to a volumetric representation of the body, and how this spatial volume is related to representations of the external world. Finally, the vestibular system signals movement of the head and of the body. However, most studies on spatial aspects of bodily self-consciousness have used static body conditions. We think that these are important research questions for the future.

PART TWO: VESTIBULAR CONTRIBUTIONS TO BODILY SELF-RELATED COGNITIVE AND PERCEPTUAL FUNCTION

The second part of the review summarizes empirical research showing vestibular effects on mental spatial transformation, self-motion perception, and body representation. These cognitive processes involve spatial representations of the body, the external world, and the relationship between body and external world. We argue therefore that bodily self-related processes closely resemble spatial aspects of bodily self-consciousness, which require volumetric representation of the body with respect to the external world and spatial reference frames.

MENTAL SPATIAL TRANSFORMATION

Mental spatial representations are an important aspect of self-conscious experience. For example, the capacity to take the visual perspective of other humans is important for spatial cognition (Maguire et al., 1998), theory-of-mind (Baron-Cohen et al., 1985; Saxe and Kanwisher, 2003; Frith and Frith, 2006) and bodily self-consciousness (Newen and Vogeley, 2003).

Mental spatial representations have been extensively studied by mental imagery tasks involving objects, body parts, or entire bodies at different locations and orientations in external space (Shepard and Metzler, 1971). Mental imagery of these objects involves mental spatial transformation without participants actually moving their body or the perceived object. Performance in these tasks, i.e., reaction times and error rates, generally depend on the object rotation angle and the shortest path of rotation (Shepard and Metzler, 1971; Parsons, 1987a; Wexler et al., 1998). Mental imagery of body parts or entire bodies additionally depends on anatomical constraints of the physical body (Parsons, 1987b, 1994) and on participant's body posture while performing the mental imagery task (Ionta and Blanke, 2009; Ionta et al., 2013).

A long tradition in cognitive neuroscience has studied egocentric imagery, which is self-centered mental spatial transformation of the own whole body or visuospatial perspective. In egocentric imagery tasks participants judge spatial attributes of objects in their environment from a location or perspective that differs from their actual location or perspective. For example, participants may judge whether a marker is at the left or right side of their imagined body location. Some researchers referred to egocentric imagery in the context of body-part imagery (Zacks and Michelon, 2005) which we argue does not necessarily draw on global representations of the whole body, but rather depends on body-part centered reference frames (Klatzky, 1997; Blanke, 2012). Therefore, we choose to refer to egocentric imagery for imagined own whole-body or perspective transformations. Egocentric imagery is typically compared to allocentric imagery, which is imagining transformations of objects in external space in order to judge their spatial attributes. Several studies have shown that egocentric vs. allocentric imagery depend on distinct functional neural activations (Mast et al., 1999; Wraga et al., 2005). For instance, egocentric, but not allocentric, imagery exhibits brain activity at the TPJ (Arzy et al., 2006)—the same brain region involved in spatial aspects of bodily self-consciousness, in out-of-body experience (Blanke et al., 2002, 2004; Blanke and Mohr, 2005) and in full-body illusions (Ionta et al., 2011).

While most previous research comparing egocentric with allocentric imagery focused on visual, motor, and proprioceptive contributions, more recent studies have shown very specific contributions of vestibular signals to egocentric mental spatial transformation. For instance, Grabherr et al. (2011) compared mental imagery in patients with vestibular loss (i.e., peripheral vestibular damage) with performance of healthy individuals (i.e., intact peripheral vestibular system). These authors found that bilateral vestibular impairment affected egocentric imagery when compared with unilateral loss or intact vestibular processing. Vestibular damage vs. intact vestibular processing did not affect allocentric imagery, thus highlighting the relevance of peripheral vestibular signals (intact or semi-intact) in egocentric imagery. Notably, egocentric imagery is known to rely on cortical activation of the TPJ (see above).

Likewise, highly specific effects of vestibular processing on egocentric imagery were found by Lenggenhager et al. (2008). Healthy participants received vestibular stimulation by left/right anodal GVS while viewing left/right rotated bodily or non-body object. Egocentric imagery was facilitated by side-congruent vestibular-visual stimulation, but only if participants viewed bodily objects. GVS had no effect on allocentric imagery and did not influence mental imagery of non-body objects. These results not only show vestibular modulation of egocentric imagery, but also vestibular processing specifically affecting body-related mental transformations for multisensory congruent directions. These results are congruent with clinical observations linking vestibular, visual, and kinesthetic processing at the TPJ and with changes of spatial aspects of bodily self-consciousness during out-of-body experience (Blanke et al., 2002).

While Grabherr et al. (2011) and Lenggenhager et al. (2008) studied the effects of vestibular damage and artificial stimulation on mental imagery, van Elk and Blanke (2014) used natural vestibular stimulation and found comparable results. Passive whole-body yaw rotations (activating the horizontal semicircular canals) facilitated egocentric body-related mental imagery if actual rotations and shortest paths of mental rotation were side-congruent. While general bilateral vestibular loss in the study by Grabherr et al. (2011), and GVS in the study by Lenggenhager et al. (2008), involved altered vestibular signals from both otoliths and semicircular canals, the study by van Elk and Blanke (2014) showed that selective stimulation of the semicircular canal signals affected egocentric mental imagery.

These data indicate that mental spatial transformation depends on vestibular signals. Vestibular processing enhances egocentric imagery when related to a visually seen bodily object. Vestibular signals from semicircular canals and otolith organs facilitate mental imagery in a spatial direction specific fashion.

Given that egocentric mental imagery draws on similar spatial representations and neural processing as spatial aspects of bodily self-consciousness, then it is likely that vestibular signals from semicircular canals contribute to spatial aspects of bodily self-consciousness and that they are processed at TPJ. To our knowledge, this hypothesis has not been studied directly. Instead, previous work on spatial aspects of bodily self-consciousness studied the effects of otolithic vestibular signals and representations of the static gravitational field.

Egocentric imagery recruits functional neural activation at the TPJ, suggesting that egocentric imagery engages similar representations, as do spatial aspects of bodily self-consciousness. Indeed, the strategy during egocentric imagery involves mental spatial displacement of one's own body or perspective to a location in external space, whose analogous physical movements would activate otolithic and semicircular canals respectively. The effects found for rotational-direction specific contributions of vestibular signals to egocentric imagery suggest that cortical processing of semicircular canal signals may contribute to spatial aspects of bodily self-consciousness. Finally, vestibular signals facilitates egocentric imagery when viewing a human body shape, suggesting that egocentric imagery and spatial aspects of bodily self-consciousness are highly tuned to visual representations of the human body.

SELF-MOTION PERCEPTION

Most everyday activities imply bodily movement in the environment. Planning and controlling these actions require accurate self-motion perception with respect to the environment and for this the brain must be able to monitor body movements based on multisensory signals. Furthermore, self-motion perception is important for balance, walking, and tracking the motion of objects under the influence of gravity. Research has shown that self-motion perception depends on integrating redundant sensory signals about body movement from vestibular, visual, proprioceptive, auditory and kinesthetic signals. Although vestibular signals alone indicate head posture and movement with respect to the environment, they are poor at sensing very slow movements (Kolev et al., 1996) and prolonged constant-velocity movements (Brandt et al., 1998). Similarly, the otoliths cannot distinguish between linear acceleration from head motion and constant gravitational acceleration (Einstein, 1907). Research on self-motion perception studied therefore multisensory integration mechanisms, i.e., most extensively visual-vestibular integration, in non-human primates (Andersen et al., 2000; Bremmer et al., 2002; Gu et al., 2007; Bremmer, 2011). These studies found that in the non-human primate brain the medial temporal region and dorsal MST region integrate optokinetic stimuli and vestibular signals about head rotation and heading direction. Another area integrating vestibular, visual, and somatosensory signals relevant for self-motion perception is VIP (Bremmer et al., 1999; Chen et al., 2013a). Neuroimaging in humans found comparable activation for visual-vestibular integration for self-motion in posterior parietal, parietooccipital, and medial temporal regions (Brandt et al., 1998; Kleinschmidt et al., 2002; Kovács et al., 2008; Becker-Bense et al., 2012).

While these studies showed that self-motion perception depends on an optimal comparison of dynamic multisensory stimuli, including vestibular signals about bodily movement, more recent studies have shown that also constant gravitational acceleration signals are important for self-motion perception. For instance, De Saedeleer et al. (2013) found that under normal terrestrial conditions (with constant gravitational acceleration acting in the downward direction), the velocity of perceived self-motion depends on the spatial direction of visual implied motion, and that self-motion velocity perception shows an asymmetric pattern for upward vs. downward, but not for leftward vs. rightward motion. Specifically, visual self-motion is experienced as slower when directed upwards (opposite to the downward direction of gravitational acceleration) than when directed downward (in the same direction as gravitational acceleration). In microgravity, when no otolithic vestibular signals are present, this upward-downward asymmetry is abolished. Interestingly, the transition between asymmetric to symmetric perceptual bias is delayed by several days when astronauts in microgravity are presented with tactile cues that mimic foot sole pressure, as if they were standing upright in a gravitational field. These results suggest that constant gravitational acceleration, but also multisensory cues, affect self-motion perception.

Neural correlates of self-motion perception as related to the gravitational field have been studied by Indovina et al. (2013). During fMRI, these authors presented visual self-motion cues in a virtual rollercoaster. For motion in the vertical, but not in the horizontal, direction the PIVC region was activated—a key region in the cortex receiving vestibular inputs. The activation depended on motion acceleration constant and showed strongest activation for direction-acceleration congruent motion at earth-gravity constant 9.81 m/s^2.

Several studies from the same research group have previously shown that an internal model of gravity is recruited for visual motion perception. An internal model of gravity during these tasks recruited activation at of PIVC region, which was similarly activated by peripheral vestibular stimulation (McIntyre et al., 2001; Indovina et al., 2005). More recently, Maffei et al. (2010) found that visual object motion with a gravitational acceleration profile activated insula cortex and inferior parietal cortex. Both visually seen motion and unseen apparent motion cues similarly activated these regions. Activations were stronger when these signals were behaviorally relevant during an object interception task as compared to passive observation.

These recent studies in human subjects showed that self-motion perception is not only based on dynamic signals about body movement, but also on vestibular signal about the static gravitational field. Behavioral responses and functional neuroimaging suggest that the brain accounts for the effects of gravity on self- and environmental object motion by using an internal model of gravity that was found to overlap with cortical processing of vestibular signals in the PIVC region (Indovina et al., 2005, 2013)—a key region for vestibular input to the cortex (see Section Part Three: Vestibular Cortex and Spatial Aspects of Bodily Self-Consciousness of this review). Together, these findings suggest that vestibular signals about movement and position of the head are critical for self-motion perception, which draws on spatially representing one's own-body movements with respect to the external environment.

Experiments on self-motion perception have extensively inquired about participants' subjective experience of whether or not, and in which direction, they experienced to be moving. These are self-related perceptual judgments that are likely based on multisensory spatial representations of the bodily self ("I") and the external world. Thus, self-motion perception likely draws on similar neural representations underlying the spatial aspects of bodily self-consciousness, i.e., self-location and first-person perspective. It is important for the brain to spatially update self-location and first-person perspective while the body is in motion, and to withhold from spatial update when there is motion in the environment. However, research on bodily self-consciousness has mostly studied static body conditions and thus to date the exact relationship between functional and neural representations of self-motion perception and spatial aspects of bodily self-consciousness is not well understood.

BODY REPRESENTATION

Spatial aspects of bodily self-consciousness include a volumetric spatial representation of the body. Yet, no single sensory modality in isolation encodes such volumetric body representation. Instead, the brain integrates multisensory, body-related signals from the somatosensory, proprioceptive, visual, and, as it has been shown more recently, the vestibular system.

Longo and Haggard (2010) developed a task to assess perception of hand shape. They found that hand shape judgments were deformed in a manner partially resembling the cortical representation of the hand in primary somatosensory cortex. Using a similar task, Lopez et al. (2012c) studied the effect of vestibular stimulation by CVS on body representation and found that hand size judgments were generally enlarged by vestibular stimulation. A different study by Ferre et al. (2013)

applied vestibular stimulation by GVS during a homologous task and found that finger representations were enlarged while hand dorsum was shrunk by vestibular stimulation. The specific differences between the results in these studies, i.e., enlargement or shrinkage of hand shape judgments, may reflect differences in the spatial directionality of the vestibular signals applied. Specifically, vestibular stimulation by CVS mostly activates the horizontal canals that encode yaw rotation, whereas GVS activates mostly the vertical canals (i.e., anterior and posterior canals) that encode roll and pitch rotation (Lopez et al., 2012b). Alternatively, these results may be based on additional factors to the stimulation technique utilized; for instance, sensory co-activation of thermal and nociceptive sensory signals. Despite differences between studies, both findings show that vestibular stimulation deforms hand shape representation. Thus, in addition to visual, somatosensory and proprioceptive signals (Serino and Haggard, 2010), the brain also integrates vestibular signals in order to determine the volumetric representation of the body.

Vestibular stimulation temporarily altered participant's perception of the internal spatial configuration of the hand in the studies by Lopez et al. (2012c) and Ferre et al. (2013). These results differ from experienced changes of hand location during the rubber hand illusion (Botvinick and Cohen, 1998). Specifically, participants experience their own hand at a location different from their physical hand, but do not experience changes of hand shape. It seems that vestibular signals differently contribute to human position sense of implicit hand representations and overall hand location in external space. Two studies provide indirect support for this idea by showing that vestibular stimulation during the rubber hand illusion did not affect proprioceptive drift (Lopez et al., 2010, 2012a).

Generally, adult physical bodies undergo little change of shape over time, but vestibular stimulation immediately affected the internal representation of the hand shape. This suggests that highly plastic mechanisms underlie volumetric representations of the body. Such representations may be critical for spatial aspects of bodily self-consciousness, which can be manipulated rapidly during full-body illusions.

PART TWO: CONCLUSION

We reviewed data showing that vestibular signals from otolith organs and semicircular canals, as well as internal models of gravity, contribute to cognitive, sensorimotor, and perceptual functions. These self-related functions depend on vestibular processing at the TPJ, the intraparietal sulcus, the parietal-occipital and the medial temporal cortices. Because the TPJ also encodes spatial aspects of bodily self-consciousness, it is likely that vestibular processing at the TPJ is involved in both self-related processes and spatial aspects of bodily self-consciousness.

