Vestibular Contributions to the Sense of Body, Self, and Others

Bigna Lenggenhager & Christophe Lopez

There is increasing evidence that vestibular signals and the vestibular cortex are not only involved in oculomotor and postural control, but also contribute to higher-level cognition. Yet, despite the effort that has recently been made in the field, the exact location of the human vestibular cortex and its implications in various perceptional, emotional, and cognitive processes remain debated. Here, we argue for a vestibular contribution to what is thought to fundamentally underlie human consciousness, i.e., the bodily self. We will present empirical evidence from various research fields to support our hypothesis of a vestibular contribution to aspects of the bodily self, such as basic multisensory integration, body schema, body ownership, agency, and self-location. We will argue that the vestibular system is especially important for global aspects of the self, most crucially for implicit and explicit spatiotemporal self-location. Furthermore, we propose a novel model on how vestibular signals could not only underlie the perception of the self but also the perception of others, thereby playing an important role in embodied social cognition.

Keywords
Agency | Bodily self | Consciousness | Interoception | Multisensory integration | Ownership | Self-location | Vestibular system

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1 Introduction

There is an increasing interest from both theoretical and empirical perspectives in how the central nervous system dynamically represents the body and how integrating bodily signals arguably gives rise to a stable sense of self and self-consciousness (e.g., Blanke & Metzinger 2009; Blanke 2012; Gallagher 2005; Legrand 2007; Metzinger 2007; Seth 2013). Discussion of the "bodily self"—which is thought to be largely pre-reflective and thus independent of higher-level aspects such as language and cognition—has played an important role in various theoretical views (e.g., Alsmith 2012; Blanke 2012; Legrand 2007; Metzinger 2003; Metzinger 2013; Serino et al. 2013). For example in the conceptualisation of minimal phenomenal selfhood (MPS), which constitutes the simplest form of self-consciousness, Blanke & Metzinger (2009) suggested three key features of the MPS: a globalized form of identification with the body

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as a whole (as opposed to ownership for body parts), self-location—by which one's self seems to occupy a certain volume in space at a given time—and a first-person perspective that normally originates from this volume of space.[1] In recent years, an increasing number of studies has tried to manipulate and investigate these aspects of the minimal self as well as other aspects of the bodily self empirically. This chapter aims to show that including the oft-neglected vestibular sense of balance (Macpherson 2011) into this research might enable us to enrich and refine such empirical research as well as its theoretical models and thus gain further insights into the nature of the bodily self. We agree with Blanke & Metzinger (2009) that self-identification, self-location, and perspective are fundamental for the sense of a bodily self and argue that exactly these components are most strongly influenced by the vestibular system. Yet, we additionally want to stress that the phenomenological sense of a bodily self is—at least in a normal conscious waking state—much richer and involves various fine-graded and often fluctuating bodily sensations. We will thus also describe how the vestibular system might contribute to these (maybe not minimal) aspects of bodily self (e.g., the feeling of agency).

The aim of this book chapter is thus to combine findings from human and non-human animal vestibular research with the newest insights from neuroscientific investigations of the sensorimotor foundations of the sense of self. We present several new experimentally testable hypotheses out of this convergence, especially regarding the relation between vestibular coding and the sense of self-location. We first describe the newest advances in the field of experimental studies of the bodily self (section 2) and give a short overview of vestibular processing and multisensory integration along the vestibulo-thalamo-cortical pathways (section 3). In section 4, we present several lines of evidence and hypotheses on how the vestibular system contributes to various bodily experiences thought to underpin our sense of bodily self. We conclude this section by suggesting that the vestibular system not only contributes to the sense of self, but may also play a significant role in self-other interactions and social cognition.

2 Multisensory mechanisms underlying the sense of the body and self

How the body shapes human conscious experience is an old and controversial philosophical debate. Yet, recent theories converge on the importance of sensory and motor bodily signals for the experience of a coherent sense of self and hence for self-consciousness in general (Berlucchi & Aglioti 2010; Bermúdez 1998; Blanke & Metzinger 2009; Carruthers 2008; Gallagher 2000; Legrand 2007; Metzinger 2007; Tsakiris 2010). Even the emergence of self-consciousness in infants has been linked to their ability to progressively detect intermodal congruence (e.g., Bahrick & Watson 1985; Filippetti et al. 2013; Rochat 1998).[2] The assumption that multisensory integration of bodily signals underpins the sense of a bodily self has opened up—next to clinical research—a broad and exciting avenue of experimental investigations in psychology and cognitive neuroscience as well as interdisciplinary projects integrating philosophy and neuroscience. Experiments in these fields typically provided participants with conflicting information about certain aspects of their body and assessed how it affected implicit and explicit aspects of the body and self. The first anecdotal evidence of an altered sense of self through exposure to a multisensory conflict dates back at least to the nineteenth century with the work of Stratton (1899). More systematic, well-controlled paradigms from experimental psychology have gained tremendous influence since the first description of the *rubber*

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[1] Jennifer Windt (2010) suggested, based on dream research, an even more basic form of minimal phenomenal selfhood, which she defined as a "sense of immersion or of (unstable) location in a spatiotemporal frame of reference", thus not needing a global full-body representation (see also Metzinger 2013, 2014 for an interesting discussion of this view). We believe that for this more basic sense of a self especially, the vestibular system should be of importance, as a vestibular signal unambiguously tells us that our self was moving (i.e., change in self-location and perspective) without an actual sensation from the body (i.e., a specific body location as it is the case in touch, proprioception, or pain).

[2] It is interesting to note for the frame of this chapter that these authors describe the importance of the detection of coherence of all self-motion specific information (including the vestibular system), despite the fact that their experimental setup involved only proprioceptive and visual information (leg movements in a sitting position).

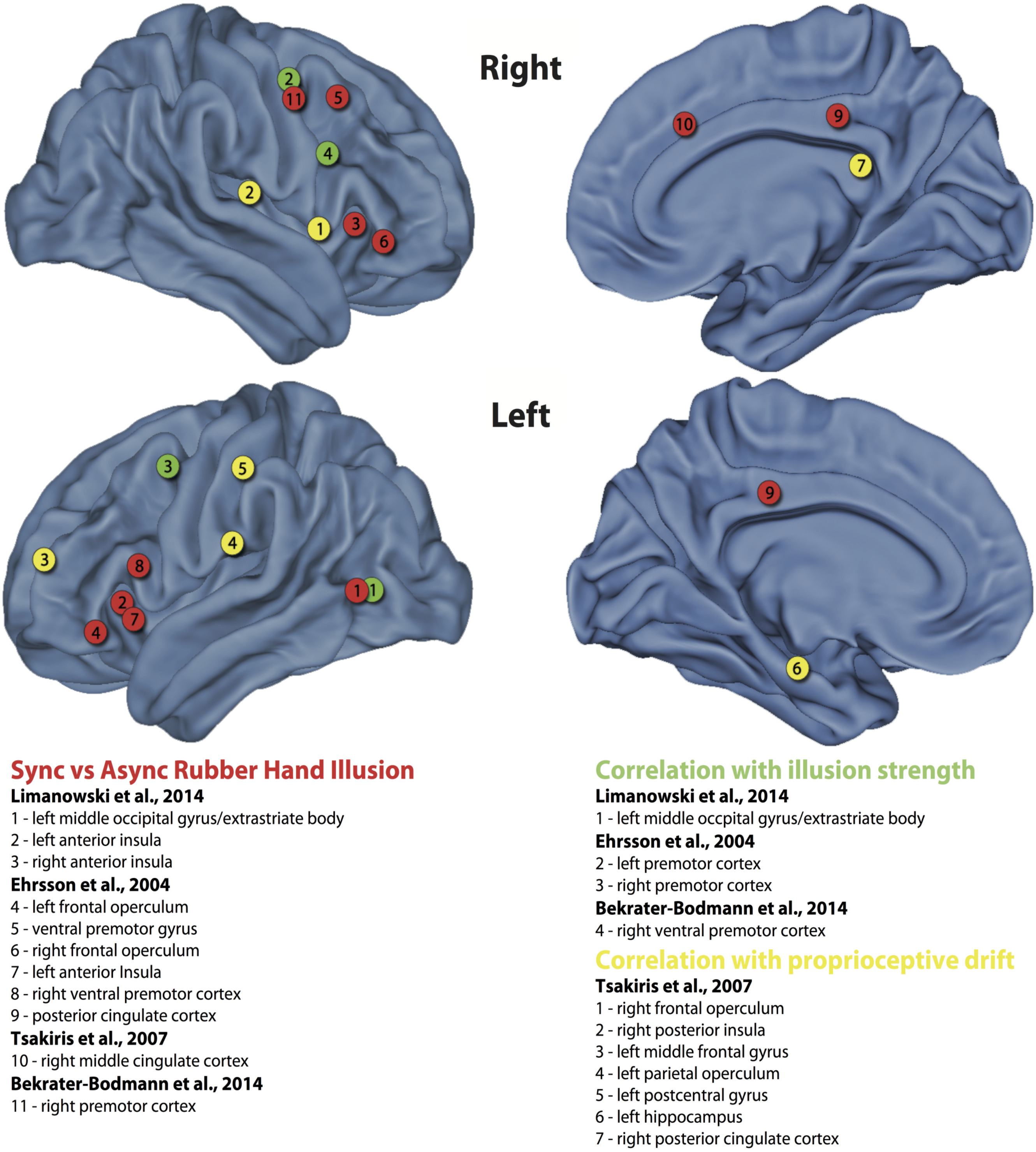

Figure 1: An overview of brain imaging studies of the rubber hand illusion (Bekrater-Bodmann et al. 2014; Ehrsson et al. 2004; Limanowski et al. 2014; Tsakiris et al. 2006). Red circles indicate significant brain activation in the comparison of synchronous visuo-tactile stimulation (illusion condition) to the control asynchronous visuo-tactile stimulation. Green circles indicate brain areas where the hemodynamic response correlates with the strength of the rubber hand illusion. Yellow circles indicate areas that significantly correlate with the proprioceptive drift. For the generation of the figure, MNI coordinates were extracted from the original studies and mapped onto a template with caret (http://www.nitrc.org/projects/caret/ (van Essen et al. 2001)).

hand illusion seventeen years ago (Botvinick & Cohen 1998). Since then, different important components underlying the bodily self have been identified, described, and experimentally modified. Most prominently: *self-location*—the feeling of being situated at a single location in space; *first-person perspective*—the centeredness of the subjective multidimensional and multimodal experiential space upon one's own body (Vogeley & Fink 2003); *body ownership*—the sense of ownership of the body (Blanke & Metzinger 2009; Serino et al. 2013); and *agency*—the sense of being the agent of one's own actions (Jeannerod 2006). In this section, we briefly describe these components of the bodily self as well as experimental paradigms that allow their systematic manipulation and investigation of their underlying neural mechanisms. Later, in section 4, we will describe how and to what extent vestibular signals might influence these components as well as their underlying multisensory integration.

2.1 Ownership, self-location, and the first-person perspective

2.1.1 Body part illusions

Both ownership and self-location[3] have traditionally been investigated in healthy participants using the rubber hand illusion paradigm (Botvinick & Cohen 1998). Synchronous stroking of a hidden real hand and a seen fake hand in front of a participant causes the fake hand to be self-attributed (i.e., quantifiable subjective change in ownership) and the real hand to be mis-localized towards the rubber hand (i.e., objectively quantifiable change in self-location). During the last ten years, various other correlates of the illusion have been described. For example, illusory ownership for a rubber hand is accompanied by a reduction of the skin temperature of the real hand (Moseley et al. 2008), an increased skin conductance and activity in pain-related neural networks in response to a threat toward the rubber hand (Armel & Ramachandran 2003; Ehrsson et al. 2007), and increased immune response to histamine applied on the skin of the real hand (Barnsley et al. 2011). Several variants of the illusion have been established using conflicts between tactile and *proprioceptive information,*[4] between visual and nociceptive information (Capelari et al. 2009), between visual and *interoceptive information*, and between visual and motor information (Tsakiris et al. 2007). All these multisensory manipulations have in common that they can induce predictable changes in the implicit and explicit sense of a bodily self. Yet, the question of what components of the bodily self are really altered during such illusions and how the various measures relate to them is still under debate. Longo et al. (2008) used a psychometric analysis of an extended questionnaire presented after the induction of the rubber hand illusion to identify three components of the illusion: (1) *ownership*, i.e., the perception of the rubber hand as part of oneself; (2) *location*, i.e., the localization of one's own hand or of touch applied to one's own hand in the position of the rubber hand; and (3) *sense of agency*, i.e., the experience of control over the rubber hand. These different components seem also to be reflected in differential neural activity as revealed by recent functional neuroimaging studies.[5]

Figure 2 summarizes the main brain regions found to be involved in the rubber hand illusion during functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) studies (Bekrater-Bodmann et al. 2014; Ehrsson et al. 2004; Limanowski et al. 2014; Tsakiris et al. 2006). The activation patterns depend on how the illusion was quantified. The pure contrast of the illusion condition (i.e., synchronous stroking) to the control condition reveals a network including the insular, cingulate, premotor, and lateral occipital (extrastriate body area) cortex. Areas in which haemodynamic responses correlate with the strength of illusory ownership include the premotor cortex

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[3] This component is in such context usually termed self-location, but a more accurate formulation is "body part location with respect to the self" (Blanke & Metzinger 2009; Lenggenhager et al. 2007).

