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

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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 perceptual, 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

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*

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).

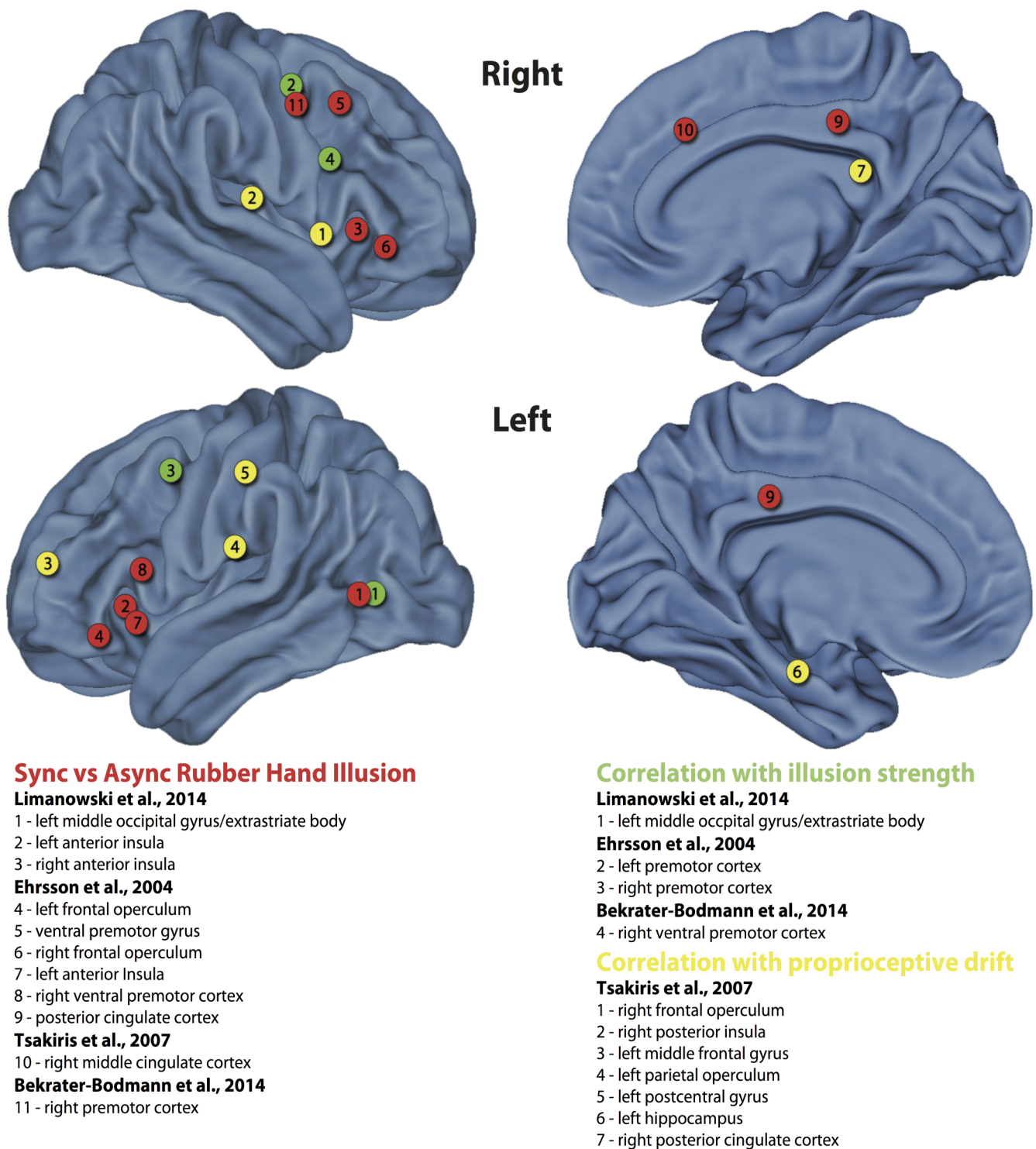


Figure 1: An overview of brain imaging studies of the rubber hand illusion (Bekrater-Bodmann et al. 2014; Ehrsson et al. 2004; Limanowski et al. 2014; Tsakiris et al. 2006). Red circles indicate significant brain activation in the comparison of synchronous visuo-tactile stimulation (illusion condition) 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-location³ 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

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.