Vestibular signals are special sensory signals because the peripheral vestibular organs are fixed with respect to the head and therefore signal head movement relative to the external environment. Vestibular signals are thus likely to contribute in locating and updating location during movement of the body in the external world. However, vestibular signals alone are not sufficient, as they are signaling head position, but not the position of other body parts with respect to the external world. A multisensory integrated global representation of the whole body is necessary for bodily self-consciousness and thus vestibular signals need to be integrated with other spatially informative multisensory signals from the body. A full body representation can be achieved only by integrating multisensory body-related signals within a unique body-centered reference frame. Together vestibular world-related signals, when integrated with multisensory bodily signals, can provide a representation of the volumetric spatial body and its momentary position and orientation in space. Such representation of the whole body in space must be dynamically updated as the body and its parts continuously move. In this function, the vestibular signals are important to signal self-motion and thus to update spatial aspects of bodily self-consciousness with respect to the environment.

We think that for these functions, i.e., the spatial relationship between external world and a global full-body representation, and the update of the body-environment relationship in motion, vestibular processing in posterior brain regions is critical. In the final part of the present review we will present evidence supporting this view.

PART THREE: VESTIBULAR CORTEX AND SPATIAL ASPECTS OF BODILY SELF-CONSCIOUSNESS

What are the neural correlates of vestibular processing contributing to bodily self-consciousness? Empirical data shows that in the right hemisphere posterior cortical regions process both vestibular signals and spatial aspects of bodily self-consciousness (Dieterich et al., 2003; Blanke and Mohr, 2005; Ionta et al., 2011). In the third part of this review we summarize the functional characteristics of three important posterior vestibular cortex regions, i.e., PIVC, MST, and VIP, and a region causally involved in bodily self-consciousness, i.e., TPJ, which together may encode self-location and first-person perspective.

PIVC

It is commonly accepted that PIVC is a key region of vestibular input into the animal cortex (Grüsser et al., 1990a,b). This area also receives somatosensory and proprioceptive inputs (Lopez and Blanke, 2011). There is no consensus about the exact location and function of the PIVC in the human cortex. Different authors localized PIVC in the posterior insular and retroinsular cortex (Fasold et al., 2002; Indovina et al., 2005; Lopez et al., 2012b), in the parietal operculum (zu Eulenburg et al., 2012) and in different regions in the TPJ (Bense et al., 2001; Deutschländer et al., 2002; Lopez et al., 2012b). The available functional neuroimaging data in humans show that PIVC encodes vestibular signals from artificial stimulations by GVS and CVS (Fasold et al., 2002; Lopez et al., 2012b), proprioceptive signals from the neck (Fasold et al., 2008), and also visual signals (Brandt et al., 1998; Bense et al., 2001; Brandt et al., 2002; Deutschländer et al., 2002; Indovina et al., 2005, 2013). Although from non-human primate electrophysiology there is evidence for visual processing in PIVC (Grüsser et al., 1990a) there are also reports of no visual encoding in this region (Chen et al., 2010). Brandt et al. (1998) proposed that human PIVC and parietal occipital region encode visual and vestibular signals related to self-motion by a reciprocal visual vestibular inhibition mechanism. Specifically, these authors proposed that vestibular input activates PIVC and simultaneously deactivates parietooccipital region. Optokinetic stimulation, on the other hand, would activate parietooccipital region and simultaneously deactivate PIVC. Accordingly, the dynamic interaction between activation and inhibition from PIVC to parietooccipital region and *vice versa* would allow for determining self-motion. The PIVC projects to all other vestibular cortex regions, which is why some authors have discussed PIVC as the main vestibular input region to the human cortex (zu Eulenburg et al., 2012).

What could be the role of PIVC in encoding the spatial aspects of bodily self-consciousness? Because PIVC can be considered a subregion of the TPJ (see **Figure 3**), on top of the evidence for PIVC as a major input area of vestibular signals into the cortex, in addition to PIVC's strong connection to pSTG region, the PIVC seems to be critical in encoding vestibular signals contributing to self-location and first-person perspective. During experimentally induced changes in self-location and first-person perspective, vestibular otolithic signals play a critical role (Ionta et al., 2011) and these otolithic inputs as well as internal models of gravity have been reported to be encoded by PIVC and immediately neighboring regions (Indovina et al., 2005). It is thus likely that PIVC encodes body orientation and motion in the gravitational field and that these signals interact with neural processing regions at the TPJ coding for spatial aspects of bodily self-consciousness. Determining a clear functional and anatomical localization of PIVC in humans and its distinction from other neighboring regions involved in bodily self-consciousness will be an important goal for future research.

MST

In non-human primates, the dorsal MST region is located in the extrastriate cortex. It processes visual optic flow stimuli, in addition to vestibular signals from body translation and rotation (Bremmer et al., 2002; Gu et al., 2007). Recent models proposed that MST neurons process the perceptual decision about self-motion by integrating visual and vestibular cues according to a Bayesian optimal integration model (Tanaka et al., 1986; Duffy and Wurtz, 1991; Gu et al., 2008; Fetsch et al., 2013; Chen et al., 2013a). While in primates next to MST also VIP neurons process optic flow, both regions are different in terms of their reference frame encoding such vestibular signals. While VIP encodes vestibular signals in body- and world-centered coordinates, MST encodes vestibular signals in eye-centered coordinates (Chen et al., 2013a,b). These data suggest that in primates, MST is a critical region of visuovestibular integration and self-motion perception. Due to morphological changes of the cortical structures between non-human primates and humans, the exact human homologue

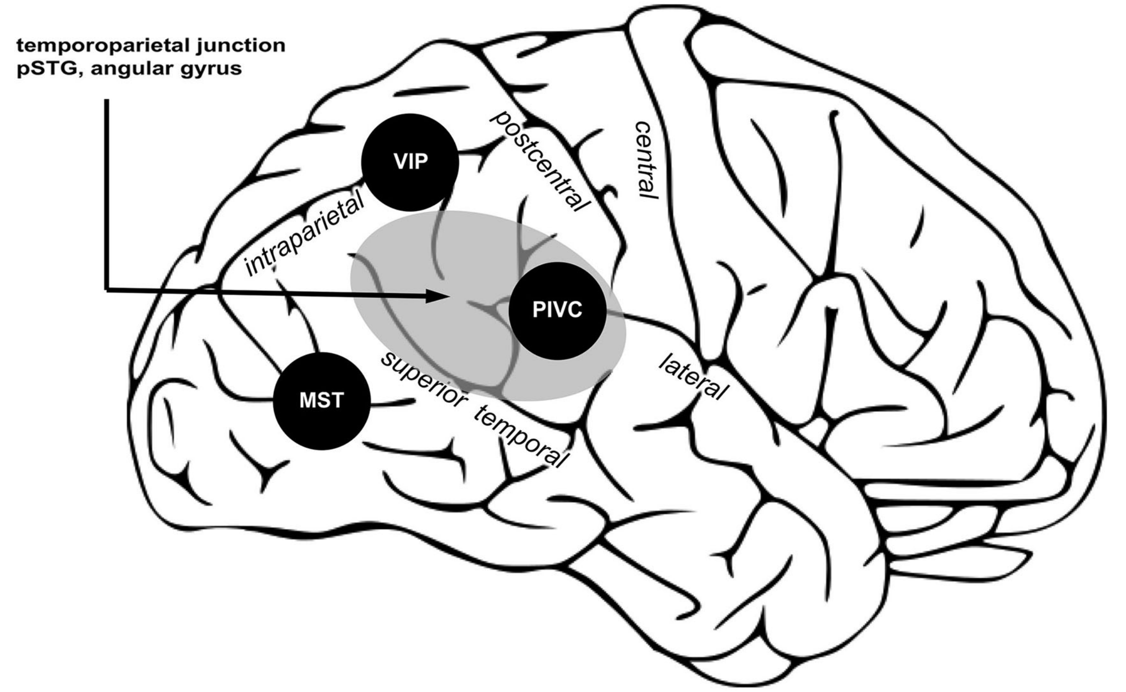

FIGURE 3 | Three posterior cortical regions processing vestibular signals are proposed important for bodily self-consciousness. PIVC encodes vestibular signals about position and movement of the head; VIP, integrates multisensory signals and computes reference frames transformation to common body and world-centered spatial reference frames; MST integrate vestibular and visual signals necessary for self-motion perception. Area in gray shows the TPJ, an area causally involved in encoding spatial aspects of bodily self-consciousness. Within TPJ, the pSTG and angular gyrus are regions associated to changes in spatial aspects of bodily self-consciousness in out-of-body experience and full-body illusion, and also the vestibular cortex region PIVC is part of the TPJ. (Image is a derivative of work licensed under creative commons.)

of MST (in terms of functional properties) is not precisely located in the human, however, functional neuroimaging studies have shown optic flow induced activity in the parietooccipital region (Brandt et al., 1998, 2002; Deutschländer et al., 2002). It is likely that the human homologue of MST is contributing to spatial aspects of bodily self-consciousness during self-motion by integrating visuovestibular signals. Therefore, vestibular processing in MST may play an important role in updating self-location and first-person while the body is in motion.

VIP

VIP is a critical region for multisensory spatial coding. First of all, several findings both in humans and animals show that VIP processes visual, tactile, proprioceptive, and auditory stimuli (Duhamel et al., 1997, 1998; Bremmer et al., 2001; Avillac et al., 2005; Schlack et al., 2005; Sereno and Huang, 2006; Huang et al., 2012). A main function of VIP neurons is to integrate spatial information from different sensory modalities, which initially encode space in peripheral sensory system centered coordinates (e.g., visual stimuli in retinotopic coordinates; auditory stimuli in head coordinates; somatosensory stimuli in somatotopic coordinates) into common body-centered reference frames. Most neurons in area VIP respond selectively to visual stimuli presented close the animal's body. Indeed, about half of VIP neurons respond best to visual stimuli within 30 cm of the body, and many neurons respond only within a few centimeters range (Colby et al., 1993). However, more distant space is also represented in VIP, since some neurons have visual receptive fields that are not confined in depth. In most neurons in VIP visual stimuli are encoded in body-part centered reference frames (typically centered at the head), some neurons are encoded in visual (retinal) reference frames, and some neurons have mixed reference frames (Avillac et al., 2005). Therefore, most VIP neurons preferentially represent the space near the body, in body-centered reference frames (Colby et al., 1993; Bremmer et al., 2002; Schlack et al., 2005). Although some neurons in VIP also encode visual-based representations of extrapersonal space, these extrapersonal space representations and the body-centered spatial representations are implemented in rather distinct neural populations within VIP (Colby et al., 1993), which supports the idea of distinct representations for near and far space, rather than a continuous representation from near to far space.

Interestingly, VIP also receives vestibular input. For instance, linear translations of the body, that are signaled by the otoliths, are encoded in VIP in body- or world-centered reference frames (Chen et al., 2013a). VIP may thus integrate vestibular with multisensory signals to compute spatial representations of the whole body—which are an important aspect of self-location (Blanke and Metzinger, 2009; Blanke, 2012; Metzinger, 2013). For all these reasons, computational models have proposed that VIP plays a critical role in coordinates transformation (Pouget et al., 2002; Avillac et al., 2005) and suggest that this region, together with other portions of the posterior parietal cortex plays a key role in remapping multisensory body-related signals into a common, whole-body centered, reference frames. Such computation is necessary to build a multisensory representation of the body in space, which is critical for spatial aspects of bodily self-consciousness.

TPJ

The TPJ can be defined as a larger region including the pSTG, angular gyrus, supramarginal gyrus, and the parietal operculum (**Figure 3**, gray region). The TPJ receives somatosensory, visual, and vestibular inputs (zu Eulenburg et al., 2012; Bzdok et al., 2013). Note that PIVC is a subregion of the TPJ (Lopez and Blanke, 2011; Lopez et al., 2012b). The TPJ is important for multisensory signal coding (Downar et al., 2000), theory of mind (Saxe and Kanwisher, 2003), and bodily self-consciousness (Blanke, 2012). Several findings presented in the first and second part of this review show that damage or stimulation at the TPJ can induce changes in self-location and first-person perspective (Blanke et al., 2002, 2004; Ionta et al., 2011). In the same vein, changes in self-location and first-person perspective, induced in healthy subject by the full-body illusion, are encoded at the TPJ, and in particular in the pSTG region. Thus, the TPJ seems to be a critical region for encoding spatial aspects of bodily self-consciousness. We think that vestibular inputs from PIVC, MST, and VIP to the TPJ are critical for that function. In particular, TPJ might integrate inputs from VIP contributing to a global body representation, from MST to update body orientation and direction during movement, from PIVC for the orientation of the body in the gravitational field. When these vestibular inputs are absent or in conflict with other sensory signals, e.g., visual or somatosensory, the brain may generate an inaccurate spatial representation of the bodily self, inducing illusions in healthy participants or disorders of bodily self-consciousness in patients.

CONCLUSION

The vestibular system processes head posture relative to constant gravitational acceleration and head motion in three-dimension space, thus providing important information related to the body with respect to the earth gravitational system, which is essential for coding the spatial orientation of the body in the external world. By reviewing recent data about bodily illusions, mental spatial representations, self-motion perception, and body representation, we argue that vestibular information is integrated with other sensory modalities to underlie bodily self-consciousness. Visual-vestibular interactions and internal models of gravity are processed at the TPJ, contributing to self-location and first-person perspective. We propose that this information depends on neural processing in the posterior cortical areas, which integrates and computes multisensory signals to build body representations in global whole-body centered reference frames and therefore contributes to stable representations of the bodily self. Integration of vestibular signals in PIVC, MST, and VIP, and further processing at the TPJ might be critical for the experience of the self as placed within a body, which occupies a specific location of space and faces the world from the first-person perspective. Vestibular processing may thus serve as a spatial reference for these spatial determinants of bodily self-consciousness.