[4] Proprioception classically refers to information about the position of body segments originating from muscle spindles, articular receptors, and Golgi tendon organs, while interoception refers to information originating from internal organs such as the heart, gastrointestinal tract, and bladder.

[5] The sense of agency has not yet been investigated using neuroimaging studies in the context of the rubber hand illusion.

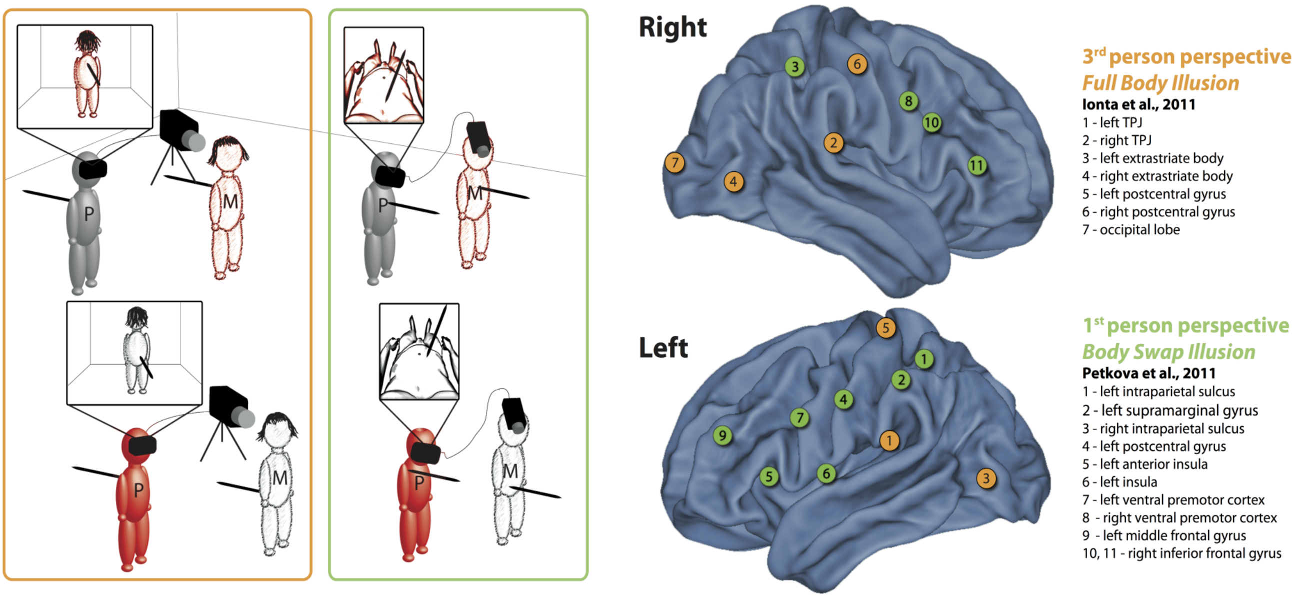

Figure 2: A comparison of brain activity associated with two illusions targeting the manipulation of more global aspects of the bodily self, i.e., the full body illusion (Lenggenhager et al. 2007, setup in orange frame) and the body swap illusion (Petkova & Ehrsson 2008, setup in green frame). In both variants of the illusion, synchronous stroking of one's own body and the seen mannequin led to self-identification with the latter (locus of self-identification is indicated in red colour). Two recent fMRI studies using either the full body illusion (Ionta et al. 2011 in orange circles) or the body swap illusion (Petkova et al. 2011, in green circles) are compared and plotted. Only areas significantly more activated during synchronous visuo-tactile stimulation (illusion condition), as compared to control conditions, are shown. For the generation of the figure, MNI coordinates were extracted from the original studies and mapped onto a template with caret (http://www.nitrc.org/projects/caret/). Adapted from Serino et al. 2013, Figure 2.

and extrastriate body area, whereas illusory mis-localization of the physical hand (referred to as "proprioceptive drift") correlates particularly with responses in the right posterior insula, right frontal operculum, and left middle frontal gyrus (see figure 1 for the detailed list). The fact that different brain regions are involved in illusory ownership and mis-localization of the physical hand provides further evidence for distinct sub-components underlying the bodily self.

2.1.2 Full-body illusions

Several authors claimed that research on body part illusions is unable to provide insight into the mechanisms of global aspects of the bodily self, such as self-identification with a body as a whole, self-location in space, and first-person perspective (e.g., Blanke & Metzinger 2009; Blanke 2012; Lenggenhager et al. 2007). Thus, empirical studies have more recently adapted the rubber hand illusion paradigm to a *full-body illusion* paradigm where the whole body (instead of just a body part) is seen using video-based techniques and virtual reality.

Two main versions of multisensory illusions targeting more global aspects of the self have been used (but see also Ehrsson 2007), one in which the participants saw the back-view of their own body (or a fake body) in front of them as if it were seen from a third-person perspective (full-body illusion [see figure 2, orange frame]; Lenggenhager et al. 2007) and one in which a fake body was seen from a first-person perspective (body swap illusion [see figure 2 green frame; Petkova & Ehrsson 2008]). In both versions of the illusion, synchronous visuo-tactile stroking of the fake and the real body increased self-identification (i.e., full-body ownership)[6] with a virtual or fake body as compared

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[6] While these experiments are targeting illusory full-body ownership, it has recently been criticized (Smith 2010; see also Metzinger 2013) that it has not empirically been shown that it really

to asynchronous stroking. Importantly, it has been argued that only the former is associated with a change in self-location[7] (Aspell et al. 2009; Lenggenhager et al. 2007; Lenggenhager et al. 2009) and in some cases with a change in the direction of the first-person visuo-spatial perspective (Ionta et al. 2011; Pfeiffer et al. 2013).

A recent psychometric approach identified three components of the bodily self in a full-body illusion set up: bodily self-identification, space-related self-perception, which is closely linked to the feeling of presence in a virtual environment (see section 4.5.1.3), and agency (Dobricki & de la Rosa 2013). Again, these subcomponents seem to rely on different brain mechanisms. Figure 2 contrasts two recent brain imaging studies using full-body illusions (see Serino et al. 2013, for a more thorough comparison). While self-identification with a fake body seen from a first-person perspective is associated with activity in premotor areas (Petkova et al. 2011), changes in self-location and visuo-spatial perspective are associated with activity in the temporo-parietal junction (TPJ) (Ionta et al. 2011). The TPJ is a region located close to the parieto-insular vestibular cortex (see section 3.2.3), suggesting that the vestibular cortex might play a role in the experienced self-location and visuo-spatial perspective, as we will elaborate on in the following sections.

2.2 Agency

Agency, the feeling that one is initiating, executing, and controlling one's own volitional actions, has been described as another key aspect of the bodily self and self-other discrimination (Gallagher 2000; Jeannerod 2006; Tsakiris et al. 2007). Experimental investigations of the sense of agency started in the 1960s with a study by Nielsen (1963) In this seminal study, as well as in follow-up studies, a spatial or a temporal bias was introduced between a physical action (e.g., reaching movement toward a target) and the visual feedback from this action (Farrer et al. 2003b; Fourneret & Jeannerod 1998). These studies measured the degree of discrepancy for which the movement is still self-attributed. Theories of the sense of agency have mostly been based on a "forward model," which has been defined in a predictive coding framework (Friston 2012). The forward model uses the principle of the *efference motor copy*, which is a copy from the motor commands predicting the sensory consequences of an action. Such efference copies allow the brain to distinguish self-generated actions from externally generated actions (Wolpert & Miall 1996). This idea is supported by a large body of empirical evidence showing that the sense of agency increases with increasing congruence of predicted and actual sensory input (e.g., Farrer et al. 2003a; Fourneret et al. 2001). Neurophysiological and brain imaging studies showed a reduction of activation in sensory areas in response to self-generated, as compared to externally generated, movements (e.g., Gentsch & Schütz-Bosbach 2011). As well as suppression of activity in specific sensory areas, agency has also been linked to activity in a large network including the ventral premotor cortex, supplementary motor area, cerebellum, dorsolateral prefrontal cortex, posterior parietal cortex, posterior superior temporal sulcus, angular gyrus, and the insula (David et al. 2006; Farrer et al. 2008; Farrer et al. 2003a).

While studies on agency have almost exclusively investigated agency for arm and hand movements, a recent study has addressed "full-body agency" during locomotion using full-body tracking and virtual reality (Kannape et al. 2010). As the vestibular system is importantly involved in locomotion, we will argue for a strong implication of the vestibular system in full-body agency during locomotion (see section 4.4).

3 The vestibular system

In this section, we describe the basic mechanisms of the peripheral and central vestibular

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affects the full body (as opposed to just certain body parts). We agree that this argument is justified and that further experiments are needed to address this issue (see also Lenggenhager et al. 2009).

[7] Similarly to the rubber hand illusion, changes in self-location and self-identification have been associated with physiological changes such as increased pain thresholds, decreased electrodermal response to pain (Romano et al. 2014), and decreased body temperature (Salomon et al. 2013).

system for coding self-motion and self-orientation, as we believe that these aspects are crucial bases for a sense of the bodily self. It is, however, beyond the scope of this paper to provide a comprehensive description of the vestibular system anatomy and physiology, and the reader is referred to recent review articles (e.g., Angelaki & Cullen 2008; Lopez & Blanke 2011).

3.1 Peripheral mechanisms

The peripheral vestibular organs in the inner ear contain sensors detecting three-dimensional linear motions (two otolith organs) and angular motions (three semicircular canals). The characteristic of these sensors is that they are *inertial sensors*, a type of accelerometers and gyroscopes found in inertial navigation systems. When an individual turns actively his or her head, or when the head is moved passively (e.g., in a train moving forward), the head acceleration is transmitted to the vestibular organs. Head movements create inertial forces—due to the inertia of the otoconia, the small crystals of calcium carbonate above the otolith organs, and to the inertia of the endolymphatic fluid in the semicircular canals—inducing an activation or inactivation of the vestibular sensory hair cells.

It is important to note here that the neural responses of the vestibular sensory hair cells depend on the direction of head movements with respect to head-centred inertial sensors and not with respect to any external reference. For this reason, the vestibular system enables the coding of *absolute* head motion in a *head-centred reference frame* (Berthoz 2000). This way of coding body motion differs from the motion coding done by other sensory systems. The coding by the visual, somatosensory, and auditory system is ambiguous because these sensory systems detect a body motion *relative to* an external reference, or the motion of an external object with respect to the body. For example, the movement of an image on the retina can be interpreted either as a motion of the body with respect to the visual surrounding, or as a motion of the visual scene in front of a static observer (e.g., Dichgans & Brandt 1978), leading to an ambiguous sense of ownership for the movement. Similarly, if a subject detects changes of pressures applied to his skin (e.g., under his foot soles), this can be related either to a body movement, with respect to the surface on which he is standing, or to the movement of this surface on his skin (Kavounoudias et al. 1998; Lackner & DiZio 2005). Similar observations have been made in the auditory system and illusory sensations of body motion have been evoked by rotating sounds (Väljamäe 2009). By contrast, a vestibular signal is a non-ambiguous neural signal that the head moved or has been moved; thus there is no ambiguity regarding whether the own body moved or the environment moved. It should, however, be noted that the vestibular information on its own does not distinguish between passive or active movements of the subject's whole body (i.e., the self-motion associated with the feeling of agency; see also section 4.4).[8]

The otolith organs are not only activated by head translations, such as those produced by a train moving forward or by an elevator moving upward, but also by Earth's gravitational pull. Otolith receptors are sensitive to *gravito-inertial forces* (Angelaki et al. 2004; Fernández & Goldberg 1976) and thus provide the brain with signals about head orientation with respect to gravity. Such information is crucial to maintain one's body in a vertical orientation and to orient oneself in the physical world (Barra et al. 2010).

3.2 Central mechanisms

The vestibulo-thalamo-cortical pathways that transmit vestibular information from the peripheral vestibular organs to the cortex involve several structures relaying and processing vestibular sensory signals. We describe below vestibular sensory processing in the vestibular nuclei complex, thalamus, and cerebral cortex.

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[8] As we will see below, the neural signal provided by the peripheral vestibular organs does not allow us to distinguish whether the self is (active motion) or is not (passive motion) the agent of the action. Therefore, peripheral vestibular signals are ambiguous regarding the sense of agency. Yet, comparisons with motor efference copy in several vestibular neural structures allow such distinction and provide a sense of agency.

3.2.1 The vestibular nuclei complex and thalamus

The eighth cranial nerve transmits vestibular signals from the vestibular end organs to the vestibular nuclei complex and cerebellum (Barmack 2003). The vestibular nuclei complex is located in the brainstem and is the main relay station for vestibular signals. From the vestibular nuclei, descending projections to the spinal cord are responsible for vestibulo-spinal reflexes and postural control. Ascending projections to the oculomotor nuclei support eye movement control, while ascending projections to the thalamus and subsequently to the neocortex support the vestibular contribution to higher brain functions. Vestibular nuclei are also strongly interconnected with several nuclei in the brainstem and limbic structures, enabling the control of autonomic functions and emotion (see section 4.1.3) (Balaban 2004; Taube 2007).

The role of the vestibular nuclei is not limited to a relay station for vestibular signals. Complex sensory processing takes place in vestibular nuclei neurons, involving, for example, the distinction between active, self-generated head movements and passive, externally imposed head movements (Cullen et al. 2003; Roy & Cullen 2004). As we will argue in section 4.4, this processing is likely to play a crucial role in the sense of agency, especially concerning full-body agency during locomotion. Another characteristic of the vestibular nuclei complex is the large extent of *multisensory convergence* that occurs within it (Roy & Cullen 2004; Tomlinson & Robinson 1984; Waespe & Henn 1978), which leads to the perceptual “disappearance” of vestibular signals as they are merged with eye movement, visual, tactile, and proprioceptive signals. Because there is “no overt, readily recognizable, localizable, conscious sensation” from the vestibular organs during active head movements, excluding artificial passive movements and pathological rotatory vertigo, the vestibular sense has been termed a “silent sense” (Day & Fitzpatrick 2005).

Ascending projections from the vestibular nuclei complex reach the thalamus. These projections are bilateral and very distributed as there is no thalamic nucleus specifically dedicated to vestibular processing, as compared to visual, auditory, or tactile processing.[9] Anatomical and electrophysiological studies in rodents and primates identified vestibular neurons in many thalamic nuclei (review in Lopez & Blanke 2011). Important vestibular projections have been noted in the ventroposterior complex of the thalamus, a group of nuclei typically involved in somatosensory processing (Marlinski & McCrea 2008a; Meng et al. 2007). Other vestibular projections have been identified in the ventroanterior and ventrolateral nuclear complex, intralaminar nuclei, as well as in the lateral and medial geniculate nuclei (Kotchabhakdi et al. 1980; Lai et al. 2000; Meng et al. 2001). Electrophysiological studies revealed that similarly to vestibular nuclei neurons, thalamic vestibular neurons can distinguish active, self-generated head movements from passive head movements, showing a convergence of vestibular and motor signals in the thalamus (Marlinski & McCrea 2008b).

3.2.2 Vestibular projections to the cortex

Vestibular processing occurs in several cortical areas as demonstrated as early as the 1940s in the cat neocortex and later in the primate neocortex (reviews in Berthoz 1996; Fukushima 1997; Grüsser et al. 1994; Guldin & Grüsser 1998; Lopez & Blanke 2011). Figure 3 summarizes the main vestibular areas found in the monkey and human cerebral cortex. More than ten vestibular areas have been identified to date.

Electrophysiological and anatomical studies in animals have revealed important vestibular projections to a region covering the posterior parts of the insula and lateral sulcus, an area referred to as the parieto-insular vestibular cortex (PIVC) (Grüsser et al. 1990a; Guldin et al. 1992; Liu et al. 2011). Other vestibular regions include the primary somatosensory cortex (the hand and neck somatosensory representations of postcentral areas 2 and 3 [Ödkvist et al. 1974;

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[9] Olfactory processing in the thalamus seems also to be different from processing of the main senses as there is no direct relay between sensory neurons and primary cortex, and olfactory thalamic nuclei have been identified only recently (Courtiol & Wilson 2014).

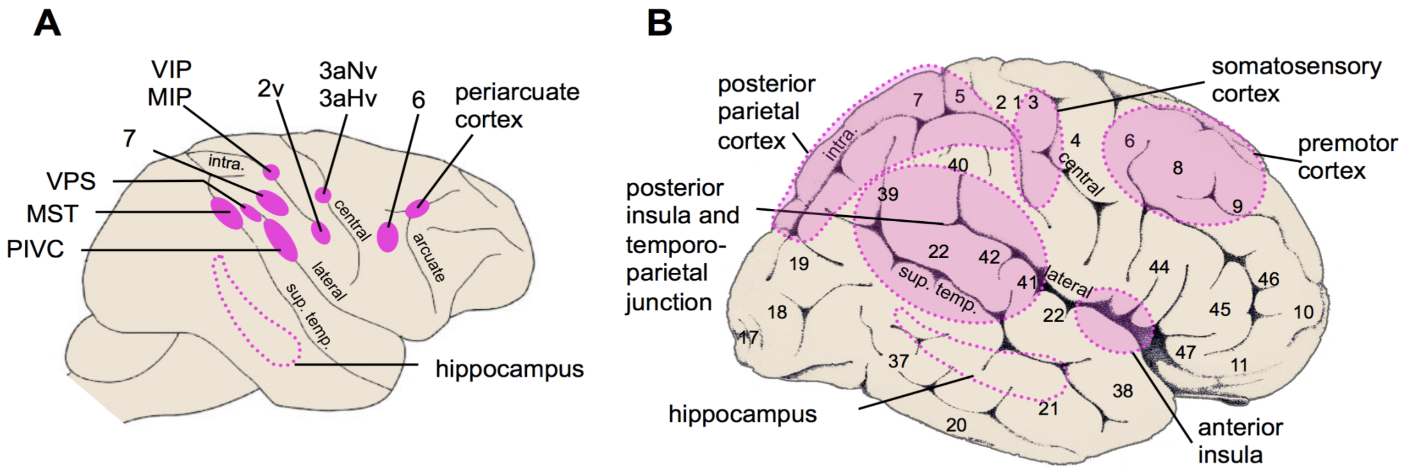

Figure 3: Schematic representation of the main cortical vestibular areas. (A) Main vestibular areas in monkeys are somatosensory areas 2v and 3av (3aHv (3a-hand-vestibular region), 3aNv (3a-neck-vestibular region)) in the postcentral gyrus, frontal area 6v and the periarcuate cortex, parietal area 7, MIP (medial intraparietal area) and VIP (ventral intraparietal area), extrastriate area MST (medial superior temporal area), PIVC (parieto-insular vestibular cortex), VPS (visual posterior sylvian area), and the hippocampus. Major sulci are represented: arcuate sulcus (arcuate), central sulcus (central), lateral sulcus (lateral), intraparietal sulcus (intra.), and superior temporal sulcus (sup. temp.). Adapted from Lopez and Blanke after Sugiuchi et al. (2005). (B) Main vestibular areas in the human brain identified by noninvasive functional neuroimaging techniques. Numbers on the cortex refer to the cytoarchitectonic areas defined by Brodmann. Adapted from Lopez & Blanke (2011) after Sugiuchi et al. (2005).

Schwarz et al. 1973; Schwarz & Fredrickson 1971]); ventral and medial areas of the intraparietal sulcus (Bremmer et al. 2001; Chen et al. 2011; Schlack et al. 2005); visual motion sensitive area MST (Bremmer et al. 1999; Gu et al. 2007); frontal cortex (motor and premotor cortex and the frontal eye fields [Ebata et al. 2004; Fukushima et al. 2006]); cingulate cortex (Guldin et al. 1992) and hippocampus (O'Mara et al. 1994). These findings indicate that vestibular processing in the animal cortex relies on a highly distributed cortical network.

A similar conclusion has been drawn from neuroimaging studies conducted in humans. These studies have used fMRI and PET during caloric and galvanic vestibular stimulation[10] and revealed that the human vestibular cortex closely matches the vestibular regions found in animals. Vestibular responses were found in the insular cortex and parietal operculum as well as in several regions of the temporo-parietal junction (superior temporal gyrus, angular and supramarginal gyri). Other vestibular activations are located in the primary and secondary somatosensory cortex, precuneus, cingulate cortex, frontal cortex, and hippocampus (Bense et al. 2001; Bottini et al. 1994; Bottini et al. 1995; Dieterich et al. 2003; Eickhoff et al. 2006; Indovina et al. 2005; Lobel et al. 1998; Suzuki et al. 2001).

It is of note that the non-human animal and human vestibular cortex differs from other sensory cortices as there is apparently no *primary vestibular cortex*; that is, there is no koniocortex dedicated to vestibular processing and containing only or mainly vestibular responding neurons (Grüsser et al. 1994; Guldin et al. 1992; Guldin & Grüsser 1998), stressing again the multisensory character of the vestibu-

[10] Caloric and galvanic vestibular stimulations are the two most common techniques to artificially (i.e., without any head or full-body movements) stimulate the vestibular receptors. Caloric vestibular stimulation was developed by Robert Bárány and consists of irrigating the auditory canal with warm (e.g., 45°C) or cold (e.g., 20°C) water (or air), creating convective movements of the endolymphatic fluid mainly in the horizontal semicircular canals. This stimulation evokes a vestibular signal close to that produced during head rotations. Galvanic vestibular stimulation consists of the application of a transcutaneous electrical current through electrodes placed on the skin over the mastoid processes (i.e., behind the ears). Galvanic vestibular stimulation is often applied binaurally, with the anode fixed behind one ear, and the cathode on the opposite side. The cathodal current increases the firing rate in the ipsilateral vestibular afferents.