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REFERENCES

Andersen, R. A., Shenoy, K. V., Crowell, J. A., and Bradley, D. C. (2000). Neural mechanisms for self-motion perception in area MST. *Int. Rev. Neurobiol.* 44, 219–233. doi: 10.1016/s0074-7742(08)60744-8

Arthur, J. C., Philbeck, J. W., and Chichka, D. (2009). Non-sensory inputs to angular path integration. *J. Vestib. Res.* 19, 111–125. doi: 10.3233/VES-2009-0354

Arzy, S., Thut, G., Mohr, C., Michel, C. M., and Blanke, O. (2006). Neural basis of embodiment: distinct contributions of temporoparietal junction and extrastriate body area. *J. Neurosci.* 26, 8074–8081. doi: 10.1523/jneurosci.0745-06.2006

Aspell, J. E., Heydrich, L., Marillier, G., Lavanchy, T., Herbelin, B., and Blanke, O. (2013). Turning body and self inside out: visualized heartbeats alter bodily self-consciousness and tactile perception. *Psychol. Sci.* 24, 2445–2453. doi: 10.1177/0956797613498395

Avillac, M., Deneve, S., Olivier, E., Pouget, A., and Duhamel, J. R. (2005). Reference frames for representing visual and tactile locations in parietal cortex. *Nat. Neurosci.* 8, 941–949. doi: 10.1038/nn1480

Baron-Cohen, S., Leslie, A. M., and Frith, U. (1985). Does the autistic child have a "theory of mind"? *Cognition* 21, 37–46. doi: 10.1016/0010-0277(85)90022-8

Becker-Bense, S., Buchholz, H. G., zu Eulenburg, P., Best, C., Bartenstein, P., Schreckenberger, M., et al. (2012). Ventral and dorsal streams processing visual motion perception (FDG-PET study). *BMC Neurosci.* 13:81. doi: 10.1186/1471-2202-13-81

Bense, S., Stephan, T., Yousry, T. A., Brandt, T., and Dieterich, M. (2001). Multisensory cortical signal increases and decreases during vestibular galvanic stimulation (fMRI). *J. Neurophysiol.* 85, 886–899.

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nat. Rev. Neurosci.* 13, 556–571. doi: 10.1038/nrn3292

Blanke, O., Landis, T., Spinelli, L., and Seeck, M. (2004). Out-of-body experience and autoscopy of neurological origin. *Brain* 127, 243–258. doi: 10.1093/brain/awh040

Blanke, O., and Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends Cogn. Sci.* 13, 7–13. doi: 10.1016/j.tics.2008.10.003

Blanke, O., and Mohr, C. (2005). Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin implications for neurocognitive mechanisms of corporeal awareness and self-consciousness. *Brain Res. Brain Res. Rev.* 50, 184–199. doi: 10.1016/j.brainresrev.2005.05.008

Blanke, O., Ortigue, S., Landis, T., and Seeck, M. (2002). Stimulating illusory own-body perceptions. *Nature* 419, 269–270. doi: 10.1038/419269a

Botvinick, M., and Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature* 391:756. doi: 10.1038/35784

Brandt, T., Bartenstein, P., Janek, A., and Dieterich, M. (1998). Reciprocal inhibitory visual-vestibular interaction. Visual motion stimulation deactivates the parieto-insular vestibular cortex. *Brain* 121(Pt. 9), 1749–1758. doi: 10.1093/brain/121.9.1749

Brandt, C., Brechtelsbauer, D., Bien, C. G., and Reiners, K. (2005). [Out-of-body experience as possible seizure symptom in a patient with a right parietal lesion]. *Nervenarzt* 76, 1259–1262. doi: 10.1007/s00115-005-1904-y

Brandt, T., Glasauer, S., Stephan, T., Bense, S., Yousry, T. A., Deutschlander, A., et al. (2002). Visual-vestibular and visuovisual cortical interaction: new insights from fMRI and pet. *Ann. N Y Acad. Sci.* 956, 230–241. doi: 10.1111/j.1749-6632.2002.tb02822.x

Bremmer, F. (2011). Multisensory space: from eye-movements to self-motion. *J. Physiol.* 589(Pt. 4), 815–823. doi: 10.1113/jphysiol.2010.195537

Bremmer, F., Klam, F., Duhamel, J. R., Ben Hamed, S., and Graf, W. (2002). Visual-vestibular interactive responses in the macaque ventral intraparietal area (VIP). *Eur. J. Neurosci.* 16, 1569–1586. doi: 10.1046/j.1460-9568.2002.02206.x

Bremmer, F., Kubischik, M., Pekel, M., Lappe, M., and Hoffmann, K. P. (1999). Linear vestibular self-motion signals in monkey medial superior temporal area. *Ann. N Y Acad. Sci.* 871, 272–281. doi: 10.1111/j.1749-6632.1999.tb09191.x

Bremmer, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K., et al. (2001). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron* 29, 287–296. doi: 10.1016/s0896-6273(01)00198-2

Bzdok, D., Langner, R., Schilbach, L., Jakobs, O., Roski, C., Caspers, S., et al. (2013). Characterization of the temporo-parietal junction by combining data-driven parcellation, complementary connectivity analyses, and functional decoding. *Neuroimage* 81, 381–392. doi: 10.1016/j.neuroimage.2013.05.046

Chen, A., DeAngelis, G. C., and Angelaki, D. E. (2010). Macaque parieto-insular vestibular cortex: responses to self-motion and optic flow. *J. Neurosci.* 30, 3022–3042. doi: 10.1523/JNEUROSCI.4029-09.2010

Chen, X., Deangelis, G. C., and Angelaki, D. E. (2013a). Diverse spatial reference frames of vestibular signals in parietal cortex. *Neuron* 80, 1310–1321. doi: 10.1016/j.neuron.2013.09.006

Chen, X., Deangelis, G. C., and Angelaki, D. E. (2013b). Eye-centered representation of optic flow tuning in the ventral intraparietal area. *J. Neurosci.* 33, 18574–18582. doi: 10.1523/JNEUROSCI.2837-13.2013

Cheyne, J. A., and Girard, T. A. (2009). The body unbound: vestibular-motor hallucinations and out-of-body experiences. *Cortex* 45, 201–215. doi: 10.1016/j.cortex.2007.05.002

Colby, C. L., Duhamel, J. R., and Goldberg, M. E. (1993). Ventral intraparietal area of the macaque: anatomic location and visual response properties. *J. Neurophysiol.* 69, 902–914.

Craig, A. D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. *Nat. Rev. Neurosci.* 3, 655–666. doi: 10.1038/nrn894

Craig, A. D. (2009). How do you feel–now? The anterior insula and human awareness. *Nat. Rev. Neurosci.* 10, 59–70. doi: 10.1038/nrn2555

De Ridder, D., Van Laere, K., Dupont, P., Menovsky, T., and Van de Heyning, P. (2007). Visualizing out-of-body experience in the brain. *N. Engl. J. Med.* 357, 1829–1833. doi: 10.1056/NEJMoa070010

De Saedeleer, C., Vidal, M., Lipshits, M., Bengoetxea, A., Cebolla, A. M., Berthoz, A., et al. (2013). Weightlessness alters up/down asymmetries in the perception of self-motion. *Exp. Brain Res.* 226, 95–106. doi: 10.1007/s00221-013-3414-7

Deutschländer, A., Bense, S., Stephan, T., Schwaiger, M., Brandt, T., and Dieterich, M. (2002). Sensory system interactions during simultaneous vestibular and visual stimulation in PET. *Hum. Brain Mapp.* 16, 92–103. doi: 10.1002/hbm.10030

Devinsky, O., Feldmann, E., Burrowes, K., and Bromfield, E. (1989). Autoscopic phenomena with seizures. *Arch. Neurol.* 46, 1080–1088. doi: 10.1001/archneur.1989.00520460060015

Dieterich, M., Bense, S., Lutz, S., Drzezga, A., Stephan, T., Bartenstein, P., et al. (2003). Dominance for vestibular cortical function in the non-dominant hemisphere. *Cereb. Cortex* 13, 994–1007. doi: 10.1093/cercor/13.9.994

Downar, J., Crawley, A. P., Mikulis, D. J., and Davis, K. D. (2000). A multimodal cortical network for the detection of changes in the sensory environment. *Nat. Neurosci.* 3, 277–283. doi: 10.1038/72991

Duffy, C. J., and Wurtz, R. H. (1991). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *J. Neurophysiol.* 65, 1329–1345.

Duhamel, J. R., Bremmer, F., Ben Hamed, S., and Graf, W. (1997). Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389, 845–848. doi: 10.1038/39865

Duhamel, J. R., Colby, C. L., and Goldberg, M. E. (1998). Ventral intraparietal area of the macaque: congruent visual and somatic response properties. *J. Neurophysiol.* 79, 126–136.

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science* 317:1048. doi: 10.1126/science.1142175

Ehrsson, H. H. (2012). "The concept of body ownership and it's relationship to multisensory integration," in *The New Handbook of Multisensory Processes*, ed B. Stein (Cambridge, MA: MIT Press).

Einstein, A. (1907). Uber das relativitatsprinzip und die aus demselben gezogenen folgerungen. *Yearb. Radioact. Electron.* 4, 411–462.

Fasold, O., Heinau, J., Trenner, M. U., Villringer, A., and Wenzel, R. (2008). Proprioceptive head posture-related processing in human polysensory cortical areas. *Neuroimage* 40, 1232–1242. doi: 10.1016/j.neuroimage.2007.12.060

Fasold, O., von Brevern, M., Kuhberg, M., Ploner, C. J., Villringer, A., Lempert, T., et al. (2002). Human vestibular cortex as identified with caloric stimulation in functional magnetic resonance imaging. *Neuroimage* 17, 1384–1393. doi: 10.1006/nimg.2002.1241

Ferre, E. R., Bottini, G., and Haggard, P. (2011). Vestibular modulation of somatosensory perception. *Eur. J. Neurosci.* 34, 1337–1344. doi: 10.1111/j.1460-9568.2011.07859.x

Ferre, E. R., Vagnoni, E., and Haggard, P. (2013). Vestibular contributions to bodily awareness. *Neuropsychologia* 51, 1445–1452. doi: 10.1016/j.neuropsychologia.2013.04.006

Fetsch, C. R., DeAngelis, G. C., and Angelaki, D. E. (2013). Bridging the gap between theories of sensory cue integration and the physiology of multisensory neurons. *Nat. Rev. Neurosci.* 14, 429–442. doi: 10.1038/nrn3503

Frith, C. D., and Frith, U. (2006). The neural basis of mentalizing. *Neuron* 50, 531–534. doi: 10.1016/j.neuron.2006.05.001

Gallagher, S. (2005). *How the Body Shapes the Mind.* USA: Oxford University Press.

Goldberg, J. M., Wilson, V. J., Cullen, C. E., Angelaki, D. E., Boussard, D. M., Buettner-Ennever, J. A., et al. (2012). *The Vestibular System: A Sixth Sense (Vol. 1).* USA: Oxford University Press.

Grabherr, L., Cuffel, C., Guyot, J. P., and Mast, F. W. (2011). Mental transformation abilities in patients with unilateral and bilateral vestibular loss. *Exp. Brain Res.* 209, 205–214. doi: 10.1007/s00221-011-2535-0

Green, C. E. (1968). *Out-Of-Body Experiences.* London: Hamish Hamilton.

Grüsser, O. J., Pause, M., and Schreiter, U. (1990a). Localization and responses of neurones in the parieto-insular vestibular cortex of awake monkeys (Macaca fascicularis). *J. Physiol.* 430, 537–557.

Grüsser, O. J., Pause, M., and Schreiter, U. (1990b). Vestibular neurones in the parieto-insular cortex of monkeys (Macaca fascicularis): visual and neck receptor responses. *J. Physiol.* 430, 559–583.

Gu, Y., Angelaki, D. E., and Deangelis, G. C. (2008). Neural correlates of multisensory cue integration in macaque MSTd. *Nat. Neurosci.* 11, 1201–1210. doi: 10.1038/nn.2191

Gu, Y., DeAngelis, G. C., and Angelaki, D. E. (2007). A functional link between area MSTd and heading perception based on vestibular signals. *Nat. Neurosci.* 10, 1038–1047. doi: 10.1038/nn1935

Guldin, W. O., Akbarian, S., and Grusser, O. J. (1992). Cortico-cortical connections and cytoarchitectonics of the primate vestibular cortex: a study in squirrel monkeys (Saimiri sciureus). *J. Comp. Neurol.* 326, 375–401. doi: 10.1002/cne.903260306

Haggard, P., Taylor-Clarke, M., and Kennett, S. (2003). Tactile perception, cortical representation and the bodily self. *Curr. Biol.* 13, R170–R173. doi: 10.1016/s0960-9822(03)00115-5

Hänsel, A., Lenggenhager, B., von Kanel, R., Curatolo, M., and Blanke, O. (2011). Seeing and identifying with a virtual body decreases pain perception. *Eur. J. Pain* 15, 874–879. doi: 10.1016/j.ejpain.2011.03.013

Huang, R. S., Chen, C. F., Tran, A. T., Holstein, K. L., and Sereno, M. I. (2012). Mapping multisensory parietal face and body areas in humans. *Proc. Natl. Acad. Sci. U S A* 109, 18114–18119. doi: 10.1073/pnas.1207946109

Indovina, I., Maffei, V., Bosco, G., Zago, M., Macaluso, E., and Lacquaniti, F. (2005). Representation of visual gravitational motion in the human vestibular cortex. *Science* 308, 416–419. doi: 10.1126/science.1107961

Indovina, I., Maffei, V., Pauwels, K., Macaluso, E., Orban, G. A., and Lacquaniti, F. (2013). Simulated self-motion in a visual gravity field: sensitivity to vertical and horizontal heading in the human brain. *Neuroimage* 71, 114–124. doi: 10.1016/j.neuroimage.2013.01.005

Ionta, S., and Blanke, O. (2009). Differential influence of hands posture on mental rotation of hands and feet in left and right handers. *Exp. Brain Res.* 195, 207–217. doi: 10.1007/s00221-009-1770-0

Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., et al. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron* 70, 363–374. doi: 10.1016/j.neuron.2011.03.009

Ionta, S., Sforza, A., Funato, M., and Blanke, O. (2013). Anatomically plausible illusory posture affects mental rotation of body parts. *Cogn. Affect. Behav. Neurosci.* 13, 197–209. doi: 10.3758/s13415-012-0120-z

Jeannerod, M. (2003). The mechanism of self-recognition in humans. *Behav. Brain Res.* 142, 1–15. doi: 10.1016/s0166-4328(02)00384-4

Klatzky, R. L. (1997). "Allocentric and egocentric spatial representations: definitions, distinctions and interconnections," in *Spatial Cognition: Lecture Notes in Computer Science*, (Vol. 1404), eds C. Freska, C. Habel and K. F. Wender (Berlin: Springer), 1–17.