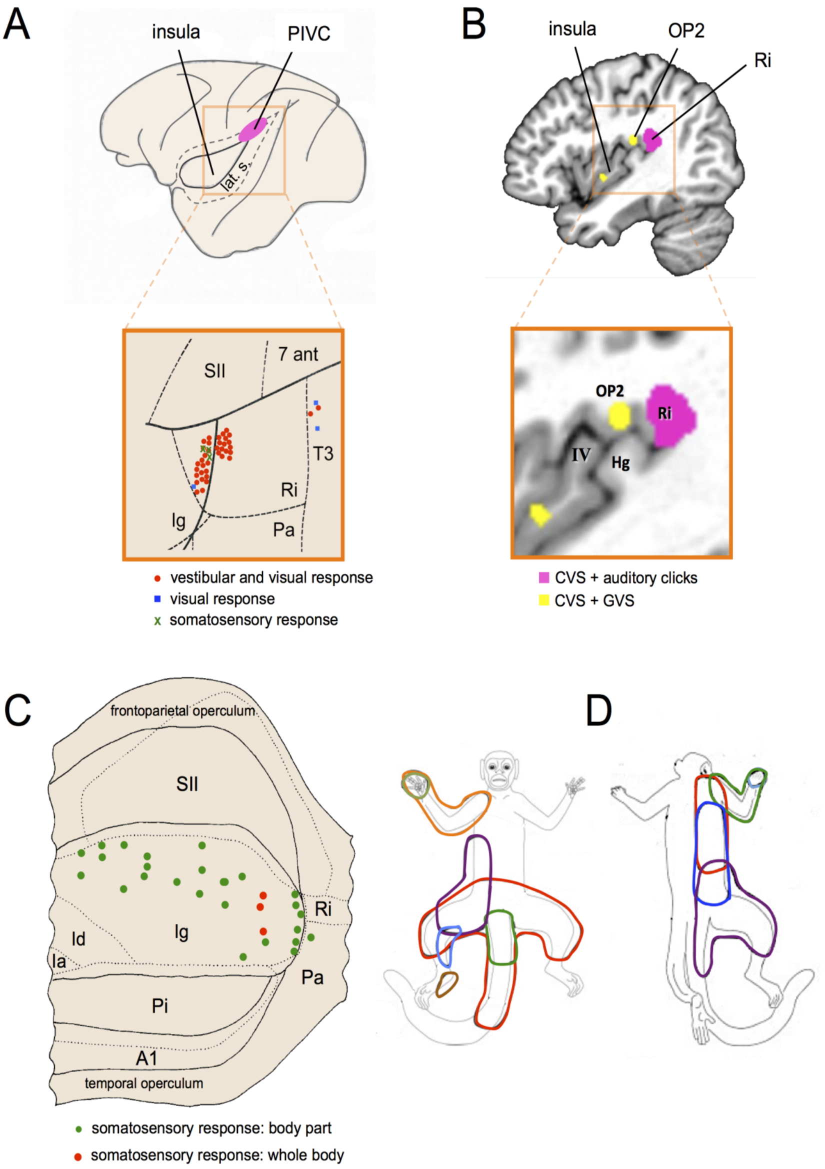

Figure 4: Anatomical location and functional properties of the parieto-insular vestibular cortex (PIVC). (A) Schematic representation of the macaque brain showing the location of the PIVC. For the purpose of illustration, the lateral sulcus (lat. s.) is shown unfolded. The macaque PIVC is located in the parietal operculum at the posterior end of the insula and retroinsular cortex. Modified from Grüsser et al. (1994). The insert illustrates the location of vestibular neurons in different regions of the lateral sulcus in a squirrel monkey (*Saimiri sciureus*). The lateral sulcus is shown unfolded to visualize the retroinsular cortex (Ri), secondary somatosensory cortex (SII), granular insular cortex (Ig), and auditory cortex (PA). Vestibular neurons (red dots) were mostly located in Ri and Ig. Adapted from Guldin et al. (1992). (B) Vestibular activations found in the human PIVC using meta-analysis of functional neuroimaging data. The Ri showed a convergence of activations evoked by caloric vestibular stimulation (CVS) of the semicircular canals and auditory activation of the otolith organs (*pink*). The parietal operculum (OP2) and posterior insula showed a convergence of activations evoked by CVS and galvanic vestibular stimulation (GVS) of all primary vestibular afferents (*yellow*). Hg (Heschl's gyrus). Adapted from Lopez et al. (2012). (C) View of the unfolded lateral sulcus of the rhesus monkey (*Macaca mulatta*) showing somatosensory neurons (*green dots*) in the granular insula, of which some have large somatosensory receptive fields covering the whole body (*red dots*). Ia (agranular insular field); Id (dysgranular insular field); A1 (first auditory field); Pa (postauditory field); Pi (parainsular field). Modified from Schneider et al. (1993). (D) Representation of the size of the receptive fields of neurons recorded in somatosensory representations of the body found in the dorsal part of the insula (ventral somatosensory area) of the titi monkey (*Callicebus moloch*). Modified from Coq et al. (2004).

lar system. All areas processing vestibular signals are multimodal, integrating visual, tactile, and proprioceptive signals. The PIVC has been shown to occupy a key role in the cortical vestibular network and is the only vestibular area that is connected to all other vestibular regions described above. The PIVC also receives signals from the primary somatosensory cortex, premotor cortex, posterior parietal cortex, and the cingulate cortex (Grüsser et al. 1994; Guldin et al. 1992), and it integrates signals from personal and extrapersonal spaces. Given these characteristics, we believe that the PIVC should be importantly involved in a coherent representation of the bodily self and the body embedded in the world.

3.2.3 The PIVC as a core, multimodal, vestibular cortex

The group of Grüsser was the first to describe vestibular responses in the monkey PIVC. Vestibular neurons were located in several regions of the posterior end of the lateral sulcus "in the upper bank of the lateral sulcus around the posterior end of the insula, sometimes also within the upper posterior end of the insula [... and] more posteriorly in the retroinsular region or more anteriorly in the parietal operculum" (Grüsser et al. 1990a, pp. 543-544; Grüsser et al. 1990b; Guldin et al. 1992; Guldin & Grüsser 1998). Figure 4A illustrates the location of PIVC in the macaque brain. Recent investigations of PIVC in rhesus monkeys revealed that vestibular neurons were mostly located in the retroinsular cortex and at the junction between the secondary somatosensory cortex, retroinsular cortex, and granular insular cortex (area Ig) (Chen et al. 2010; Liu et al. 2011).

In humans, functional neuroimaging studies used caloric and galvanic vestibular stimulation and showed activations in and around the posterior insula and temporo-parietal junction (Bense et al. 2001; Bottini et al. 1994; Dieterich et al. 2003; Eickhoff et al. 2006; Lobel et al. 1998; Suzuki et al. 2001). Because these activations also extend to the superior temporal gyrus, posterior and anterior insula, and inferior parietal lobule, the exact location of human PIVC is still debated (review in Lopez & Blanke 2011). Recent meta-analyses of vestibular activations suggest that the core vestibular cortex is in the *parietal operculum*, *retroinsular cortex,* and/or *posterior insula* (Lopez et al. 2012; zu Eulenburg et al. 2012) (figure 4B). Of note, several neuroimaging studies have also implicated the anterior insula in vestibular processing (Bense et al. 2001; Bottini et al. 2001; Fasold et al. 2002). The insula is crucial for interoceptive awareness (Craig 2009) and could provide the neural substrate for vestibulo-interoceptive interactions that impact several aspects of the bodily self (see section 4.1.3).

4 Vestibular contributions to various aspects of the bodily self

The aim of this section is to describe several mechanisms by which the vestibular system might influence multisensory mechanisms underlying the bodily self. Again, we would like to stress that the vestibular system seems of utter importance for the most minimal aspects of self-consciousness (i.e., the sense of location in a spatial reference frame) (Windt 2010; Metzinger 2013, 2014) but at the same time also contributes to our rich sense of a bodily self in daily life. We will try to include both aspects in the following section. We further point out that while some mechanisms of a vestibular contribution to the sense of a self are now accepted, others are still largely speculative. We start by pinpointing the influence of the vestibular system on basic bodily senses such as touch and pain (section 4.1, which are subjectively experienced as bodily, i.e., as coming from within one's own bodily borders, and thus importantly contribute to a sense of bodily self. We then outline evidence for a vestibular contribution to several previously identified and experimentally modified components of the multisensory bodily self: body schema and body image, body ownership, agency, and self-location (sections 4.2–4.5). On the basis of recent data on self-motion perception in a social context and on the existence of shared sensorimotor representations between one's own body and others' bodies, we propose a vestibular contribution to the socially embedded self (section 4.6).

4.1 The sensory self

4.1.1 Touch

The feeling of touch, as its subjective perception is confined within the bodily borders, is considered as crucial for the feeling of ownership and other aspects of the bodily self (Makin et al. 2008) and a loss of somatosensory signals has been associated with a disturbed sense of the bodily self (e.g., Lenggenhager et al. 2012). Vestibular processes have been shown to interact with the perception and location of tactile stimulation. Clinical studies in brain-damaged patients suffering from altered somatosensory perceptions showed transient improvement of somatosensory perception during artificial vestibular stimulation (Kerkhoff et al. 2011; Vallar et al. 1990). Furthermore, studies in healthy participants showed that caloric vestibular simulation can alter conscious perception of touch (Ferrè et al. 2011), probably due to interfering effects in the parietal operculum (Ferrè et al. 2012). A recent study further suggests that vestibular stimulations not only modify tactile perception thresholds, but also the perceived location of stimuli applied to the skin (Ferrè et al. 2013), a finding likely related to a vestibular influence on the body schema (see section 4.2).

Behavioural evidence of vestibulo-tactile interactions is in line with both human and animal physiological and anatomical data. Human neuroimaging studies identified areas responding to tactile, proprioceptive, and caloric vestibular stimulation in the posterior insula, retroinsular cortex, and parietal operculum (Bottini et al. 1995; Bottini et al. 2001; Bottini et al. 2005; zu Eulenburg 2013). Electrophysiological recordings in monkeys revealed a *vestibulo-somesthetic convergence* in most of the PIVC neurons. Bimodal neurons in the PIVC have large somatosensory receptive fields often located in the region of the neck and respond to muscle pressure, vibrations, and rotations applied to the neck (Grüsser et al. 1990b).

To date, the influence of caloric vestibular stimulation on somatosensory perception has been measured at the level of peripheral body parts only (e.g., the capacity to detect touch applied to the hand, or to locate touch on the hand), but not on more central body parts or *the entire body*. Here, we propose that vestibular signals are not only important for sensory processes and awareness of body parts, but even more for *full-body awareness*. This hypothesis is supported by findings from mapping of the posterior end of the lateral sulcus in rhesus monkey that revealed neurons in the granular field of the posterior insula with *large* and *bilateral* tactile receptive fields (Schneider et al. 1993). The range of stimuli used included brushing and stroking the hair, touching the skin, muscles and other deep structures, and manipulating the joints. Importantly, the authors noted that some neurons had receptive fields covering the entire surface of the animal body, excluding the face. As can be seen in figure 4C, those neurons (red dots) were located in the most posterior part of the insula. Functional mapping conducted in the dorsal part of the insula in other monkey species has also identified neurons with large and sometimes bilateral tactile receptive fields (Coq et al. 2004) (figure 4D). So far, there is no direct evidence that neurons with full-body receptive fields receive vestibular inputs, probably because to date few electrophysiological studies have directly investigated the convergence of vestibular and somatosensory signals in the lateral sulcus (Grüsser et al. 1990a; Grüsser et al. 1990b; Guldin et al. 1992). We hypothesize that caloric and galvanic vestibular stimulation, as well as physical head rotations and translations, are likely to interfere with populations of neurons with whole-body somatosensory receptive fields and therefore may strongly impact full-body awareness. Indeed, in daily life the basic sense of touch, especially regarding large body segments, should be crucial to experience a bodily self. While full-body tactile perception hasn't been directly assessed during vestibular stimulation, the fact that caloric vestibular stimulation in healthy participants as well as acute vestibular dysfunction can evoke the feeling of strangeness and numbness for the entire body might point in this direction (see Lopez 2013, for a review).

4.1.2 Pain

Similar to touch, the experience of pain has been described as crucial to self-consciousness and the feeling of an embodied self. In his book “Still Lives—Narratives of Spinal Cord Injury” (Cole 2004), the neurophysiologist Jonathan Cole reports the case of a patient with a spinal cord lesion who described that “the pain is almost comfortable. Almost my friend. I know it is there, it puts me in contact with my body” (p. 89). This citation impressively illustrates how important the experience of pain might be in some instances for the sense of a bodily self. Reciprocal relations between pain and the sense of self are further supported by observations of altered pain perception and thresholds during dissociative states of bodily self-consciousness, such as depersonalization (Röder et al. 2007), dissociative hypnosis (Patterson & Jensen 2003) and out-of-body experiences (Green 1968). Similarly, acting in an immersive virtual environment is also associated with an increase in pain thresholds (Hoffman et al. 2004), a fact that is now increasingly exploited in virtual reality based pain therapies. This increase in pain threshold depends on the strength of *feeling of presence* in the virtual environment, i.e., the sense of “being there,” located in the virtual environment (Gutiérrez-Martínez et al. 2011; see also section 4.5.2.1). These analgesic effects of immersion and presence in virtual realities are usually explained by attentional resource mechanisms (i.e., attention is directed to the virtual environment rather than the painful event). Yet, all described instances involve also illusory self-location which has shown in full-body illusions to be accompanied by an increasing in pain thresholds or altered arousal response to painful stimuli (Hänsel et al. 2011; Romano et al. 2014). We thus speculate that analgesic effects of immersion could also be linked to disintegrated multisensory signals and a related illusory change in self-location and global self-identification. Since the vestibular system is crucially involved in self-location (see section 4.5), we suggest that some interaction effects between altered self-location and pain may be mediated by the vestibular system.[11] Interestingly, galvanic and caloric stimulation, which also induce illusory changes in self-location, increase pain thresholds in healthy participants (Ferrè et al. 2013). This result and several clinical observations suggest an interplay between vestibular processes, nociceptive processes, and the sense of the bodily self (André et al. 2001; Balaban 2011; Gilbert et al. 2014; McGeoch et al. 2008; Ramachandran et al. 2007).