Kleinschmidt, A., Thilo, K. V., Buchel, C., Gresty, M. A., Bronstein, A. M., and Frackowiak, R. S. (2002). Neural correlates of visual-motion perception as object- or self-motion. *Neuroimage* 16, 873–882. doi: 10.1006/nimg.2002.1181

Kolev, O., Mergner, T., Kimmig, H., and Becker, W. (1996). Detection thresholds for object motion and self-motion during vestibular and visuo-oculomotor stimulation. *Brain Res. Bull.* 40, 451–457; discussion 457–458. doi: 10.1016/0361-9230(96)00141-4

Kovács, G., Raabe, M., and Greenlee, M. W. (2008). Neural correlates of visually induced self-motion illusion in depth. *Cereb. Cortex* 18, 1779–1787. doi: 10.1093/cercor/bhm203

Lenggenhager, B., Lopez, C., and Blanke, O. (2008). Influence of galvanic vestibular stimulation on egocentric and object-based mental transformations. *Exp. Brain Res.* 184, 211–221. doi: 10.1007/s00221-007-1095-9

Lenggenhager, B., Tadi, T., Metzinger, T., and Blanke, O. (2007). Video ergo sum: manipulating bodily self-consciousness. *Science* 317, 1096–1099. doi: 10.1126/science.1143439

Longo, M. R., and Haggard, P. (2010). An implicit body representation underlying human position sense. *Proc. Natl. Acad. Sci. U S A* 107, 11727–11732. doi: 10.1073/pnas.1003483107

Lopez, C., and Blanke, O. (2011). The thalamocortical vestibular system in animals and humans. *Brain Res. Rev.* 67, 119–146. doi: 10.1016/j.brainresrev.2010.12.002

Lopez, C., Bieri, C. P., Preuss, N., and Mast, F. W. (2012a). Tactile and vestibular mechanisms underlying ownership for body parts: a non-visual variant of the rubber hand illusion. *Neurosci. Lett.* 511, 120–124. doi: 10.1016/j.neulet.2012.01.055

Lopez, C., Blanke, O., and Mast, F. W. (2012b). The human vestibular cortex revealed by coordinate-based activation likelihood estimation meta-analysis. *Neuroscience* 212, 159–179. doi: 10.1016/j.neuroscience.2012.03.028

Lopez, C., Schreyer, H.-M., Preuss, N., and Mast, F. W. (2012c). Vestibular stimulation modifies the body schema. *Neuropsychologia* 50, 1830–1837. doi: 10.1016/j.neuropsychologia.2012.04.008

Lopez, C., Halje, P., and Blanke, O. (2008). Body ownership and embodiment: vestibular and multisensory mechanisms. *Neurophysiol. Clin.* 38, 149–161. doi: 10.1016/j.neucli.2007.12.006

Lopez, C., Lacour, M., Ahmadi, A. E., Magnan, J., and Borel, L. (2007). Changes of visual vertical perception: a long-term sign of unilateral and bilateral vestibular loss. *Neuropsychologia* 45, 2025–2037. doi: 10.1016/j.neuropsychologia.2007.02.004

Lopez, C., Lenggenhager, B., and Blanke, O. (2010). How vestibular stimulation interacts with illusory hand ownership. *Conscious. Cogn.* 19, 33–47. doi: 10.1016/j.concog.2009.12.003

Maffei, V., Macaluso, E., Indovina, I., Orban, G., and Lacquaniti, F. (2010). Processing of targets in smooth or apparent motion along the vertical in the human brain: an fMRI study. *J. Neurophysiol.* 103, 360–370. doi: 10.1152/jn.00892.2009

Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S., Frith, C. D., and O'Keefe, J. (1998). Knowing where and getting there: a human navigation network. *Science* 280, 921–924. doi: 10.1126/science.280.5365.921

Mast, F., Kosslyn, S. M., and Berthoz, A. (1999). Visual mental imagery interferes with allocentric orientation judgements. *Neuroreport* 10, 3549–3553. doi: 10.1097/00001756-199911260-00016

McIntyre, J., Zago, M., Berthoz, A., and Lacquaniti, F. (2001). Does the brain model Newton's laws? *Nat. Neurosci.* 4, 693–694. doi: 10.1038/89477

Metzinger, T. (2003). *Being No One.* Boston: MIT Press.

Metzinger, T. (2013). Why are dreams interesting for philosophers? The example of minimal phenomenal selfhood, plus an agenda for future research. *Front. Psychol.* 4:746. doi: 10.3389/fpsyg.2013.00746

Mian, O. S., Li, Y., Antunes, A., Glover, P. M., and Day, B. L. (2013). On the vertigo due to static magnetic fields. *PLoS One* 8:e78748. doi: 10.1371/journal.pone.0078748

Newen, A., and Vogeley, K. (2003). Self-representation: searching for a neural signature of self-consciousness. *Conscious. Cogn.* 12, 529–543. doi: 10.1016/s1053-8100(03)00080-1

Oltman, P. K. (1968). A portable rod-and-frame apparatus. *Percept. Mot. Skills* 26, 503–506. doi: 10.2466/pms.1968.26.2.503

Palluel, E., Aspell, J. E., and Blanke, O. (2011). Leg muscle vibration modulates bodily self-consciousness: integration of proprioceptive, visual and tactile signals. *J. Neurophysiol.* 105, 2239–2247. doi: 10.1152/jn.00744.2010

Parsons, L. M. (1987a). Imagined spatial transformations of one's hands and feet. *Cogn. Psychol.* 19, 178–241. doi: 10.1016/0010-0285(87)90011-9

Parsons, L. M. (1987b). Imagined spatial transformations of one's body. *J. Exp. Psychol. Gen.* 116, 172–191. doi: 10.1037/0096-3445.116.2.172

Parsons, L. M. (1994). Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *J. Exp. Psychol. Hum. Percept. Perform.* 20, 709–730. doi: 10.1037/0096-1523.20.4.709

Petkova, V. I., Bjornsdotter, M., Gentile, G., Jonsson, T., Li, T. Q., and Ehrsson, H. H. (2011). From part- to whole-body ownership in the multisensory brain. *Curr. Biol.* 21, 1118–1122. doi: 10.1016/j.cub.2011.05.022

Petkova, V. I., and Ehrsson, H. H. (2008). If I were you: perceptual illusion of body swapping. *PLoS One* 3:e3832. doi: 10.1371/journal.pone.0003832

Pfeiffer, C., Lopez, C., Schmutz, V., Duenas, J. A., Martuzzi, R., and Blanke, O. (2013). Multisensory origin of the subjective first-person perspective: visual, tactile and vestibular mechanisms. *PLoS One* 8:e61751. doi: 10.1371/journal.pone.0061751

Pouget, A., Deneve, S., and Duhamel, J. R. (2002). A computational perspective on the neural basis of multisensory spatial representations. *Nat. Rev. Neurosci.* 3, 741–747. doi: 10.1038/nrn914

Pozzo, T., Berthoz, A., and Lefort, L. (1990). Head stabilization during various locomotor tasks in humans. I. Normal subjects. *Exp. Brain Res.* 82, 97–106. doi: 10.1007/bf00230842

Prsa, M., Gale, S., and Blanke, O. (2012). Self-motion leads to mandatory cue fusion across sensory modalities. *J. Neurophysiol.* 108, 2282–2291. doi: 10.1152/jn.00439.2012

Saxe, R., and Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind". *Neuroimage* 19, 1835–1842. doi: 10.1016/s1053-8119(03)00230-1

Schlack, A., Sterbing-D'Angelo, S. J., Hartung, K., Hoffmann, K. P., and Bremmer, F. (2005). Multisensory space representations in the macaque ventral intraparietal area. *J. Neurosci.* 25, 4616–4625. doi: 10.1523/jneurosci.0455-05.2005

Schwarz, D. W. (1976). Clinically relevant physiology of the vestibulo-ocular reflex. *J. Otolaryngol.* 5, 425–436.

Seizova-Cajic, T., Smith, J. L., Taylor, J. L., and Gandevia, S. C. (2007). Proprioceptive movement illusions due to prolonged stimulation: reversals and aftereffects. *PLoS One* 2:e1037. doi: 10.1371/journal.pone.0001037

Sereno, M. I., and Huang, R. S. (2006). A human parietal face area contains aligned head-centered visual and tactile maps. *Nat. Neurosci.* 9, 1337–1343. doi: 10.1038/nn1777

Serino, A., Alsmith, A., Costantini, M., Mandrigin, A., Tajadura-Jimenez, A., and Lopez, C. (2013). Bodily ownership and self-location: components of bodily self-consciousness. *Conscious. Cogn.* 22, 1239–1252. doi: 10.1016/j.concog.2013.08.013

Serino, A., and Haggard, P. (2010). Touch and the body. *Neurosci. Biobehav. Rev.* 34, 224–236. doi: 10.1016/j.neubiorev.2009.04.004

Shepard, R. N., and Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science* 171, 701–703. doi: 10.1126/science.171.3972.701

Tajadura-Jiménez, A., Kitagawa, N., Valjamae, A., Zampini, M., Murray, M. M., and Spence, C. (2009). Auditory-somatosensory multisensory interactions are spatially modulated by stimulated body surface and acoustic spectra. *Neuropsychologia* 47, 195–203. doi: 10.1016/j.neuropsychologia.2008.07.025

Tanaka, K., Hikosaka, K., Saito, H., Yukie, M., Fukada, Y., and Iwai, E. (1986). Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *J. Neurosci.* 6, 134–144.

van Elk, M., and Blanke, O. (2014). Imagined own-body transformations during passive self-motion. *Psychol. Res.* 78, 18–27. doi: 10.1007/s00426-013-0486-8

Wexler, M., Kosslyn, S. M., and Berthoz, A. (1998). Motor processes in mental rotation. *Cognition* 68, 77–94. doi: 10.1016/s0010-0277(98)00032-8

Wraga, M., Shephard, J. M., Church, J. A., Inati, S., and Kosslyn, S. M. (2005). Imagined rotations of self versus objects: an fMRI study. *Neuropsychologia* 43, 1351–1361. doi: 10.1016/j.neuropsychologia.2004.11.028

Zacks, J. M., and Michelon, P. (2005). Transformations of visuospatial images. *Behav. Cogn. Neurosci. Rev.* 4, 96–118. doi: 10.1177/1534582305281085

zu Eulenburg, P., Caspers, S., Roski, C., and Eickhoff, S. B. (2012). Meta-analytical definition and functional connectivity of the human vestibular cortex. *Neuroimage* 60, 162–169. doi: 10.1016/j.neuroimage.2011.12.032

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Appendix 5

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Multisensory Spatial Mechanisms of the Bodily Self and Social Cognition

A Commentary on Vittorio Gallese and Valentina Cuccio

Christian Pfeiffer

This commentary aims to find the right description of the pre-reflective brain mechanisms underlying our phenomenal experience of being a subject bound to a physical body (bodily self) and basic cognitive, perceptual, and subjective aspects related to interaction with other individuals (social cognition). I will focus on the proposal by Gallese and Cuccio that embodied simulation, in terms of motor resonance, is the primary brain mechanism underlying the pre-reflective aspects of social cognition and the bodily self. I will argue that this proposal is too narrow to serve a unified theory of the neurobiological mechanisms of both target phenomena. I support this criticism with theoretical considerations and empirical evidence suggesting that multisensory spatial processing, which is distinct from but a pre-requisite of motor resonance, substantially contributes to the bodily self and social cognition.

My commentary is structured in three sections. The first section addresses social cognition and compares embodied simulation to an alternative account, namely the attention schema theory. According to this theory we pre-reflectively empathize with others by predicting their current state of attention which involves predicting the spatial focus of attention. Thereby we derive a representational model of their state of mind. On this account, spatial coding of attention, rather than motor resonance, is the primary mechanism underlying social cognition. I take this as a theoretical alternative complementing motor resonance mechanisms.

The second section focuses on the bodily self. Comparison of the brain networks of the bodily self and social cognition reveals strong overlap, suggesting that both phenomena depend on shared multisensory and sensorimotor mechanisms. I will review recent empirical data about altered states of the bodily self in terms of self-location and the first-person perspective. These spatial aspects of the bodily self are encoded in brain regions distinct from the brain network of embodied simulation. I argue that while motor resonance might contribute to body ownership and agency, it does not account for spatial aspects of the bodily self. Thus, embodied simulation appears to be a necessary but insufficiently "primary" brain mechanism of the bodily self and social cognition.

The third section discusses the contributions of the vestibular system, i.e., the sensory system encoding head motion and gravity, to the bodily self and social cognition. Vestibular cortical processing seems relevant to both processes, because it directly encodes the world-centered direction of gravity and allows us to distinguish between motions of the own body and motions of other individuals and the external world. Furthermore, the vestibular cortical network largely overlaps with those neural networks relevant to the bodily self and social cognition. Thus, the vestibular system may play a crucial role in multisensory spatial coding relating the bodily self to other individuals in the external world.

Keywords
Attention schema | Bodily self | Embodied simulation | First-person perspective | Mirror neurons | Self-location | Social cognition | Vestibular system

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1 Introduction

The paper by Gallese and Cuccio provides an integrated theoretical framework explaining how the brain and body relate to social cognition, the human self, and language. The authors review empirical evidence from electrophysiological and neuroimaging studies supporting embodied simulation (ES) theory (Gallese & Cuccio this collection, p. 8). According to ES, the brain covertly simulates the bodily actions, perceptions, and emotions observed in other individuals by using parts of our neural architecture involved in acting, sensing, and feeling emotions. Thereby, we infer the goals, intentions, and states of mind of others in a pre-reflective and non-conceptual fashion. But the authors take this a step further and propose that ES is the key mechanism underlying, and hence unifying, both social cognition, the human self, and language. Throughout the paper, the authors emphasize the tight functional coupling between the body and the brain, which when taken into account bears the potential to significantly advance the scientific study of the hard problem of consciousness (Chalmers 1996).

This commentary on Gallese and Cuccio aims to find the right description of the brain mechanisms underlying pre-reflective aspects of both the bodily self and social cognition. Specifically, I will focus on Gallese and Cuccio's central claim that ES, based on motor resonance and neural processing in the motor system, is the primary brain mechanism underlying pre-reflective representations of the bodily self and social cognition (Gallese & Cuccio this collection, pp. 8–14). I ask the following questions: Could there be an alternative theory or empirical evidence countering the claim of a primacy of motor resonance underlying social cognition and the bodily self? Which brain mechanisms in addition to motor resonance might contribute to pre-reflective aspects of social cognition and the bodily self? I will defend the following three theses:

(1) Social cognition and the bodily self depend on multisensory spatial coding, which is distinct from motor resonance. Thus, motor resonance may be a necessary but insufficiently "primary" brain mechanism of social cognition and the bodily self (cf. section Fehler: Referenz nicht gefunden, 2).

(2) The brain networks underlying social cognition and the bodily self largely overlap. Specific functional associations exist (a) between motor resonance and body ownership/agency and (b) between multisensory spatial coding and self-location/the first-person perspective (cf. section 2).

(3) The vestibular system, i.e., the sensory system encoding head motion and gravity, might provide unique information used for multisensory spatial coding that relates the bodily self to other individuals and the external world. This is further suggested by the large overlap existing between the human vestibular cortex and the brain networks underlying the bodily self and social cognition (cf. section 3).

My commentary is structured in three sections. In the first section I shall compare ES to an alternative theory of social cognition that assigns priority to spatial coding of attention, rather than to motor resonance. I shall show that both theories bear the potential that their proposed brain mechanisms cooperatively work together in order to support social cognition. The second section addresses the bodily self. I shall review data from neurological patients and full-body illusion experiments, which highlight the importance of two spatial aspects of the bodily self not mentioned by Gallese and Cuccio, i.e., self-location and the first-person perspective. These spatial aspects of the bodily self depend primarily on multisensory integration and on cortical processing outside regions involved in ES. Furthermore, comparisons between the brain networks encoding the bodily self and social cognition show large overlaps, suggesting shared functional mechanisms. In the third section I propose that because multisensory spatial processing appears to be critical for the bodily self and social cognition, important contributions may come from the vestibular system (Lenggenhager & Lopez this collection). I shall show that the vestibular cortical network largely overlaps with the brain networks underlying the bodily self and social cognition. I shall discuss potential contributions of vestibular cortical processing to these target phenomena and suggest directions for future research.

2 Is social cognition based on motor resonance or attention tracking?

Social cognition refers to cognitive processes, perceptions, and subjective experiences related to interaction with conspecifics. This section asks: Which are the brain mechanisms underlying pre-reflective aspects of social cognition? Could there be alternative theories and empirical evidence countering the primary role of motor resonance?

Gallese and Cuccio propose that social cognition mainly depends on ES based on motor resonance and processing of mirror neurons (see citations in Gallese & Cuccio this collection). Mirror neurons were initially discovered in fronto-parietal networks of the macaque monkey brain. They are a specific type of canonical neuron involved in planning and executing hand actions and were found to be activated both when the monkey executed a specific grasping or reaching action and when the monkey passively observed somebody performing similar actions (Gallese et al. 1996; Rizzolatti et al. 1996). Neuroimaging studies in humans also showed mirror neuron-like activation patterns at the level of populations of neurons in distinct brain regions—mainly the ventral premotor cortex (vPM), the intraparietal sulcus (IPS), but also the insula cortex and the secondary somatosensory cortex (Rizzolatti & Sinigaglia 2010; see also figure 1a gray dots). ES proposes that based on mirror neurons the brain maps observed actions into an action space, into motor potentialities, within our hierarchically-organized motor system, and thereby infers and predicts the action goals of the individual. In this way it penetrates the state of mind of the other, and thus links self and other in a pre-reflective empathical fashion (Gallese & Cuccio this collection, p. 7).

I would like to point out that motor resonance, i.e., the mapping of observed actions into motor potentialities, necessarily depends on multisensory spatial coding. I argue that this is the case because of five points: First, the brain has access to the physical world only through the different sensory receptors of the body that bombard it with exteroceptive (e.g., vision, audition), proprioceptive (somatosensory, vestibular), and interoceptive (somatosensory, visceral) signals. Second, these multisensory signals must be integrated according to their spatial and temporal parameters (Stein & Stanford 2008) to inform neural representations of the states of the body and of the world around us—including the agents whose actions are subject to motor resonance. Third, the observed movements of these agents are coded in coordinates distinct from the egocentric spatial frame of reference upon which our motor system operates. Fourth, the brain must necessarily perform spatial transformations of the observed movements by the other agent into the egocentric frame of reference, upon which motor resonance can operate. In sum, multisensory spatial coding is a pre-requisite of motor resonance.

According to Gallese and Cuccio, the outcomes of such multisensory spatial coding are readily available to the brain network of ES through anatomical connections to the vPM that are “anatomically connected to visual and somatosensory areas in the posterior parietal cortex and to frontal motor areas” (Gallese & Cuccio this collection, p. 10). However, it seems that the multisensory spatial coding required for a precise description of complex motor acts might be computationally costly. Might there be a computationally more effective alternative by which multisensory spatial coding is used to decode the intentions of observed agents?

The attention schema (AS) theory of awareness (Graziano 2013; Graziano & Kastner 2011) proposes that brain mechanisms related to attention and spatial coding, which are distinct from neural processing relevant to ES, primarily underlie pre-reflective aspects of social cognition. Graziano and Kastner define *attention* as an information-handling mechanism of the brain that serves to give priority to some information (e.g., representational features) out of several equally probable alternatives that are in constant competition for awareness. Furthermore, *awareness* is defined as the process of consciously experiencing something, it is the process of relating the subject (i.e., a phenomenal self, see also Metzinger 2003) to the object/content of experience. Graziano and Kastner summarize AS as follows:

> [Awareness is information and] depends on some system in the brain that must have computed [it] […]; otherwise, the information would be unavailable for report. […] People routinely compute the state of awareness of other people [and] the awareness we attribute to another person is our reconstruction of that person's attention. […] The same machinery that computes socially relevant information […] also computes […] information about our own awareness. […] Awareness is […] a perceptual model […] a rich informational model that includes, among other computed properties, a spatial structure. […] Through the use of the social perceptual machinery, we assign the property of awareness to a location within ourselves. (Graziano & Kastner 2011, pp. 98–99)

Related to social cognition, AS proposes that by using a schematic representation of the state of attention of other individuals—including a prediction of the spatial location of their focus of attention—we predict the current state of awareness of the individual, which is informative about their intentions and potential future actions. In short: Awareness of others is an attention schema. As compared to ES, AS is a relatively recent theory that requires extensive empirical studies. Yet the evidence so far shows that indeed the brain has a neural circuitry for monitoring the spatial configuration of one's own attention independent of the sensory modality (Downar et al. 2000), including the direction of gaze (Beck & Kastner 2009; Desimone & Duncan 1995). These structures are the proposed neural expert system upon which AS is based and consist of the right-hemispheric temporo-parietal junction (TPJ) and superior temporal sulcus (STS) (see figure 1a in black). Notably, this expert system relevant to AS shows little anatomical overlap with the neural structures relevant to ES (figure 1a compare black with gray).

Because the AS relies on coding of the spatial relationship between the location of the observed individual and the likely spatial location of this individual's attention (i.e., independent of a particular sensory modality), the required spatial computations seem simple and straightforward. They require two points, i.e., the individual as a reference point and the potential spatial location of the attention of that individual. According to AS, using such spatial labeling the brain is able to simultaneously track the aware and attending minds of several individuals simultaneously. Thus, spatial coding in the context of AS appears to be less complex and less computationally demanding than spatial transformations underlying ES (see above).

Which of these seemingly distinct brain mechanisms proposed by AS and ES more plausibly underlies social cognition: the neural expert system decoding the state of attention according to AS or the mirror mechanism system decoding observed motor plans according to ES? It has been proposed that AS and ES may in principle work together. Graziano and Kastner propose that the expert system of AS may take a leading role by formulating a hypothesis about the state of awareness of an individual that is likely to drive further behavior and therefore provide a set of predictions based upon which motor resonance could more efficiently perform simulations (Graziano & Kastner 2011). Motor resonance would thus add richer detail to the state-of-attention hypothesis made by the expert system.

This combined mechanism is compatible with the predictive processing principle (Clark this collection; Hohwy 2013, this collection), which has been proposed relevant to the bodily

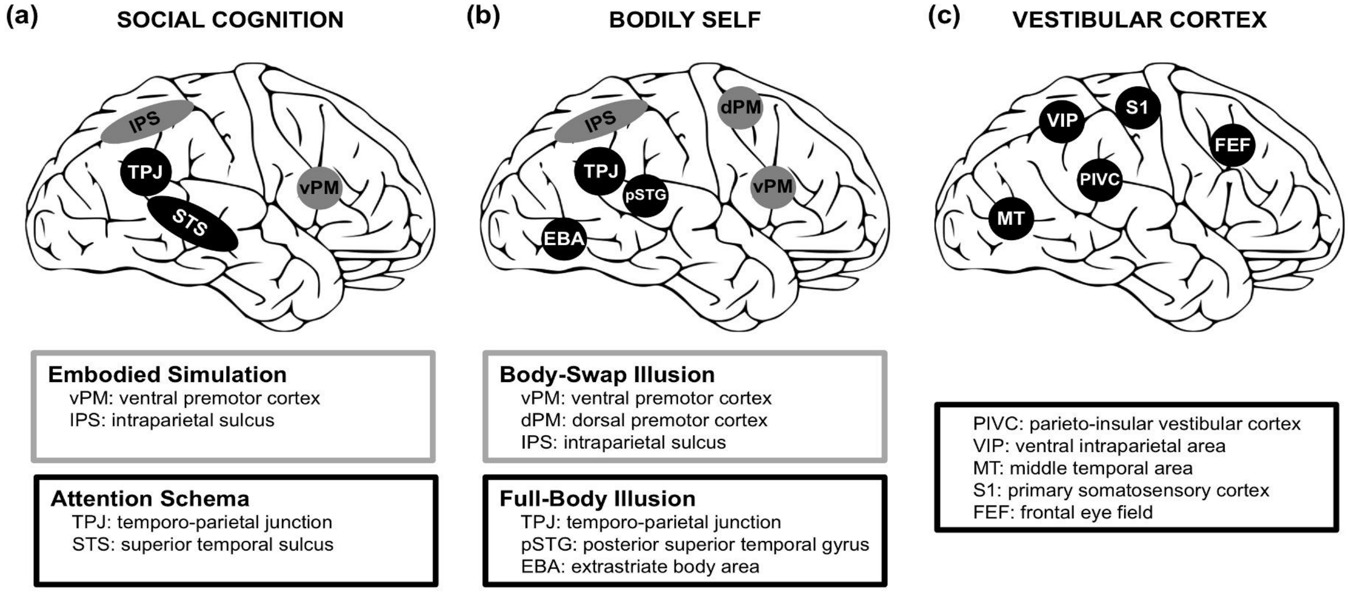

Figure 1: Summary of cortical brain regions involved in social cognition, the bodily self, and vestibular processing. (a) Whereas for social cognition there is little overlap between the brain regions proposed relevant for the attention schema (*in black*) and embodied simulation (*in gray*), both sets of brain regions overlap with (b) the brain network of the bodily self as identified by full-body illusion experiments manipulating self-location and first-person perspective (*in black*) and the body-swap illusion manipulating mainly body ownership (*in gray*). (c) The human vestibular cortical regions (*in black*) are widely distributed and overlap with several regions relevant to both the bodily self and social cognition. (The images are derived from images by NASA, licensed under creative commons.)

self (Apps & Tsakiris 2013; Limanowski & Blankenburg 2013; Seth this collection). According to *predictive processing* the brain constantly predicts the potential causes of sensory input by minimizing prediction errors via update of the predicted causes or by action that changes sensory input (Friston 2005). Applying the predictive processing principle to Graziano and Kastner's proposal that AS is a hypothesis-generating tool to which ES adds further detail, one could conceive of both mechanisms as different predictive processing modules aimed at anticipating the state of awareness and of intentional actions observed in others. Although no empirical study so far has addressed this specific hypothesis, a recent functional magnetic resonance imaging study found that predictive processing principles accounted for the blood oxygen-level dependent activity related to the perception of faces, which is an important perceptual function for social cognition in the human species (Apps & Tsakiris 2013).

These common and distinct predictions based on ES, AS, and predictive processing call for empirical research aimed at providing evidence to further refine, integrate, or reject them.

3 Multisensory and motor mechanisms of the multifaceted bodily self

The *bodily self* refers to the phenomenal experience of being an experiencing subject (i.e., a phenomenal self) bound to a physical body, which gives rise to the dual nature of the body (Husserl 1950; Gallese & Cuccio this collection, p. 2). The unified experience of being a bodily self can be decomposed into different aspects, including the experience that we identify with a particular body (self-identification or *body ownership*), the experience that the self is situated in a specific spatial location (*self-location*), that we take a specific experiential perspective at the world (*first-person perspective*), and that we are the authors of our actions, including having control of attentional focus (*agency*; (Blanke 2012; Ehrsson 2012; Jeannerod 2003; Metzinger 2003).

In their paper, Gallese & Cuccio highlight the relevance of mirror mechanisms, in particular related to processing in the cortical motor system, to the sense of body ownership and the sense of agency, in particular in the context of action and action observation:

> This minimal notion of the self, namely the bodily self as power-for-action [...], tacitly presupposes ownership of an action-capable agentive entity; hence, it primarily rests upon the functionality of the motor system. (this collection, p. 10)

However, recent philosophy of mind and cognitive neuroscience research reveals the crucial role of *spatial aspects of the bodily self*, consisting of a first-person perspective and self-location. In this section I shall compare the brain network contributing to spatial aspects of the bodily self with the brain network underlying body ownership and ask: Do these neuroimaging results support the proposal that motor resonance is a primary mechanism underlying all aspects of the bodily self? What is the relationship between the neural networks of the bodily self and social cognition? Which functional associations can be derived from this?

3.1 Brain mechanisms of spatial aspects of the bodily self

The phenomenal experience of being a subject is associated with a spatial location, which typically is the space of the physical body (see also Alsmith & Longo 2014; Limanowski & Hecht 2011). However, there are exceptions to these prototypical states of the bodily self in neurological disorders and experimental illusions pointing to a specific set of brain regions involved in spatially linking the phenomenal self to the physical body.

Which brain mechanisms link the phenomenal self to the physical body to give rise to the dual nature of the body as lived body and as physical object? Research in neurological patients who have had out-of-body experiences (OBE) shows that damage or interference with the right TPJ can lead to dissociations between the bodily self and physical body (Blanke et al. 2004; Blanke et al. 2002; De Ridder et al. 2007; Ionta et al. 2011). During an OBE, patients typically experience a disembodied self-location in elevation above their physical body, and an altered first-person perspective that originates from an elevated location in the room and is directed downwards at the physical body (Blanke et al. 2004; Metzinger 2009). These patients do not identify with their physical body but with an illusory double outside of the borders of the physical body. At the phenomenological level, self-location and the first-person perspective are often experienced as having their spatial origin in the same position. However, during OBE there are instances where self-location can be dissociated from the first-person perspective in different sensory modalities (De Ridder et al. 2007). Further evidence from asomatic OBEs and bodiless dreams suggests that a phenomenal first-person perspective may be reducible to a single point in space (Windt 2010). In fact, vestibular hallucinations systematically preceded OBEs in patients with sleep paralysis, i.e., a motor paralysis characterised by the transient inability to execute bodily actions when waking up from sleep (Cheyne & Girard 2009), showing further dissociations of the spatial location of the bodily self and the physical body and links to sensory processing. These studies seem to suggest that the first-person perspective and self-location may depend on different neural mechanisms (Blanke 2012).