These interactions are likely to rely on multimodal areas in the insular cortex. Intracranial electrical stimulations of the posterior insula in conscious epileptic patients revealed nociceptive representations with a somatotopic organization (Mazzola et al. 2009; Ostrowsky et al. 2002). Functional neuroimaging studies in healthy participants also demonstrated that painful stimuli (usually applied to the hand or foot) activate the operculo-insular complex (Baumgartner et al. 2010; Craig 2009; Kurth et al. 2010; Mazzola et al. 2012; zu Eulenburg et al. 2013). It has to be noted that vestibulo-somesthetic convergence may also exist in thalamic nuclei such as the ventroposterior lateral nucleus, known to receive both somatosensory and vestibular signals (Lopez & Blanke 2011). The parabrachial nucleus of the brainstem is also a region where vestibular and nociceptive signals converge, as shown by noxious mechanical and thermal cutaneous stimulations (Balaban 2004; Bester et al. 1995). The parabrachial nucleus is further strongly interconnected with the insula and amygdala and may control some autonomic manifestations of pain (Herbert et al. 1990). Furthermore, a recent fMRI study revealed an overlap between brain activations caused by painful stimuli and by artificial vestibular stimulation in the anterior insula (zu Eulenburg et al. 2013), a structure that has been proposed to link the homeostatic evaluation of the current state of the bodily self to broader social and motivational aspects (Craig 2009). We speculate that such association could explain why illusory changes in

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[11] A recent study investigating pain thresholds during the rubber hand illusion did not show any change in pain threshold or perception (Mohan et al. 2012), suggesting that pain perception is linked more to global aspects of the bodily self, e.g., self-location.

self-location during vestibular stimulation or during full-body illusions decrease pain thresholds.

4.1.3 Interoception

Visceral signals and their cortical representation—often referred to as *interoception*—are thought to play a core role in giving rise to a sense of self (e.g., Seth 2013). It has been proposed that visceral signals influence various aspects of emotional and cognitive processes (e.g., Furman et al. 2013; Lenggenhager et al. 2013; Werner et al. 2014; van Elk et al. 2014) and anchor the self to the physical body (Maister & Tsakiris 2014; Tsakiris et al. 2011). For this reason, various clinical conditions involving disturbed self-representation and dissociative states have been related to abnormal interoceptive processing (Seth 2013, but see also Michal et al. 2014 for an exception). Further evidence that interactions of exteroceptive with interoceptive signals play a role in building a self-representation comes again from research using bodily illusions in healthy participants. Two recent studies introduced an interoceptive version of the rubber hand illusion (Suzuki et al. 2013) and the full-body illusion (Aspell et al. 2013). In both cases, a visual cue on the body part/full body was presented in synchrony/asynchrony with the participant's own heartbeat. Synchrony increased self-identification with the virtual hand or body and modified the experience of self-location, thus suggesting a modulation of these components through interoceptive signals.

Vestibular processing in the context of such interoceptive bodily illusions has not yet been studied. Yet, we would like to emphasize the important interactions between the vestibular system and the regulation of visceral and autonomic functions at both functional and neuroanatomical levels (review in Balaban 1999). As mentioned earlier, the coding of body orientation in space relies on otolithic information signaling the head orientation with respect to gravity. Self-orientation with respect to gravity also requires that the brain integrates these vestibular signals with information from gravity receptors in the trunk (e.g., visceral signals from kidneys and blood vessels) (Mittelstaedt 1992; Mittelstaedt 1996; Vaitl et al. 2002). Other examples of interactions between the vestibular system and autonomic regulation come from the vestibular control of blood pressure, heart rate, and respiration (Balaban 1999; Jauregui-Renaud et al. 2005; Yates & Bronstein 2005). Blood pressure, for instance, needs to be adapted as a function of body position in space and the vestibular signals are crucially used to regulate the baroreflex. Vestibular-mediated symptoms of motion sickness such as pallor, sweating, nausea, salivation, and vomiting are also very well-known and striking examples of the vestibular influence on autonomic functions.

At the anatomical level, there is a large body of data showing that vestibular information projects to several brain structures involved in autonomic regulation, including the *parabrachial nucleus*, nucleus of the solitary tract, paraventricular nucleus of the hypothalamus, and the central nucleus of the amygdala. Important research has been conducted in the monkey and rat parabrachial nucleus as this nucleus contains neurons responding to natural vestibular stimulation (McCandless & Balaban 2010) and is involved in the ascending pain pathways and cardiovascular pathways to the cortex and amygdala (Bester et al. 1995; Feil & Herbert 1995; Herbert et al. 1990; Jasmin et al. 1997; Moga et al. 1990). The parabrachial nucleus receives projections from several cortical regions, including the insula, as well as from the hypothalamus and amygdala (Herbert et al. 1990; Moga et al. 1990). Accordingly, the parabrachial nucleus should be a crucial brainstem structure for basic aspects of the self as it is a place of convergence for nociceptive, visceral, and vestibular signals.

While research on the effects of vestibular stimulation on interoceptive awareness is still missing, we propose that artificial vestibular stimulation might be a particularly interesting means to manipulate interoception and investigate its influence on the sense of a bodily self.

4.2 Body schema and body image

Here, we propose that vestibular signals are not only important for the interpretation of basic somatosensory (tactile, nociceptive, interoceptive) processes, but as a consequence also contribute to *body schema* and *body image*. Body schema and body image are different types of models of motor configurations and body metric properties, including the size and shape of body segments (e.g., Gallagher 2005; de Vignemont 2010; Berlucchi & Aglioti 2010; Longo & Haggard 2010). Although body schema and body image are traditionally thought to be of mostly proprioceptive and visual origin, respectively, a vestibular contribution was already postulated over a century ago (review in Lopez 2013). Pierre Bonnier (1905) described several cases of distorted bodily perceptions in vestibular patients and coined the term *"aschématie"* (meaning a "loss" of the *schema*) to describe these distorted perceptions of the volume, shape, and position of the body. Paul Schilder (1935) also noted distorted body schema and image in vestibular patients claiming for example that their "neck swells during dizziness," "extremities had become larger," or "feet seem to elongate." The contribution of vestibular signals to mental body representations has been recognized more recently by Jacques Paillard. He proposed that "the ubiquitous geotropic constraint [i.e., gravitational acceleration, which is detected and coded by vestibular receptors] dominates the [body-, world-, object- and retina-centered] reference frames that are used in the visuomotor control of actions and perceptions, and thereby becomes a crucial factor in linking them together" (Paillard 1991, p. 472). According to Paillard, gravity signals would help merge and give coherence to the various reference frames underpinning action and perception.

Because humans have evolved under a constant gravitational field, human body representations are strongly shaped by this physical constraint. In particular, grasping and reaching movements are constrained by gravito-inertial forces and internal models of gravity (Indovina et al. 2005; Lacquaniti et al. 2013; McIntyre et al. 2001). Thus, the body schema and action potentialities must take into account signals from the otolithic sensors. For example, when a subject is instructed to reach a target while his entire body is rotated on a chair, the body rotation generates Coriolis and centrifugal forces deviating the hand. Behavioural studies demonstrate that vestibular signals generated during whole-body rotations are used to correct the hand trajectory (Guillaud et al. 2011). Other studies demonstrate that vestibular signals continuously update the body schema during hand actions. Bresciani et al. (2002) asked participants to point to previously memorized targets located in front of them (figure 5A). At the same time, participants received bilateral galvanic vestibular stimulation, with the anode on one side and the cathode on the other side. The data indicate that the hand was systematically deviated toward the side of anodal stimulation (figure 5B). It is important to note that galvanic vestibular stimulation is known to evoke illusory body displacements in the frontal plane and thus modifies the perceived self-location (Fitzpatrick et al. 2002; see also section 4.5). One possible interpretation of the change in hand trajectory during the pointing movement was that it compensated for an "apparent change in the spatial relationship between the target and the hand," evoked by the vestibular stimulation (Bresciani et al. 2002). Thus, vestibular signals are used to control the way we act and interact with objects in the environment.

After having established the contribution of vestibular signals to hand location and motion, we shall describe the role of vestibular signals in the perception of the body's metric properties (the perceived shape and size of body segments). During parabolic flights, known to create temporary weightlessness and thus mimic a deafferentation of the otolithic vestibular sensors, Lackner (1992) reported cases of participants experiencing a "telescoping motion of the feet down and the head up internally through the body," that is, an inversion of their body orientation. Experiments conducted on animals born and raised in hypergravity confirm an influence of vestibular signals on body representations. In these animals, changes in the strength of the gravita-

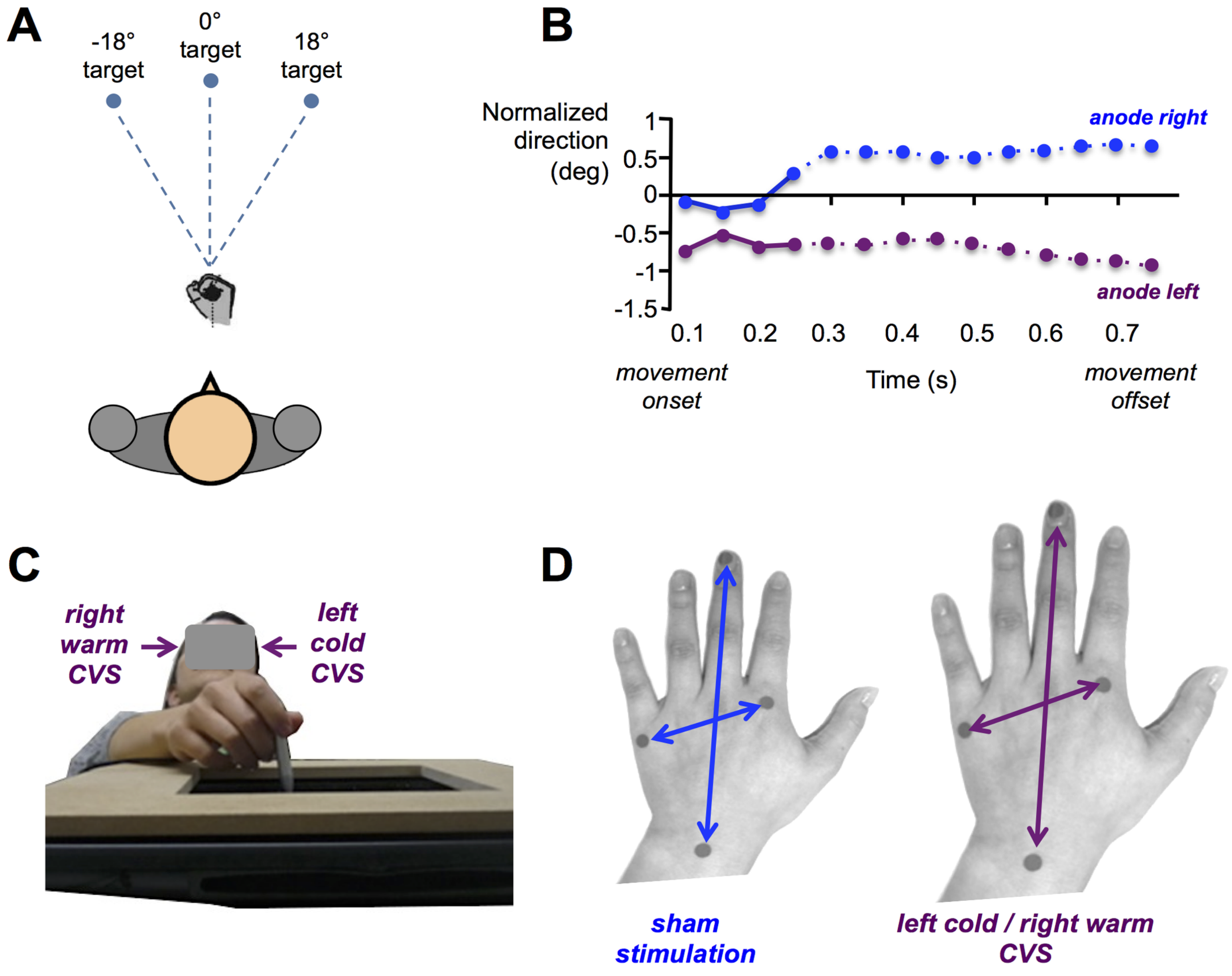

Figure 5: Influence of vestibular signals on motor control and perceived body size. (A) Pointing task toward memorized targets. Participants received binaural galvanic vestibular stimulation as soon as they initiated the hand movement (with eyes closed). (B) Deviation of the hand trajectory towards the anode (modified after Bresciani et al. 2002). (C) Proprioceptive judgment task used to estimate the perceived size of the left hand. Participants were tested blindfolded and used a stylus hold in their right hand to localize on a digitizing tablet four anatomical landmarks corresponding to the left hand under the tablet. (D) Illustration of the perception of an enlarged hand during caloric stimulation activating the right cerebral hemisphere (modified after Lopez et al. 2012).

tional field permanently disorganized the somatosensory maps recorded in their primary somatosensory cortex (Zennou-Azogui et al. 2011).