OBE in epileptic patients can be induced by subcortical electrical stimulation of a specific intensity at the TPJ. However, stimulating the same brain region with either lower or higher stimulation intensity induces bodily sensations (including vestibular, visual, somatosensory, kinesthetic sensations) without inducing an OBE (Blanke et al. 2002). These observations gave rise to the idea that the spatial aspects of the bodily self are based on the accurate integration of multisensory signals (i.e., which was perturbed by electrical stimulation in the patient in Blanke et al. 2002, which are sensory signals from personal space to sensory signals from the external environment Blanke et al. 2004).

These clinical observations in patients were corroborated by different full-body illusion experiments in healthy subjects, such as the so-called “body-swap illusion” (Petkova & Ehrsson 2008; Petkova et al. 2011; van der Hoort et al. 2011), the “full-body illusion” (Ionta et al. 2011; Lenggenhager et al. 2009; Lenggenhager 2007; Pfeiffer et al. 2013; Pfeiffer, Schmutz & Blanke 2014), and the “out-of-body illusion” (Ehrsson 2007; Guterstam & Ehrsson 2012). In these experiments, healthy subjects receive conflicting signals about the spatial location of their body and of the temporal synchrony of exteroceptive and interoceptive signals, including somatosensory, cardiac, and vestibular signals that at the same time are applied to a virtual or fake body seen by the subject (Aspell et al. 2013; Ionta et al. 2011; Pfeiffer et al. 2013; Pfeiffer et al. 2014). For example, in the *full-body illusion*, synchronous stroking of a virtual or fake body seen from a distance can induce the feeling in participants that they are more closely located to the position of the virtual or fake body, and that they experience and increase of ownership for the seen body. The brain regions involved in these spatial experimental manipulations of the experienced bodily self most consistently involve the right TPJ region, but also draw on somatosensory and visual regions that process the sensory inputs (Blanke 2012; Ionta et al. 2011; figure 1b in black). Recently, several studies have manipulated visual and vestibular signals about the direction of gravity, affecting self-location and perspective and thus showing that those visual spatial cues affect our subjective experience of the first-person perspective (Ionta et al. 2011; Pfeiffer et al. 2013). These authors presented images on virtual-reality goggles showing visual gravitational cues, similar to the visual perspective during an OBE showing a scene from an elevated spatial location and a visual viewpoint directed downwards into the room. At the same time the somatosensory and the vestibular signals received by the participant, who was lying on the back, suggested that the physical body was oriented upwards with respect to veridical gravity. Thus the visual gravity cues (i.e., downwards) and the vestibular gravity cues (i.e., upwards) were in directional conflict. When the full-body illusion was induced under these conflicting conditions, participants reported subjective changes in their experienced direction of the first-person perspective (upward or downward) in line with experimentally-induced multisensory conflict (Ionta et al. 2011; Pfeiffer et al. 2013).

3.2 Brain mechanisms of body ownership

A different brain network encodes experimental manipulations of another aspect of the bodily self: body ownership. This was shown by the *body-swap illusion* (Petkova & Ehrsson 2008; Petkova et al. 2011), during which the participant views from a first-person visual viewpoint the body of a mannequin or another person. Thus no conflict between the visual spatial coordinates of the participant’s physical body and the visually-perceived location of the mannequin is presented. However, conflicting sensory information about the shape, gender, size, or overall spatial context surrounding the virtual body were presented that typically prevented feeling ownership of the virtual body. If under these conditions visuo-tactile stroking on the abdomen of the participant and the virtual body was synchronously administered, an illusion of ownership for the body emerged, reflected in increased responses to threatening the mannequin. In different variants of the body-swap illusion subjects reported experiencing and adopting different sizes of both the virtual body and the contextual environment (Petkova & Ehrsson 2008; Petkova et al. 2011; van der Hoort et al. 2011). Neuroimaging experiments of the body-swap illusion show activation of the vPM and IPS regions, notably without involving actions made by subjects or performed by the virtual body (Petkova et al. 2011). These brain regions are key nodes of the mirror mechanism network of ES (see Serino et al. 2013). For a recent review see figure 1b.

3.3 A shared brain network of bodily self and social cognition

Although the neuroimaging evidence so far suggests that distinct brain regions encode the spatial aspects of the bodily self and body ownership (Blanke 2012; Serino et al. 2013), the ensemble of those bodily self-encoding regions closely matches the brain regions relevant for social cognition (compare in figure 1a with figure 1b). These empirical data indeed suggest that the bodily self and social cognition are encoded by at least overlapping neural circuits supporting the proposal of ES that neural capacities to control and monitor the own body are used in understanding others.

These neuroimaging data suggest particular functional associations between different aspects of social cognition and the bodily self. In particular, the brain network of ES anatomically overlaps with regions encoding experimentally-induced changes in body ownership during the body-swap illusion (figure 1a–b in gray), which involves spatial congruence of the observational viewpoint and position of the fake body and the participant's body. A second association can be observed between the brain network of AS and the brain regions encoding spatial aspects of the bodily self, as manipulated during the full-body illusion (figure 1a–b in black). During the latter, the position and observational viewpoints of the virtual body and the participant's body are in spatial conflict, and thus closely resemble social interaction settings.

Based on these functional and neuroanatomical observations, I propose that ES seems to contribute to the bodily self and social cognition in a way primarily related to the sense of body ownership and agency. However, ES does not account for multisensory spatial representations that relate the physical body to the bodily self in space. These spatial aspects of the bodily self are encoded by brain regions outside of the brain network of ES, and rather resemble those brain regions relevant for coding the spatial configuration of attention (or awareness, according to AS).

Because two crucial aspects of the bodily self, i.e., self-location and the first-person perspective, are encoded in the TPJ region, and full-body illusions show that they can be manipulated without action or motor manipulations, it seems implausible that ES as based on motor resonance is the primary brain mechanism underlying the bodily self. Instead, the brain networks coding self-location and the first-person perspective, which overlap with brain regions proposed to encode spatial aspects of an attention schema (see figure 1), seem to contribute to at least an equal degree to both the bodily self and social cognition. Thus, ES seems to be a necessary but insufficiently "primary" brain mechanism underlying the bodily self and social cognition.

I do not mean to imply that these are independent processes, because it is possible that they cooperatively work together (Graziano & Kastner 2011). However, I think that Gallese and Cuccio's claim of a primacy of motor resonance underlying the multifaceted aspects of the bodily self and social cognition is questionable on empirical and theoretical grounds.

4 Vestibular contributions to the bodily self and social cognition

In the previous sections I have provided theoretical considerations and empirical evidence assigning a critical role to multisensory spatial processing in the neural computations underlying representations of the bodily self and social cognition. This section will further examine the multisensory mechanisms relating the space of the bodily self to other individuals and the external world. I propose that important contributions to the brain's multisensory spatial coding might come from a particular sensory system, i.e., the vestibular system, which has often been neglected in studies of higher brain functions related to subjectivity and intersubjectivity. I will ask: What might be the functional contribution of the vestibular system to pre-reflective representations of the bodily self and social cognition? How does the human vestibular cortex relate to the neural networks of the bodily self and social cognition?

The *vestibular system* consists of sensory organs in the inner ear that sense accelerations of the head in space, including rotational and linear movement of the head and whole body and the constant acceleration of gravity on earth (Day & Fitzpatrick 2005). Vestibular signals are processed by subcortical and cortical structures (Angelaki & Cullen 2008; Cullen 2012; Lopez & Blanke 2011). Research initially focused on subcortical processing as related to gaze control, postural stabilization, and neural computations of head motion directions (Fernandez & Goldberg 1971; Goldberg & Fernandez 1971). More recently, studies have revealed the contribution of vestibular cortical processing to spatial cognition, body perception, and the bodily self (see Lenggenhager & Lopez this collection; Lopez & Blanke 2011; Pfeiffer et al. 2014 for reviews). These studies show that vestibular cortical processing is based on a neural network of distinct, distributed, and multisensory cortical regions. In distinction from any other sensory modality, there is no primary vestibular cortex that processes purely vestibular signals. Instead, a core vestibular cortical input region, the human parieto-insular vestibular cortex (PIVC; Lopez et al. 2012; zu Eulenburg et al. 2012), processes vestibular, somatosensory, and visual signals and is connected to a number of multisensory brain regions in the parietal, temporal, cingulate, and frontal regions (figure 1c).

The vestibular system contributes to spatial aspects of the bodily self. For instance, OBEs were associated with vestibular sensation, such as floating in elevation (Blanke et al. 2004; Blanke & Mohr 2005; Blanke et al. 2002), and vestibular sensations preceded OBEs in persons with sleep paralysis (Cheyne & Girard 2009). Other studies presented conflicting visual and vestibular signals about earth gravity during the full-body illusion and induced changes in the subjectively-experienced spatial direction of the first-person perspective and self-location (Ionta et al. 2011; Pfeiffer et al. 2013). Thus, it has been argued that vestibular cortical processing does not merely signal the motions of the own body and the external world, but is also constitutive of spatial aspects of the bodily self (Lopez et al. 2008; Pfeiffer et al. 2014).

Previously, Lopez et al. (2013), Deroualle & Lopez (2014), and Lenggenhager & Lopez (this collection) have argued that the vestibular system probably contributes to social cognition. I will briefly summarize their main arguments and complement them with own points:

First, because the human species evolved under the steady influence of the earth's gravitational field, adaptation to gravity also framed and affected action, perception, and social interaction. More recently, research has shown that the brain hosts internal models of gravity, representing the effects of gravity on the motion of objects under the influence of gravity, of self-motion, of bodily actions, and of the direction of the gravitational acceleration. Those internal models of gravity strongly overlap with the vestibular cortex (Indovina et al. 2005; Indovina et al. 2013; McIntyre et al. 2001; Sciutti et al. 2012). More evidence for a vestibular contribution to social perception comes from studies showing the effects of gravitational signals on the perception of emotional faces (Thompson 1980) and the perception of the spatial orientation of bodies (Lopez et al. 2009).

Second, the vestibular system might contribute to social cognition because it detects head motions in space and hence directly enables us, when compared to other sensory signals, to discern movements made by our own body from motions of other individuals and motions of the external environment (Deroualle & Lopez 2014).

Third, mental spatial transformation of the own visual viewpoint to that of another person presents an important underlying cognitive aspect of social cognition (Furlanetto 2013; Hamilton 2009; Newen & Vogeley 2003; also cited by Gallese & Cuccio this collection, pp. 9–11). More direct evidence supporting this hypothesis comes from a recent study that showed that physical whole-body rotations, which stimulate the vestibular sensory organs, affected the ability of participants to perform mental spatial transformations (van Elk & Blanke 2013).

Fourth, I have argued in previous sections of this commentary that multisensory spatial coding is a critical prerequisite that underlies pre-reflective brain mechanisms of the bodily self and social cognition. Because the vestibular cortical processing has been strongly associated with multisensory integration (for review see Lopez & Blanke 2011), it is likely that vestibular signals shape multisensory spatial coding relevant to the bodily self and social cognition (Deroualle & Lopez 2014; Pfeiffer et al. 2014).

Fifth, the distributed multisensory vestibular cortical network clearly overlaps with the neural structures involved in social cognition and the bodily self, which suggests that there is a functional contribution on the part of vestibular processing to these phenomena (compare figure 1c to 1a and 1b; compare also to Deroualle & Lopez 2014).

Together, these five points suggest that the vestibular system may be a promising candidate for future studies of the sensorimotor mechanisms of social cognition, which should motivate research on the intersection of vestibular cortical processing, mirror mechanisms, and intersubjectivity. These studies may, for instance, question how vestibular stimulation affects our ability to reconstruct the process of attention of another person, a function critical in the AS framework. Although the vestibular system is related to reflexive motor control, it is not clear whether it also affects motor resonance (see Deroualle & Lopez 2014 for a related proposal). One might ask whether vestibular processing facilitates or inhibits motor resonance and our understanding of intentional action observed in others. How about vestibular contributions to theory of mind and reasoning? On the other hand, does social interaction modulate vestibular functions, such as self-motion perception, postural stabilization, and gaze control? These questions address the role of vestibular processing in functional mechanisms relevant to the AS and ES frameworks. Furthermore, empirical research addressing the causal relationship between the AS and ES brain mechanisms and the bodily self and social cognition are needed, for instance by brain lesion analysis or direct brain stimulation.

5 Conclusion

At the beginning of this paper I asked which brain mechanisms underlie pre-reflective representations of the bodily self and social cognition. ES, based on motor resonance, substantially contributes to the representation of the bodily self and social cognition. However, a unified theory of the neural basis of these target phenomena cannot assign a primary role to motor resonance. I have argued that multisensory spatial coding is at least of equal importance and probably more basic than ES in contributing to several key aspects of the bodily self and social cognition.

Specifically, I have argued that:

(1) Social cognition and the bodily self depend on multisensory spatial coding, which is distinct from motor resonance. Thus, motor resonance may be a necessary but insufficiently “primary” brain mechanism of social cognition and the bodily self (cf. section 1, 2).

(2) The brain networks underlying social cognition and the bodily self largely overlap. Specific functional associations exist (a) between motor resonance and body ownership/agency and (b) between multisensory spatial coding and self-location/the first-person perspective (cf. section 2).

(3) The vestibular system, i.e., the sensory system encoding head motion and gravity, might provide unique information used for multisensory spatial coding that relates the bodily self to other individuals and the external world. This is further suggested by the large overlap existing between the human vestibular cortex and the brain networks underlying the bodily self and social cognition (cf. section 3).

A unifying theory of pre-reflective brain mechanisms of the bodily self and social cognition must be able to account for the empirical evidence reviewed here; and it seems that such a theory cannot exclusively depend on motor resonance. Multisensory spatial coding, motor mechanisms, but also representations of the process of attention appear highly relevant to bodily self and social cognition.