Experimental evidence of a vestibular contribution to the coding of body metric properties comes from the application of stimulation in healthy participants. In a recent study, Lopez et al. (2012) showed that caloric vestibular stimulation modified the perceived size of the body during a proprioceptive judgment task (figure 5C). Participants had their left hand palm down on a table. Above the left hand, there was a digitizing tablet on which participants were instructed to localize four anatomical targets enabling the calculation of the perceived width and length of the left hand. While participants pointed repeatedly to these targets, they received bilateral caloric vestibular stimulation known to stimulate the right cerebral hemisphere in which the left hand is mostly represented (e.g., warm air in the right ear and cold air in the left ear). The results showed that in comparison to a control stimulation (injection of air at 37°C in both ears), in the stimulation condition the left hand appeared significantly enlarged (figure 5D), showing that vestibular signals can modulate internal models of the body.

4.3 Body ownership

Correct self-attribution of body parts and self-identification with the entire body relies on successful integration of multisensory information as evidenced by various bodily illusions in healthy participants (e.g., Botvinick & Cohen 1998; Lenggenhager et al. 2007; Petkova & Ehrsson 2008). So far there is only little evidence of a vestibular contribution to the sense of body ownership. Bisiach et al. (1991) described a patient with a lesion of the right parieto-temporal cortex who suffered from somatoparaphrenia, claiming that her left hand did not belong to her. In this patient, caloric vestibular stimulation transiently restored normal ownership for her left hand. Similarly, Lopez et al. (2010) applied galvanic vestibular stimulation to participants experiencing the rubber hand illusion and showed that the vestibular stimulation increased the feeling of ownership for the fake hand. The authors have linked such interaction between the vestibular system, multisensory integration, and body ownership to overlapping cortical areas in temporo-parietal areas and the posterior insula. No study has so far investigated the effect of vestibular stimulation on full-body ownership. Yet, reports from patients with acute vestibular disturbances as well as reports from healthy participants during caloric vestibular stimulation (Lopez 2013; Sang et al. 2006) suggest that full-body ownership might also be modified by artificial vestibular stimulation or vestibular dysfunctions. Given the importance of the vestibular system in more global aspects of the bodily self, we predict that vestibular stimulation would influence ownership even stronger in a full-body illusion than in a body-part illusion set-up.

4.4 The acting self: Sense of agency

As mentioned earlier, the sense of being the agent of one's own actions is another crucial aspect of the sense of self. Agency relies on sensorimotor mechanisms comparing the motor efference copy with the sensory feedback from the movement, and on other cognitive mechanisms such as the expectation of a self-generated movement (Cullen 2012; Jeannerod 2003, 2006). While no study so far has directly investigated vestibular mechanisms of the sense of agency, recent progress in this direction has been made in a study investigating full-body agency during a goal-directed locomotion task (Kannape et al. 2010). Participants walked toward a target and observed their motion-tracked walking patterns applied to a virtual body projected on a large screen in front of them. Various angular biases were introduced between their real locomotor trajectory and that projected on the screen. Comparable to the classical experiments assessing agency for a body part (Fourneret & Jeannerod 1998), these authors investigated the discrepancy up to which the motion of the avatar showed on the screen was still perceived as their own. During this task, the brain does not only detect visuo-motor coherence but also vestibulo-visual coherence, and self-attribution of the seen movements is thus likely to depend on vestibular signal processing. In the following we present an example of neural coding underlying an aspect of the sense of agency in several structures of the vestibulo-thalamo-cortical pathways.

In the vestibular system, peripheral organs encode in a similar way head motions for which the subject is or is not the agent.[12] Thus, vestibular organs generate similar signals during an active rotation of the head (i.e., the person is the agent of the action) or during a passive, externally imposed, rotation of the head (i.e., the person is passively moved while sitting on a rotating chair). It is important for the central

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[12] Although the coding of movements by the peripheral vestibular organs is ambiguous regarding the sense of agency, the coding is not ambiguous regarding the sense of ownership for the movements and self-other distinction. Indeed, because vestibular sensors are inertial sensors, vestibular signals are necessarily related to one's own motion and are the basis of the perception that I have (been) moved, irrespective of whether the "self" is or is not the agent of this movement.

nervous system to establish whether afferent vestibular signals are generated by active or passive head movements, and this is done at various levels. Electrophysiological studies conducted in monkeys have revealed that some vestibular nuclei neurons were silent, or had a strongly reduced firing rate, during active head rotations, whereas their firing rate was significantly modulated by passive head rotations. This indicates that vestibular signals generated by active head rotations were suppressed or attenuated. This suppression of neural responses was found in the vestibular nuclei complex (Cullen 2011; Roy & Cullen 2004), thalamus (Marlinski & McCrea 2008b) and cerebral cortex, for example in areas of the intraparietal sulcus (Klam & Graf 2003, 2006). Several studies were conducted to determine which signal might induce such suppression. Roy & Cullen (2004) suggested that a *motor efference copy* was used. They showed that the suppression occurred "only in conditions in which the activation of neck proprioceptors matched that expected on the basis of the neck motor command", suggesting that "vestibular signals that arise from self-generated head movements are inhibited by a mechanism that compares the internal prediction of the sensory consequences by the brain to the actual resultant sensory feedback" (p. 2102). In conclusion, as early as the first relay along the vestibulo-thalamo-cortical pathways, neural mechanisms have the capacity to distinguish between the consequences of active and passive movements on vestibular sensors. Given this evidence, we suggest an important contribution of the vestibular system to the sense of agency in general and to full-body agency in particular.

4.5 The spatial self: Self-location

4.5.1 Behavioural studies in humans

Self-location is the experience of where "I" am located in space and is one of the (if not the) crucial aspects of the bodily self (Blanke 2012). Recently, self-location has been systematically investigated in human behavioural and neuroimaging studies using multisensory conflicts (Ionta et al. 2011; Lenggenhager et al. 2007; Lenggenhager et al. 2009; Pfeiffer et al. 2013). While we usually experience ourselves as located within our own bodily borders at one single location in space, the sense of self-location can be profoundly disturbed in psychiatric and neurological conditions, most prominently during *out-of-body experiences* (Bunning & Blanke 2005). Based on findings in neurological patients that revealed a frequent association between vestibular illusions (floating in the room, sensation of lightness or levitation) and out-of-body experiences, Blanke and colleagues proposed that the illusory disembodied self-location was due to a dis-integration of vestibular signals with signals from the personal (tactile and proprioceptive signals) and extrapersonal (visual) space (Blanke et al. 2004; Blanke & Mohr 2005; Blanke 2012; Lopez et al. 2008). The authors proposed that this multisensory disintegration is mostly a result of abnormal neural activity in the temporo-parietal junction (Blanke et al. 2005; Blanke et al. 2002; Heydrich & Blanke 2013; Ionta et al. 2011). In this section, we review experimental data in healthy participants that may account for the tight link between vestibular disorders and illusory or simulated changes in self-location. While the most direct evidence of such a link comes from the finding that artificial stimulation of the vestibular organs induces an illusory change in self-location[13] (Fitzpatrick & Day 2004; Fitzpatrick et al. 2002; Lenggenhager et al. 2008), we focus on three experimental set-ups that have been used to alter the experience of self-location in healthy participants.

4.5.1.1 Illusory change in self-location during full-body illusions

Full-body illusions have increasingly been used to study the mechanisms underlying self-location (see Blanke 2012, for a review). No study has so far investigated the influence of artificial vestibular stimulation on such illusions. Nevertheless, there is some experimental evidence suggesting a vestibular involvement in illusory changes in self-location. While the initial full-

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[13] Depending on the stimulation parameters and method, participants describe various sensations of movements and change in position.

body illusion was described in a standing position (Lenggenhager et al. 2007), the paradigm has later been adapted to a lying position (Ionta et al. 2011; Lenggenhager et al. 2009; Pfeiffer et al. 2013), mainly because the frequency of spontaneous out-of-body experiences is higher in lying position than in standing or sitting positions (Green 1968). It has been speculated that this influence of the body position on the sense of embodiment is related to the decreased sensitivity of otolithic vestibular receptors and decreased motor and somatosensory signals in the lying position (Pfeiffer et al. 2013). We hypothesized that under such conditions of reduced vestibular (and proprioceptive) information, visual capture is enhanced in situations of multisensory conflict, thus resulting in a stronger change in self-location during the full-body illusion. So far, the full-body illusion has not been directly compared in standing versus lying positions. However, the application of visuo-tactile conflicts in a lying position not only alters self-location but also evokes sensations of floating (Ionta et al. 2011; Lenggenhager et al. 2007). This finding hints toward a reweighting of visual, tactile, proprioceptive, and vestibular information during the illusion, plausibly in the temporo-parietal junction and human PIVC. In line with this finding, the changes in self-location and perspective have been associated with individual perceptual styles of visual-field dependence (Pfeiffer et al. 2013), i.e., weighting of visual as compared to vestibular information in a subjective visual vertical task, suggesting an individually different contribution and weighting of the various senses for the construction of the bodily self (for a similar finding regarding the rubber hand illusion, see David et al. 2014).

4.5.1.2 Mental own-body transformation and perspective taking

Another way to investigate bodily self-consciousness has been to use experimental paradigms requiring participants to put themselves "into the shoes" of another individual, that is to mentally simulate an external self-location (own-body, egocentric, mental transformation tasks) and a third-person visuo-spatial perspective. Typically, participants are instructed to make left-right judgments about a body, for example, to judge whether this other shown person is wearing a glove on his right or left hand (Blanke et al. 2005; Lenggenhager et al. 2008; Parsons 1987; Schwabe et al. 2009). Other tasks require that participants adopt the visual perspective of another person to decide whether a visual object is to the right or left of the other person (David et al. 2006; Lambrey et al. 2012; Vogeley & Fink 2003). Early studies have shown that the time needed for own-body mental transformations correlates with the distance or angle between the participant's position in the physical space and the position to be simulated (Parsons 1987). It is largely admitted that own-body mental transformation is an "embodied" mental simulation that can be influenced by various sensorimotor signals from the body (e.g., Kessler & Thomson 2010). In line with this view, various experiments demonstrated that the actual body position influences mental own-body transformation of body parts (e.g., Ionta et al. 2012). Importantly, next to proprioceptive and motor mechanisms, visuo-spatial perspective taking and own-body mental transformation also require the integration of vestibular information (active or passive body motion). Thus, while most of this research looked at how body parts' posture (e.g., of the hand) influences mental own-body (part) transformation, some recent research investigated how mental own-body transformation is influenced by vestibular cues (Candidi et al. 2013; Dilda et al. 2012; Falconer & Mast 2012; Lenggenhager et al. 2008; van Elk & Blanke 2014). All these studies revealed that vestibular signals influence mental (full) own-body transformation, confirming again the influence of the vestibular system in the sense of self-location and perspective taking.[14]

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[14] Visuo-spatial perspective-taking has not only been used in the field of spatial cognition but also in the field of social cognition. Perspective taking is a very crucial aspect of human cognition, which allows us to understand other people's actions and emotions. The fact that the vestibular system is importantly involved in such simulations might further suggest that the vestibular system is important for social cognition (see also section 5 and Deroualle & Lopez 2014).

4.5.1.3 Change in self-location and the feeling of presence

The development of immersive virtual environments has launched a powerful research area where the mechanisms of self-location can be investigated and manipulated by the *feeling of presence*. The term “presence” stems from virtual reality technologies and commonly refers to the feeling of being immersed (“being there”) in the virtual environment. Yet, it has been argued that “presence” also reflects a more general and basic state of consciousness (Riva et al. 2011). The study of presence has thus been suggested to provide useful tools to study (self-)consciousness, with the advantage of precise experimental control (Sanchez-Vives & Slater 2005).

Similar to previously mentioned full-body illusions, a participant who is immersed in a virtual environment receives contradicting multisensory information about his or her self-location: while visual information suggests that s/he is located in a virtual world, proprioceptive information suggests that s/he is located in the real world, for example, by indicating a different body position between the physical body and the avatar. Furthermore, and contrary to the full-body illusion, the visual information often indicates that the participant is moving, whereas the proprioceptive and vestibular information suggests that he or she is sitting still. The compelling feeling of presence in virtual environments indicates that participants rely strongly on visual cues. Of note, some authors have proposed that a sort of bi-location is possible in such a situation, by which one feels to a certain degree being localized simultaneously in both the real and virtual environments (Furlanetto et al. 2013; Wissmath et al. 2011), which has also been described in a clinical condition called heautoscopy (e.g., Blanke & Mohr 2005; Brugger et al. 1994).

Neuroimaging studies in healthy participants showed that self-identification with—and self-localization at—a position of a virtual avatar seen from a third-person perspective activates the left inferior parietal lobe (Corradi-Dell’acqua et al. 2008; Ganesh et al. 2012). Corroboratively, people who are addicted to video-games show altered processing in a left posterior area of the middle temporal gyrus (Kim et al. 2012). These studies converge in their conclusion that multimodal areas in the temporo-parietal junction are involved in altered self-localization in virtual reality. As mentioned before, the temporo-parietal junction is a main region for vestibular processing. We thus hypothesize that the feeling of presence might be mediated by vestibular signals, which should be directly tested by assessing whether the feeling of presence can be modified by caloric and galvanic vestibular stimulation.

4.5.2 Physiological and vestibular mechanisms of self-location

4.5.2.1 Categories of cells coding self-location and self-orientation

Electrophysiological investigations in rodents have identified three categories of neurons encoding specifically where the animal is located, how its head is oriented, and how the animal moves in its environment (see Barry & Burgess 2014, for a recent review). These neurons are referred to in the literature as “place cells,” “head-direction cells,” and “grid cells”. In rats, *place cells* have been recorded as early as the 1970s in the hippocampus, and later in the subiculum and entorhinal cortex (O’Keefe & Conway 1978; O’Keefe & Dostrovsky 1971; Poucet et al. 2003). The firing rate of these neurons increases when the animal is located at a specific position within the environment. This activity is strongly modulated by allocentric signals (visual references in the environment) and vestibular signals (Wiener et al. 2002). Place cells have later been identified in several other animal species including mice (McHugh et al. 1996), bats (Ulanovsky & Moss 2007), monkeys (Furuya et al. 2014; Ludvig et al. 2004; Matsumura et al. 1999; Ono et al. 1993) and humans (Ekstrom et al. 2003; Miller et al. 2013). *Head-direction cells* were first recorded in the rat postsubiculum and later in several nuclei constituting the Papez circuit, such as the dorsal thalamic nucleus and lateral mammillary nuclei (Taube 2007). They were also found in the retrosplenial and entorhinal cortex. Electrophysiological recordings revealed that head-direction cells “discharge allocentrically as a function of the animal’s directional heading, independent of the animal’s location and ongoing behavior” (Taube 2007). Head-direction cells have also been identified in the monkey hippocampus (Robertson et al. 1999). Finally, *grid cells* have been identified in the rat medial entorhinal cortex, but also in the pre- and parasubiculum (Boccara et al. 2010; Sargolini et al. 2006). Grid cells fire for multiple locations of the animal within its environment. Altogether, these locations form a periodic pattern, or “grid,” spanning the entire surface of the environment. More recently, electrophysiological recordings have shown grid cells in mice (Fyhn et al. 2008), bats (Yartsev et al. 2011) and monkeys (Killian et al. 2012), and even probable homologues of grid cells in the human hippocampus (Doeller et al. 2010; Jacobs et al. 2013).

4.5.2.2 Place cells in the human hippocampus and “virtual” self-location

We can only speculate about the neural mechanisms of place and head-direction specific coding in the human brain. With the non-invasive neuroimaging techniques available to date (fMRI, PET, scalp electroencephalography (EEG), near-infrared spectroscopy (NIRS)), it remains difficult to investigate neural activity of potential human homologues of place cells, head-direction cells and grid cells (for fMRI identification of grid cells, see Doeller et al. 2010). Single-unit recordings can only be achieved during rather rare intracranial EEG carried out for presurgical evaluations of drug refractory epilepsy.

In a seminal intracranial EEG study conducted in 7 epileptic patients, Ekstrom et al. (2003) identified neurons with place selectivity in the *hippocampus*. Patients were immersed in a virtual environment and played a taxi driver computer game, picking up customers at one location in the virtual town and delivering them to another location of the town. As illustrated in figure 6, a neuron recorded in the right hippocampus had a significantly stronger firing rate when the patient was virtually “located” in the upper left corner than in any other location of the virtual town, showing its place selectivity. The authors found that 24% of neurons recorded in the hippocampus displayed a pattern of place selectivity, a proportion that was significantly larger than in the other brain structures they explored. Using a very similar procedure in a virtual environment in patients with intracranial electrodes, a recent study identified probable grid-like cells in humans (Jacobs et al. 2013). They were predominantly located in the entorhinal cortex and anterior cingulate cortex.

Interestingly, in both studies, patients did not physically move but moved virtually using button presses on a keyboard or a joystick. Nevertheless, the firing rate of these neurons changed as a function of the “virtual” location of the participants within the virtual environment. This observation indicates that both hippocampal “place cells” as well as entorhinal and cingulate “grid-cells” were coding the patient’s location in the virtual word on the basis of allocentric visual signals, rather than the patient’s position in the real world. Although the findings about these properties of the hippocampus have been mostly interpreted in the research field of spatial navigation and memory Burgess & O’Keefe 2003), we make a new proposition that they can also shed light on the neural underpinnings of bodily self-consciousness, especially on how the brain localizes the self both in everyday life as well as in situations of multisensory conflicts.

As mentioned earlier, the experience of self-location can be manipulated by creating conflicts between visual cues about the location of one’s own body (or an avatar) in the external word and tactile or other somatosensory signals (Ehrsson 2007; Lenggenhager et al. 2011; Lenggenhager et al. 2009; Lenggenhager et al. 2007). These visuo-tactile conflicts can induce the perception of being located closer to the avatar. The recent use of these visual-tactile conflicts during fMRI recordings showed that the apparent changes in self-location and visuo-spatial perspective were related to signal changes in the temporo-parietal junction, not in the hippocampus (Ionta et al. 2011). It is not clear whether hippocampal place cells' activity can be recorded with the large-scale, non-invasive functional neuroimaging techniques available. Yet, we predict that visuo-tactile conflicts, by modifying the experienced self-location, should also modify the neural activity of place cells and grid cells and their vestibular modulation (see next section), as showed during navigation in immersive virtual environments (Ekstrom et al. 2003; Jacobs et al. 2013). Future research using intracranial EEG recordings in epileptic patients should endeavour to study directly the relation between place cell activity and the experience of human self-location in situations of conflicting multisensory information.

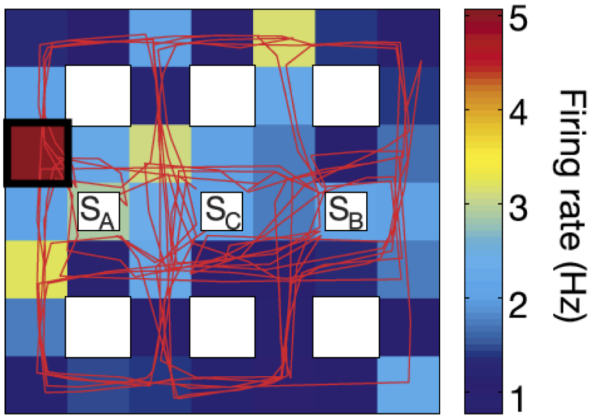

Figure 6: Map illustrating the firing rate of one cell in the right hippocampal showing a pattern of place selectivity. The rectangular map represents the virtual town explored by the participant using key presses on a keyboard and the red line represents the participant's trajectory within the virtual town. The nine white boxes indicate the location of buildings in the virtual town (SA, SB, and SC represent three shops that were "visited" by the participant). Colors from blue to red in the background represent the firing rate of the hippocampal cell as a function of the participant's location in the virtual town. This neuron displays a significantly higher firing rate when the participant was located in the left upper part of the virtual environment (location showed by a black square). Reproduced from Ekstrom et al. (2003).

4.5.2.3 Vestibular signals and place cells

In this section, we emphasize the contribution of vestibular signals to the neural coding of self-location in the hippocampus. As mentioned above, the firing rate of place cells is strongly modulated by allocentric signals, a finding replicated in several studies in rodents (Wiener et al. 2002). Vestibular signals have also been shown to modulate the firing pattern of the hippocampal place cells, which is necessary when animals navigate in darkness (O'Mara et al. 1994).

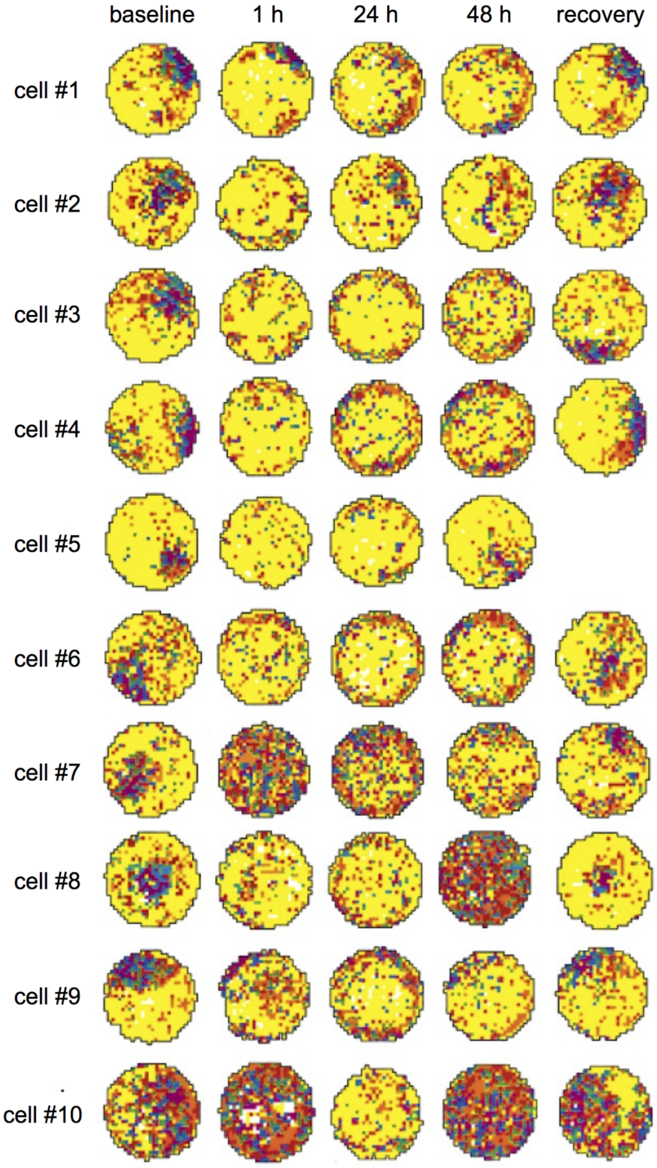

Figure 7: Modification of spatial selectivity of ten hippocampal place cells before and after inactivation of the vestibular apparatus with TTX injection. The colors ranging from yellow to purple represent the increase in firing rate of the place cells as a function of the location of the rat in the circular arena. From Stackman et al. (2002).