I agree with Gallese & Cuccio (this collection, pp. 3–7) that cognitive neuroscience cannot fully explore these exciting topics by limiting itself to a specific neuroimaging method, such as functional magnetic resonance imaging. Instead, we should exploit multi-method approaches in search for correlative and causal evidence relating brain function and anatomy to the phenomenology of the bodily self and social cognition. The body, but also the spatial representation of the world around us, are relevant to understanding brain function, and when taken into account can lead to novel approaches to phenomenal analysis of subjective experience. But we should be careful in assigning priority to a single brain mechanism when aiming to explain the human self and intersubjectivity. Scrutiny and dialogue at the intersection of philosophy of mind and cognitive neuroscience are necessary in order to advance our understanding of the nature of the human mind.

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References

Alsmith, A. J. & Longo, M. R. (2014). Where exactly am I? Self-location judgements distribute between head and torso. *Consciousness and Cognition*, *24*, 70-74. 10.1016/j.concog.2013.12.005

Angelaki, D. E. & Cullen, K. E. (2008). Vestibular system: the many facets of a multimodal sense. *Annual Reviews in Neuroscience*, *31*, 125-150. 10.1146/annurev.neuro.31.060407.125555

Apps, M. A. & Tsakiris, M. (2013). Predictive codes of familiarity and context during the perceptual learning of facial identities. *Nature Communications*, *4* (2698), 2698-2698. 10.1038/ncomms3698

Aspell, J. E., Heydrich, L., Marillier, G., Lavanchy, T., Herbelin, B. & Blanke, O. (2013). Turning body and self inside out: Visualized heartbeats alter bodily self-consciousness and tactile perception. *Psychological Science*, *24* (12). 10.1177/0956797613498395

Beck, D. M. & Kastner, S. (2009). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Research*, *49* (10), 1154-1165. 10.1016/j.visres.2008.07.012

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, *13* (8), 556-571. 10.1038/nrn3292

Blanke, O., Ortigue, S., Landis, T. & Seeck, M. (2002). Stimulating illusory own-body perceptions. *Nature*, *419* (6904), 269-270. 10.1038/419269a

Blanke, O., Landis, T., Spinelli, L. & Seeck, M. (2004). Out-of-body experience and autoscopy of neurological origin. *Brain*, *127* (Pt 2), 243-258. 10.1093/brain/awh040

Blanke, O. & Mohr, C. (2005). Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin Implications for neurocognitive mechanisms of corporeal awareness and self-consciousness. *Brain Research Reviews*, *50* (1), 184-199. 10.1016/j.brainresrev.2005.05.008

Chalmers, D. J. (1996). *The conscious mind: In search of a fundamental theory.* Oxford, UK: Oxford University Press.

Cheyne, J. A. & Girard, T. A. (2009). The body unbound: Vestibular-motor hallucinations and out-of-body experiences. *Cortex*, *45* (2), 201-215. 10.1016/j.cortex.2007.05.002

Clark, A. (2015). Embodied prediction. In T. Metzinger & J. M. Windt (Eds.) *Open MIND* (pp. 1-21). Frankfurt a. M., GER: MIND Group.

Cullen, K. E. (2012). The vestibular system: Multimodal integration and encoding of self-motion for motor control. *Trends in Neurosciences*, *35* (3), 185-196. 10.1016/j.tins.2011.12.001

Day, B. L. & Fitzpatrick, R. C. (2005). The vestibular system. *Current Biology*, *15* (15), R583-R586. 10.1016/j.cub.2005.07.053

De Ridder, D., Van Laere, K., Dupont, P., Menovsky, T. & Van de Heyning, P. (2007). Visualizing out-of-body experience in the brain. *The New England Journal of Medicine*, *357* (18), 1829-1833. 10.1056/NEJMoa070010

Deroualle, D. & Lopez, C. (2014). Toward a vestibular contribution to social cognition. *Frontiers in Integrative Neuroscience*, *8* (16). 10.3389/fnint.2014.00016

Desimone, R. & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Reviews in Neuroscience*, *18*, 193-222. 10.1146/annurev.ne.18.030195.001205

Downar, J., Crawley, A. P., Mikulis, D. J. & Davis, K. D. (2000). A multimodal cortical network for the detection of changes in the sensory environment. *Nature Neuroscience*, *3* (3), 277-283. 10.1038/72991

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science*, *317* (5841). 10.1126/science.1142175

——— (2012). *The new handbook of multisensory processes.* Cambridge, MA: MIT Press.

Fernandez, C. & Goldberg, J. M. (1971). Physiology of peripheral neurons innervating semicircular canals of the squirrel monkey. II. Response to sinusoidal stimulation and dynamics of peripheral vestibular system. *Journal of Neurophysiology*, *34* (4), 661-675.

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *360* (2456), 815-836. 10.1098/rstb.2005.1622

Furlanetto, T., Bertone, C. & Becchio, C. (2013). The bilocated mind: New perspectives on self-localization and self-identification. *Frontiers in Human Neuroscience*, *7* (71). 10.3389/fnhum.2013.00071

Gallese, V. & Cuccio, V. (2015). The paradigmatic body. Embodied simulation, intersubjectivity and the bodily self. In T. Metzinger & J. M. Windt (Eds.) *Open MIND.* Frankfurt a. M., GER: MIND Group.

Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119* (Pt 2), 593-609. 10.1093/brain/119.2.593

Goldberg, J. M. & Fernandez, C. (1971). Physiology of peripheral neurons innervating semicircular canals of the squirrel monkey. I. Resting discharge and response to constant angular accelerations. *Journal of Neurophysiology*, *34* (4), 635-660.

Graziano, M. S. (2013). *Consciousness and the social brain.* New York, NY: Oxford University Press.

Graziano, M. S. & Kastner, S. (2011). Human consciousness and its relationship to social neuroscience: A novel hypothesis. *Cognitive neuroscience*, *2* (2), 98-113. 10.1080/17588928.2011.565121

Guterstam, A. & Ehrsson, H. H. (2012). Disowning one's seen real body during an out-of-body illusion. *Consciousness and Cognition*, *21* (2), 1037-1042. 10.1016/j.concog.2012.01.018

Hamilton, A. F., Brindley, R. & Frith, U. (2009). Visual perspective taking impairment in children with autistic spectrum disorder. *Cognition*, *113* (1), 37-44. 10.1016/j.cognition.2009.07.007

Hohwy, J. (2013). *The predictive mind.* Oxford, UK: Oxford University Press.

——— (2015). The neural organ explains the mind. In T. Metzinger & J. M. Windt (Eds.) *Open MIND* (pp. 1-23). Frankfurt a. M., GER: MIND Group.

Husserl, E. (1950). *Cartesianische Meditationen und Pariser Vorträge.* The Hague, NLD: Martinus Nijhoff Publishers.

Indovina, I., Maffei, V., Bosco, G., Zago, M., Macaluso, E. & Lacquaniti, F. (2005). Representation of visual gravitational motion in the human vestibular cortex. *Science*, *308* (5720), 416-419. 10.1126/science.1107961

Indovina, I., Maffei, V., Pauwels, K., Macaluso, E., Orban, G. A. & Lacquaniti, F. (2013). Simulated self-motion in a visual gravity field: Sensitivity to vertical and horizontal heading in the human brain. *NeuroImage*, *71*, 114-124. 10.1016/j.neuroimage.2013.01.005

Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., Gassert, R. & Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron*, *70* (2), 363-374. 10.1016/j.neuron.2011.03.009

Jeannerod, M. (2003). The mechanism of self-recognition in humans. *Behavioural Brain Research*, *142* (1-2), 1-15. 10.1016/S0166-4328(02)00384-4

Lenggenhager, B., Tadi, T., Metzinger, T. & Blanke, O. (2007). Video ergo sum: Manipulating bodily self-consciousness. *Science*, *317* (5841), 1096-1099. 10.1126/science.1143439

Lenggenhager, B., Mouthon, M. & Blanke, O. (2009).

Spatial aspects of bodily self-consciousness. *Consciousness and Cognition*, *18* (1), 110-117. 10.1016/j.concog.2008.11.003

Lenggenhager, B. & Lopez, C. (2015). Vestibular contributions to the sense of body, self and others. In T. Metzinger & J. M. Windt (Eds.) *Open MIND*. Frankfurt a. M., GER: MIND Group.

Limanowski, J. & Blankenburg, F. (2013). Minimal self-models and the free energy principle. *Frontiers in Human Neuroscience*, *7* (547). 10.3389/fnhum.2013.00547

Limanowski, J. & Hecht, H. (2011). Where do we stand on locating the self? *Psychology*, *2* (4), 312-317. 10.4236/psych.2011.24049

Lopez, C. & Blanke, O. (2011). The thalamocortical vestibular system in animals and humans. *Brain Research Reviews*, *67* (1-2), 119-146. 10.1016/j.brainresrev.2010.12.002

Lopez, C., Halje, P. & Blanke, O. (2008). Body ownership and embodiment: vestibular and multisensory mechanisms. *Clinical Neurophysiology*, *38* (3), 149-161. 10.1016/j.neucli.2007.12.006

Lopez, C., Bachofner, C., Mercier, M. & Blanke, O. (2009). Gravity and observer's body orientation influence the visual perception of human body postures. *Journal of Vision*, *9* (5), 11-14. 10.1167/9.5.1

Lopez, C., Blanke, O. & Mast, F. W. (2012). The human vestibular cortex revealed by coordinate-based activation likelihood estimation meta-analysis. *Neuroscience*, *212*, 159-179. 10.1016/j.neuroscience.2012.03.028

Lopez, C., Falconer, C. J. & Mast, F. W. (2013). Being moved by the self and others: Influence of empathy on self-motion perception. *PloS one*, *8* (1), e48293-e48293. 10.1371/journal.pone.0048293

McIntyre, J., Zago, M., Berthoz, A. & Lacquaniti, F. (2001). Does the brain model Newton's laws? *Nature Neuroscience*, *4* (7), 693-694. 10.1038/89477

Metzinger, T. (2003). *Being no one*. Boston: MIT Press.

——— (2009). Why are out-of-body experiences interesting for philosophers? The theoretical relevance of OBE research. *Cortex*, *45* (2), 256-258. 10.1016/j.cortex.2008.09.004

Newen, A. & Vogeley, K. (2003). Self-representation: Searching for a neural signature of self-consciousness. *Consciousness and Cognition*, *12* (4), 529-543. 10.1016/S1053-8100(03)00080-1

Petkova, V. I. & Ehrsson, H. H. (2008). If I were you: perceptual illusion of body swapping. *PLOS ONE*, *3* (8), e3832-e3832. 10.1371/journal.pone.0003832

Petkova, V. I., Bjornsdotter, M., Gentile, G., Jonsson, T., Li, T. Q. & Ehrsson, H. H. (2011). From part- to whole-body ownership in the multisensory brain. *Current Biology*, *21* (13), 1118-1122. 10.1016/j.cub.2011.05.022

Petkova, V. I., Khoshnevis, M. & Ehrsson, H. H. (2011). The perspective matters! Multisensory integration in ego-centric reference frames determines full-body ownership. *Frontiers in Psychology*, *2* (35). 10.3389/fpsyg.2011.00035

Pfeiffer, C., Lopez, C., Schmutz, V., Duenas, J. A., Martuzzi, R. & Blanke, O. (2013). Multisensory origin of the subjective first-person perspective: Visual, tactile, and vestibular mechanisms. *PloS one*, *8* (4). 10.1371/journal.pone.0061751

Pfeiffer, C., Schmutz, V. & Blanke, O. (2014). Visuospatial viewpoint manipulation during full-body illusion modulates subjective first-person perspective. *Experimental Brain Research*. 10.1007/s00221-014-4080-0

Pfeiffer, C., Serino, A. & Blanke, O. (2014). The vestibular system: A spatial reference for bodily self-conciousness. *Frontiers in Integrative Neuroscience*, *8* (31). 10.3389/fnint.2014.00031

Rizzolatti, G., Fadiga, L., Gallese, V. & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3* (2), 131-141.

Rizzolatti, G. & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, *11* (4), 264-274. 10.1038/nrn2805

Sciutti, A., Demougeot, L., Berret, B., Toma, S., Sandini, G., Papaxanthis, C. & Pozzo, T. (2012). Visual gravity influences arm movement planning. *Journal of neurophysiology*, *107* (12), 3433-3445. 10.1152/jn.00420.2011

Serino, A., Alsmith, A., Costantini, M., Mandrigin, A., Tajadura-Jimenez, A. & Lopez, C. (2013). Bodily ownership and self-location: Components of bodily self-consciousness. *Consciousness and Cognition*, *22* (4), 1239-1252. 10.1016/j.concog.2013.08.013

Seth, A. (2014). The cybernetic Bayesian brain: From interoceptive inference to sensorimotor contingencies. In T. Metzinger & J. W. Windt (Eds.) *Open MIND*. Frankfurt am Main: MIND Group.

Stein, B. E. & Stanford, T. R. (2008). Multisensory integration: current issues from the perspective of the single neuron. *Nature Reviews Neuroscience*, *9* (4), 255-266. 10.1038/nrn2331

Thompson, P. (1980). Margaret Thatcher: A new illusion. *Perception*, *9* (4), 483-484.

van der Hoort, B., Guterstam, A. & Ehrsson, H. H. (2011). Being Barbie: The size of one's own body determines the perceived size of the world. *PLOS ONE*, *6* (5), e20195-e20195. 10.1371/journal.pone.0020195

van Elk, M. & Blanke, O. (2013). Imagined own-body transformations during passive self-motion. *Psychological Research*, *78* (1). 10.1007/s00426-013-0486-8

Windt, J. M. (2010). The immersive spatiotemporal hallucination model of dreaming. *Phenomenology and the Cognitive Sciences*, *9* (2), 295-316. 10.1007/s11097-010-9163-1

zu Eulenburg, P., Caspers, S., Roski, C. & Eickhoff, S. B. (2012). Meta-analytical definition and functional connectivity of the human vestibular cortex. *NeuroImage*, *60* (1), 162-169. 10.1016/j.neuroimage.2011.12.032

Abbreviations

1PP	First-person perspective
BSC	Bodily self-consciousness
EEG	Electroencephalography
FBI	Full-body illusion
fMRI	Functional magnetic resonance imaging
GVS	Galvanic vestibular stimulation
OBE	Out-of-body experience
PIVC	Parieto-insular vestibular cortex
RHI	Rubber hand illusion
TPJ	Temporo-parietal junction

Acknowledgments

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Next, let me thank the collaborators who contributed to the present work: Michiel, for making me catch flames for science, making me run my first ANOVA, and showing that theory and writing are our friends. Bruno for programming the stroking robot and saving my life at the sharp end of the climbing rope. Roberto, for frequent ristretto capsule-coffee breaks and for deepening my fMRI skills. Valentin, for collecting data over the weekend and positive attitude. Petr, for having given me the opportunity to supervise your master project and for efficient work. Mariia, for your insight that some projects simply do not work and for rotator-EEG team-up. Christophe, for lightening my interest in the vestibular system. Andrea, for guidance in review writing and introducing me to peripersonal space. Thomas Metzinger, for actually having a theory, and dragging me into my first single author publication. Julio, for building the robot and fixing it (sometimes). Fosco, for teaching me lemanic-style EEG and for software (i.e. every problem needs its own software). Jean-Paul, for efficient work, and availability for drinks. Silvio, for your Neuron paper paving my way through parts of my PhD studies.