For example, Stackman et al. (2002) temporarily inactivated the vestibular system of rats using bilateral transtympanic injections of tetrodotoxin (TTX). TTX abolishes almost immediately neural activity in the vestibular nerve, producing a temporary vestibular deafferentation, mimicking the situation of patients with a bilateral vestibular loss. Figure 7 illustrates changes in the firing rate of ten hippocampal neurons before and after TTX injection. Before TTX injection, hippocampal neurons displayed a typical pattern of place selectivity when the animal explored the circular environment. A major finding of this study was that as early as one hour after vestibular deafferentation, the location-specific activity of the same hippocampal neurons was strongly disturbed. In particular, the vestibular deafferentation reduced the spatial coherence and spatial information content that usually characterize the place cells. These disorders remained between thirty-six and seventy-two hours after TTX injection, despite the fact that the rats continued to explore their circular environment and had normal locomotor activity twelve hours after TTX injection. These results indicate that place cells are continuously integrating vestibular signals to estimate one's location within the physical environment and that vestibular signals strongly contribute to one of the most important neural mechanisms of self-location.

The activity of place cells or grid cells has not been recorded after vestibular deafferentation in humans. Nevertheless the neural consequences of vestibular lesions on place cells (Stackman et al. 2002) and head-direction cells (Stackman & Taube 1997) in animal models corroborate the effects of unilateral and bilateral vestibular lesions in humans. Patients with vestibular disorders may experience spatial disorientation as measured during path completion tasks (Glasauer et al. 1994) and navigation in virtual environments (Hüfner et al. 2007; Péruch et al. 1999). We propose that vestibular disorders, by disorganizing the firing pattern of place cells in the human hippocampus (and in other brain regions containing place cells) may strongly disturb the sense of self-location and thus the coherent sense of self, which could eventually even lead to disturbance of the usually very stable feeling of being located at a single place at a given time (see the strong disorganization of the place cells activity in figure 7). Another striking consequence of a bilateral vestibular loss is the induced atrophy of the hippocampus, whose volume is decreased by about seventeen percent (Brandt et al. 2005). Altogether, these data show that one neural mechanism of bodily self-location (place cells encoding of the body location in the environment) strongly relies on vestibular signals.

4.6 The socially embedded self

An important branch of research suggests that the neural mechanisms that dynamically represent multisensory bodily signals not only give rise to a sense of self, but also to the sense of others. The emerging field of social neuroscience has investigated both in animals and humans how the perception of another person modifies neural activity in body-related, sensorimotor neural processing and vice versa.[15] "Sensorimotor sharing" and related mechanisms such as emotional contagion, sensorimotor resonance, or mimicry are thought to enable individuals to understand others' emotions, intentions, and actions and are thus fundamental for our social functioning. This line of research has evolved from an influential electrophysiological study that identified *mirror neurons* activated both when a monkey was performing a (body part) action and when observing someone else executing the same action (Gallese et al. 1996; Rizzolatti et al. 1996). A human mirror-neuron-like system has been suggested based on neuroimaging studies that revealed similar brain activations when acting and when observing the same action being executed by another person (e.g., Rizzolatti & Craighero 2004). Importantly, similar mechanisms were found in various sensory systems as further experiments have shown common neural activity when experiencing and

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[15] The research on bodily illusions has recently extended to social neuroscience by investigating how sensorimotor self-other confusion (during the rubber hand, full-body, and enfacement illusions) affects the perception of another person and, vice versa, how the perception of another person influences illusory self-other confusion (e.g., Bufalari et al. 2014; Paladino et al. 2010; Tajadura-Jiménez et al. 2012).

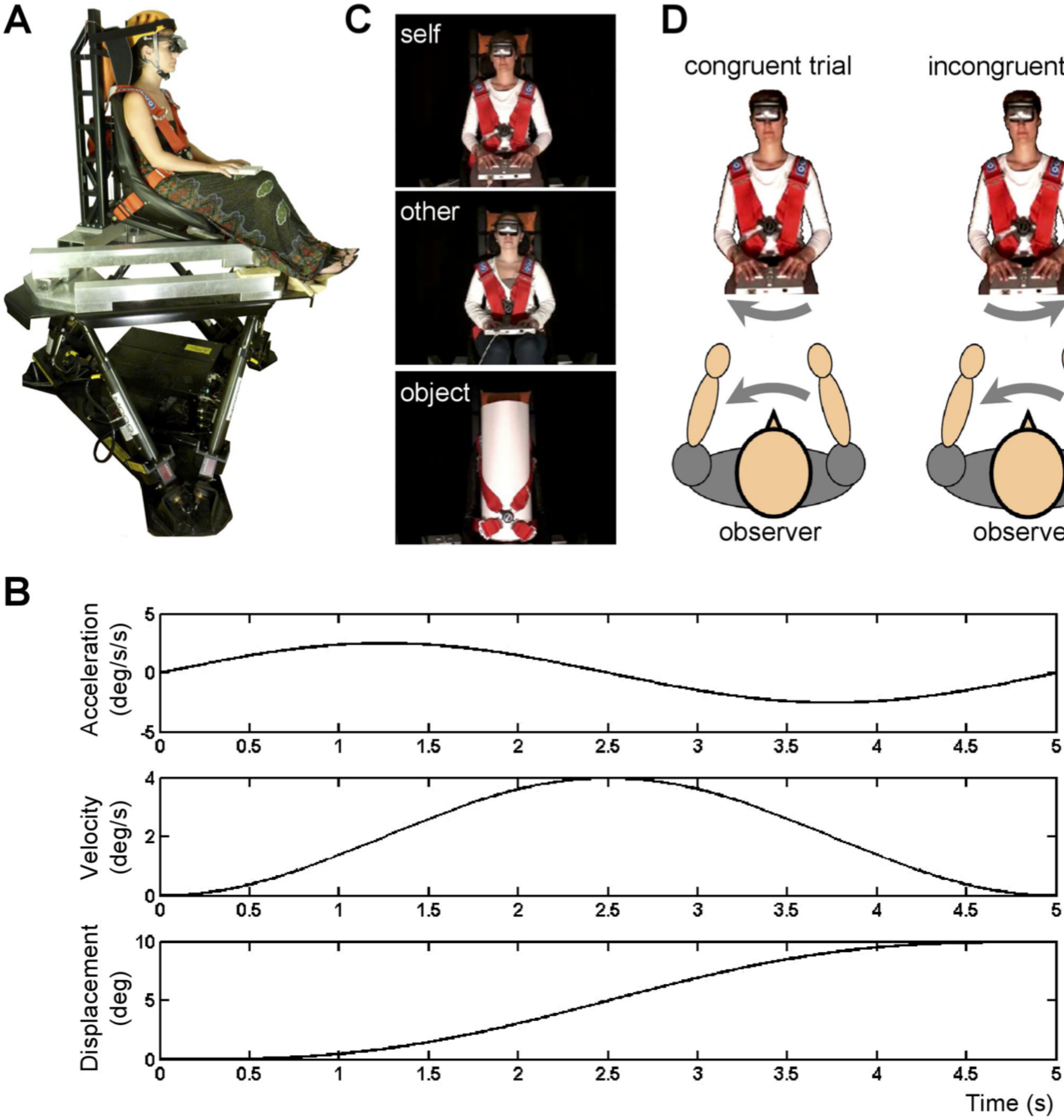

Figure 8: Experimental setup used to measure the influence of body movement observation on whole body self-motion perception. (A) Self-motion perception was tested in twenty-one observers seated on a motion platform. Motion stimuli were yaw rotations lasting for 5s with peak velocity of 0.1°/s, 0.6°/s, 1.1°/s, and 4°/s. (B) Example of a motion profile consisting of a single cycle sinusoidal acceleration. Acceleration, velocity, and displacement are illustrated for the highest velocity used at 4°/s. (C) Observers wore a head-mounted display through which 5-s videos were presented, depicting their own body, the body of another participant matched for gender and age, or an inanimate object. (D) During congruent trials, the observers and the object depicted in the video were rotated in the same direction (specular congruency). Reproduced from Lopez et al. (2013).

observing pain (Lamm et al. 2011, for a recent meta-analysis), when being touched and observing someone being touched (Keysers et al. 2004), and when inhaling disgusting odorants and observing the face of someone inhaling disgusting odorants (Wicker et al. 2003)

No human neuroimaging study so far has investigated brain mechanisms when experiencing a vestibular sensation and seeing somebody experiencing a vestibular sensation (e.g., being passively moved in space). Yet, recent findings from a behavioural study in humans suggest that the observation of another person's whole-body motion might influence vestibular self-motion perception (Lopez et al. 2013; see figure 8). In this study, participants were seated on a whole-body motion platform and passively rotated around their main vertical body axis. They were asked in a purely vestibular task to indicate in which direction (clockwise vs. counter-clockwise) they were rotated while looking at videos depicting their own body, another body, or an object rotating in the same plane. The spatial congruency between self-motion and the item displayed in the video was manipulated by creating congruent trials (specular congruency) and incongruent trials (non-specular congruency). The results indicated self-motion perception was influenced by the observation of videos showing passive whole-body motion. Participants were faster and more accurate when the motion depicted in the video was congruent with their own body motion. This effect depended on the agent depicted in the video, with significantly stronger congruency effects for the "self" videos than for the "other" videos, which is in line with the effects previously reported for the tactile system (Serino et al. 2009; Serino et al. 2008). Lopez et al. (2013) speculated on the existence of a *vestibular mirror neuron system* in the human brain, that is a set of brain regions activated both by vestibular signals and by observing bodies being displaced. As noted earlier, vestibular regions show important patterns of visuo-vestibular convergence in the parietal cortex, which could underlie such effects (Bremmer et al. 2002; Grüsser et al. 1990b).

On the basis of these findings as well as the data presented above on the importance of vestibular processes in spatial, cognitive, and social perspective-taking, we propose that the vestibular system is not only involved in shaping and building the perception of a bodily self but is also involved in better understanding and predicting another person's (full-body) action through sensorimotor resonance (see also Deroualle & Lopez 2014).

5 General conclusion

During the last years, various theories from psychological, neuroscientific, philosophical, and interdisciplinary perspectives have claimed the importance of multisensory signals and neural body representations for general theories of self-consciousness. Influential theories stated that very basic, and largely implicit and pre-reflective bodily processes crucially underlie the self (Alsmith 2012; e.g., Blanke & Metzinger 2009; Blanke 2012; Gallagher 2005; Legrand 2007). Such theories fueled experimental investigations on multisensory integration and its influence on various aspects of the self. Yet, similarly to Aristotle, who claimed that "there is no sixth sense in addition to the five enumerated—sight, hearing, smell, taste and touch"—this line of research has largely neglected the *vestibular sense of balance*. This is particularly surprising as a recent theory has claimed the importance of more global aspects of the bodily self (Blanke & Metzinger 2009), most importantly probably the sense of immersion or location in a spatiotemporal frame of reference (Windt 2010). This process, as we speculated above, should fundamentally rely on vestibular cues, plausibly among others coded by specific cells in the hippocampus. The vestibular system is activated by gravity, the constant force under which we have evolved, and also during all sorts of passive and active head and whole body movements. Moving in an environment is necessary for the development of a sense of bodily self, and the vestibular system is thus likely to contribute not only to the most basic (or minimal) aspects of the self but also to the different fine-graded implicit and explicit aspects of the experience of our bodily self in daily life such as body perception, body ownership, agency, and self-other distinction. It is thus not surprising that the vestibular system is intrinsically, highly linked to other sensory systems such as touch, pain, interoception, and proprioception. While some of the links between the vestibular system and the bodily self are rather well-established and the underlying neurophysiological processes known from both non-human animal and human research, several of the relations presented here are still largely speculative. Yet, we believe that the specific and testable hypotheses we have given here—once they are tested and possibly confirmed by experimental studies—might enable us to better describe neural and physiological mechanisms underlying minimal phenomenal selfhood (Blanke & Metzinger 2009) as well as refine current models of the multisensory mechanisms underlying the various aspects of the bodily self.

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