Last but not least, my deepest gratitude goes to my family: Gwendoline, for your love, support, our marriage, and two wonderful children. Noemi, for your energy and curiosity. Nathanael, for being with us, healthy. Maria, Hilde, Evelyn, for always having stayed close although at distant locations. Evelyne and Herve for food supply, helping hands, and interest.

Curriculum Vitae

Christian Pfeiffer, Dipl.-Psych., Ph.D. Candidate in Cognitive Neuroscience

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RESEARCH INTERESTS

I am interested in the interrelationship between consciousness, the self, spatial perception, body representation, multisensory processing, and the vestibular system.

EDUCATION

04/2010 – present	**Doctoral studies** in cognitive neuroscience, EPFL, Lausanne, Switzerland.
03/2010	**Diploma in Psychology** (equivalent to a Master's Degree) Free University, Berlin, Germany. Thesis title: "*Sensorimotor language processing: Behavioral and neural correlates of embodied lexical representations*." Grade: 1.2 = A, the best grade possible is 1 = A; Advisors: H. Bekkering, M. Niedeggen
09/2008 – 03/2010	**University studies in Psychology**, Free University, Berlin, Germany
09/2007 – 09/2008	**University studies in Cognitive Neuroscience** (Master Program), Radboud University, Nijmegen, The Netherlands.
03/2005	**Pre-diploma in Psychology**, Free University, Berlin, Germany Grade: 1.7 = B, the best grade possible is 1 = A
04/2003	**University studies in Psychology**, Free University, Berlin, Germany.
10/2003 – 09/2007	**High school diploma (German Abitur)**, Martinus-Gymnasium, Linz am Rhein, Germany. Grade: 1.7 = B, the best grade possible is 1 = A

POSITIONS SINCE 2007

04/2010 – present	**Doctoral student**, Laboratory of Cognitive Neuroscience, Swiss Federal Institute of Technology (EPFL); conducting experimental and neuroimaging work in various projects investigating bodily perception; mentored by O. Blanke
10/2008 – 03/2010	**Research assistant**, Neurophysics Group, Department of Neurology, Charite Campus Benjamin Franklin, Berlin, Germany; working on electrical neuroimaging (EEG) and visual perception; mentored by G. Curio and R. Schubert
09/2007 – 09/2008	**Internship and Diploma project**, Action Semantics Group, Donders Institute, Nijmegen, The Netherlands; conducting several experimental and functional neuroimaging (fMRI) studies on action and language; mentored by H. Bekkering, S.-A. Rueschemeyer, and M. van Elk

PUBLICATIONS

FORTHCOMING JOURNAL ARTICLES

[1] Pfeiffer C, Grivaz P, Serino A, Herbelin B, Blanke O (in preparation). *Visual gravity contribution to subjective first-person perspective*.

[2] Pfeiffer C, Van Elk M, Bernasconi F, Blanke O (under review). *Distinct vestibular effects on early and late somatosensory cortical processing in humans*. **Under review at The Journal of Neurophysiology.**

[3] Pfeiffer C, Lopez C, Bernasconi F, Blanke O (in preparation). *Vestibular modulation of visual cortical processing*.

[4] Noel J-P, Pfeiffer C, Serino A, Blanke O (under review). *Peripersonal space as the space of the bodily self*. **Under review at Cognition**.

[5] Pfeiffer C, Noel J-P, Serino A, Blanke O (in preparation). *Vestibular stimulation modulates peripersonal space boundaries*.

PEER-REVIEWED JOURNAL ARTICLES

[1] Pfeiffer C (2015). *Multisensory mechanisms of the bodily self and social cognition – A commentary on Vittorio Gallese and Valentina Cuccio*. In Metzinger T & Windt J M (Eds.) **Open MIND**: 14(C). Frankfurt am Main: MIND Group

[2] Pfeiffer C, Schmutz V, Blanke O (2014). *Visuospatial viewpoint manipulation during full-body illusion modulates subjective first-person perspective*. **Experimental Brain Research**. 232(12):4021-33. doi: 10.1007/s00221-014-4080-0.

[3] Pfeiffer C, Serino A, Blanke O (2014). *The vestibular system: a spatial reference for bodily self-consciousness*. **Frontiers in Integrative Neuroscience.** 8:31. doi: 10.3389/fnint.2014.00031.

[4] Romano D, Pfeiffer C, Maravita A, Blanke O (2014). *Illusory self-identification with an avatar reduces arousal responses to painful stimuli*. **Behavioural Brain Research**. 261:275-81. doi: 10.1016/j.bbr.2013.12.049.

[5] Salomon R, Lim M, Pfeiffer C, Gassert R, Blanke O (2013). *Full body illusion is associated with widespread skin temperature reduction*. **Frontiers in Behavioral Neuroscience**. 7:65. doi: 10.3389/fnbeh.2013.00065.

[6] Pfeiffer C, Lopez C, Schmutz V, Duenas J, Martuzzi R, Blanke O (2013). *Multisensory origin of the subjective first-person perspective: visual, tactile, and vestibular mechanisms*. **Plos One**. 8(4):e61751. doi: 10.1371/journal.pone.0061751. Print 2013.

[7] Duenas J, Chapuis D, Pfeiffer C, Martuzzi R, Ionta S, Blanke O, Gassert R (2012). *Neuroscience robotics to investigate multisensory integration and bodily awareness*. **Conference Proceedings IEEE Engineering in Medicine and Biology**. 2011:8348-52. doi: 10.1109/IEMBS.2011.6092059.

[8] Pfeiffer C, Palluel E, Blanke O (2011). *Neuroscience of bodily self-consciousness*. **Vereinigung der Schweizer Hochschuldozierenden Bulletin**. 2:25-29.

[9] Van Elk M, Paulus M, Pfeiffer C, van Schie HT, Bekkering H (2011). *Learning to use novel objects: a training study on the acquisition of novel action representations*. **Consciousness and Cognition**. 20(4):1304-14. doi: 10.1016/j.concog.2011.03.014.

[10] Rueschemeyer S-A, Pfeiffer C, Bekkering H (2010). *Body schematics: on the role of the body schema in embodied lexical-semantic representations*. **Neuropsychologia**. 48(3):774-81. doi: 10.1016/j.neuropsychologia.2009.09.019.

REVIEWING

Neuropsychologia (1 paper), Experimental Brain Research (1 paper), Plos One (1 paper), Frontiers in Psychology (1 paper), Multisensory Research (1 paper), Open Mind Project, http://open-mind.net (2 papers), Das Gehirn Project, http://dasgehirn.info (1 article)

FUNDING

06/2012	**Funding for conference fees and travel expenses; 16th** Annual Meeting of Young Philosophers of Mind, Frankfurt, Germany; value: **300 EUR.**
06/2011	**Funding for conference fees and travel expenses; 15th** Annual Conference of the Association of the Scientific Study of Consciousness, Kyoto, Japan; value: **1,600 CHF.**

01/2011 **Funding for conference fees and travel expenses;** Feldenkrais Science Symposium, Berlin, Germany; value: **100 EUR.**

09/2007 - 09/2008 **Scholarship from the ERASMUS Program of the European Union;** awarded a monthly stipend for university studies at Raboud University, Nijmegen, The Netherlands; value: **3,600 EUR**.

ADVISING

05/2010 – 02/2014 **Advising M.A. / B.A. students, & interns** (5 students).

TEACHING

10/2010 – 08/2011 **Courses and laboratory exercises** (M.A. program: *Neuroscience III*; B.A. program: *Neuroscience for Engineers, EEG Recording in Physiology Laboratory Exercises, Introduction to Life Sciences*) in the department of Life Sciences, EPFL, Lausanne, Switzerland.

INVITED PRESENTATIONS

05/2014 **La journee de movement et de l'equilibre**, talk in French entitled: *Moi, mon corp (virtuel) et le cerveau.* Bussigny, Switzerland.

04/2014 3rd **International Congress on Epilepsy, Brain and Mind**, talk entitled: *From epilepsy to neuroscience of bodily self-consciousness*. Brno, Czech Republic.

05/2013 8th **Annual Meeting of the German-Swiss-Austrian Society for Epileptology**, talk entitled: *Autoscopy in the context of body perception and consciousness*. Interlaken, Switzerland.

04/2013 **Interdisciplinary workshop on consciousness research** "Befluegeltes Gehirn – Spielformen des Bewusstseins", talk entitled: *Cognitive neuroscience of bodily self-consciousness*. Ascona, Switzerland.

06/2012 16th **Annual Meeting of Young Philosophers of Mind**, talk entitled: *The multisensory first-person perspective: Individual differences in visuo-vestibular integration support minimal phenomenal selfhood.* Frankfurt, Germany.

01/2011 **Annual Meeting of the Feldenkrais Society**, talk entitled: *The body in the brain: Multisensory basis the bodily self*. Berlin, Germany.

REGULAR CONFERENCE PRESENTATIONS

- Pfeiffer C, Van Elk M, Bernasconi F, Blanke O (2015, January). *Spatiotemporal brain dynamics underlying vestibular modulation of somatosensory processi*ng. **Poster presented twice:** at the Annual Alpine Brain Imaging Meeting, Les Diablerets, Switzerland, and at the Annual Meeting of the Swiss Society for Neuroscience, Fribourg, Switzerland.

- Pfeiffer C, Noel J-P, Serino A, Blanke O (2014, April). *Passive whole-body rotation shapes peripersonal space*. **Poster presentation** at the Neural Control of Movement 24th Annual Meeting, Amsterdam, The Netherlands.

- Pfeiffer C, Van Elk M, Blanke O (2013, November). *Vestibular inhibition of somatosensory cortical processing in humans: A high-density EEG study*. **Poster presentation** at the Annual Meeting of the Society for Neuroscience, San Diego, United States.

- Pfeiffer C, Van Elk M, Blanke O (2013, September). *Vestibular modulation of somatosensory cortical processing as revealed by high-density EEG*. **Oral presentation** at the Lemanic Neuroscience Annual Meeting, Les Diablerets, Switzerland.

- Pfeiffer C, Martuzzi R, Duenas J, Gassert R, Blanke O (2011, June). *Upside Down: Visuo-vestibular conflict induces illusory changes in the experienced direction of the first-person perspective.* **Oral presentation and poster presentation** at the 15th annual meeting of the Association for the Scientific Study of Consciousness, Kyoto, Japan.

- Duenas J, Chapuis D, Pfeiffer C, Martuzzi R, Ionta S, Blanke O, Gassert R (2011, September). *Neuroscience robotics to investigate multisensory integration and bodily awareness.* **Poster presentation** (by Julio Duenas) at the 33rd annual international conference of the IEEE Engineering in Medicine and Biology Society, Boston, USA.

- Pfeiffer C, Martuzzi R, Duenas J, Gassert R, Blanke O. (2010, October). *Visual gravity information in a virtual body modulates bodily self-consciousness.* **Poster presentation** at the Lemanic Neuroscience Annual Meeting, Geneva, Switzerland.

- Pfeiffer C, Rueschemeyer S-A, Bekkering H (2008, June). *Body schematics: On the relation between object knowledge and movement direction.* **Oral presentation** at the Interdisciplinary Summer School on Body Representation 'The Sense of Body', Bologna, Italy.

- Pfeiffer C, van Elk M, Paulus M, van Schie HT, Bekkering H (2008, February). *Function learning: Acquisition of action knowledge about novel actions.* **Poster presentation** at the 1st annual Cognitive Neuroscience Conference, Raboud University, Nijmegen, The Netherlands.

RESEARCH TECHNIQUES AND PROGRAMMING SKILLS

- **Electrical neuroimaging** (EEG): Evoked potentials, frequency analysis, source estimations

- **Functional neuroimaging** (fMRI): Blocked and event-related designs, multivariate analysis.

- **Structural neuroimaging** (MRI): Voxel-based morphometry.

- **Vestibular stimulation**: Whole-body motion platform, galvanic vestibular stimulation (GVS).

- **Somatosensory stimulation**: median nerve electrical stimulation, muscle tendon vibration.

- **Programming** in MATLAB (e.g. SPM8, EEGlab, Statistics toolbox), PYTHON (i.e. OpenGL, VisionEgg, ExpyVR), CARTOOL (and STEN, RAGU), LABVIEW, Presentation, Eprime, and SPSS.

SELECTED COURSES

05/2013	**Research proposal writing.** Lecturer: G. Margaritondo, Lausanne, Switzerland.
02/2013	**Academic writing.** Lecturer: A. Bless, Lausanne, Switzerland.
10/2012	**Machine learning.** Online course from Stanford University. Lecturer: Andrew Ng, Lausanne, Switzerland.
06/2012	**Advanced topics in fMRI in cognitive and clinical neuroscience**. Graduate course. Lecturer: P. Vuilleumier, Geneva Neuroscience Center, Switzerland.
05/2012	**Social cognition, engagement and the second-person-perspective**, Conference, University of Cologne, Germany.
04/2012	**Statistic Parametric Mapping (SPM) course**, on structural neuroimaging data analysis. Lecturer: B. Draganski, University of Lausanne, Switzerland.
02/2012	**Swiss real-time fMRI neurofeedback conference**, Eidgenössische Technische Hochschule, Zurich, Switzerland.

LANGUAGE SKILLS

- **German** (mother tongue)
- **English** (negotiation level – almost like mother tongue)
- **French** (fluent)
- **Dutch** (basic)

PRESS RELEASE

- Newspaper article on own work and other work from my laboratory: Neue Züricher Zeitung (2011). Title: *Grenzen des Körperbewusstseins austesten.*