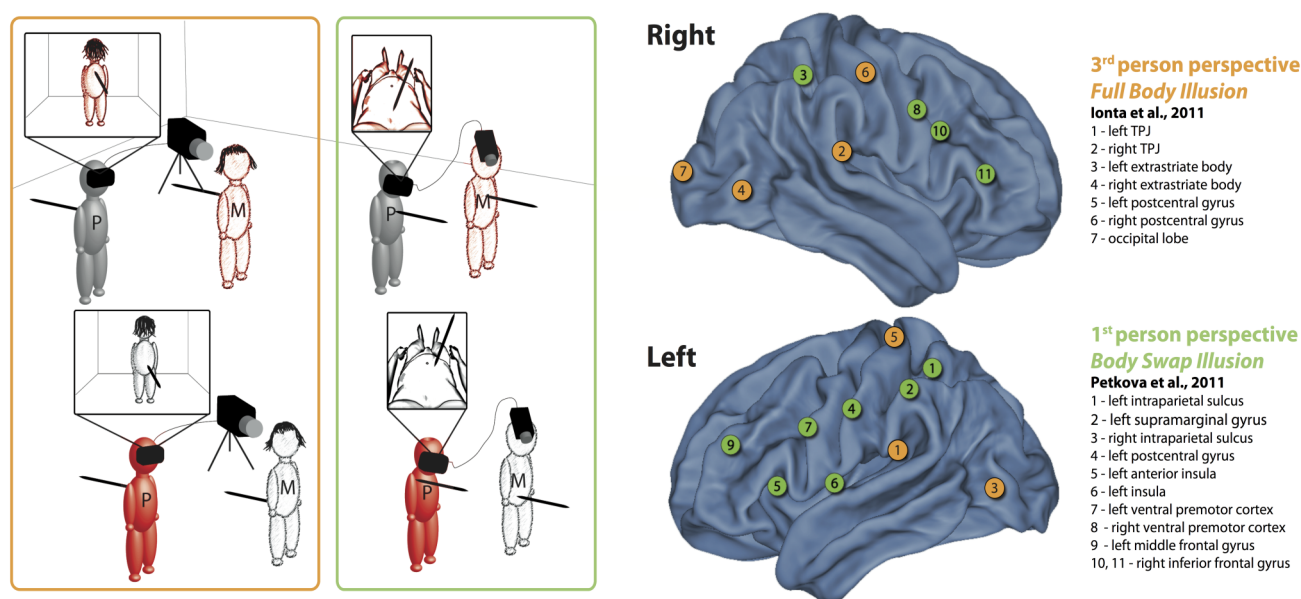


Figure 2: A comparison of brain activity associated with two illusions targeting the manipulation of more global aspects of the bodily self, i.e., the full body illusion (Lenggenhager et al. 2007, setup in orange frame) and the body swap illusion (Petkova & Ehrsson 2008, setup in green frame). In both 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

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-location⁷ (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 sub-components 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,

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 (Salmom et al. 2013).

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; Fournier & 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; Fournier 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

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 am-

biguous 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.

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;

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 (Courtillot & Wilson 2014).

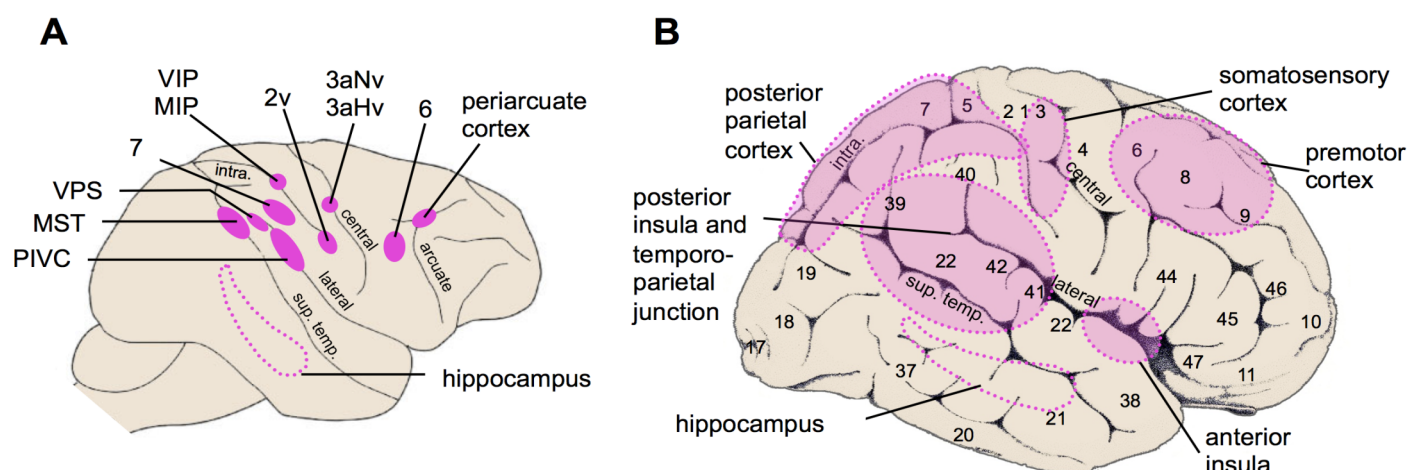


Figure 3: Schematic representation of the main cortical vestibular areas. (A) Main vestibular areas in monkeys are somatosensory areas 2v and 3av (3aHv (3a-hand-vestibular region), 3aNv (3a-neck-vestibular region)) in the postcentral gyrus, frontal area 6v and the periarculate cortex, parietal area 7, 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 stimulation¹⁰ 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 vestibular

behind one ear, and the cathode on the opposite side. The cathodal current increases the firing rate in the ipsilateral vestibular afferents.

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

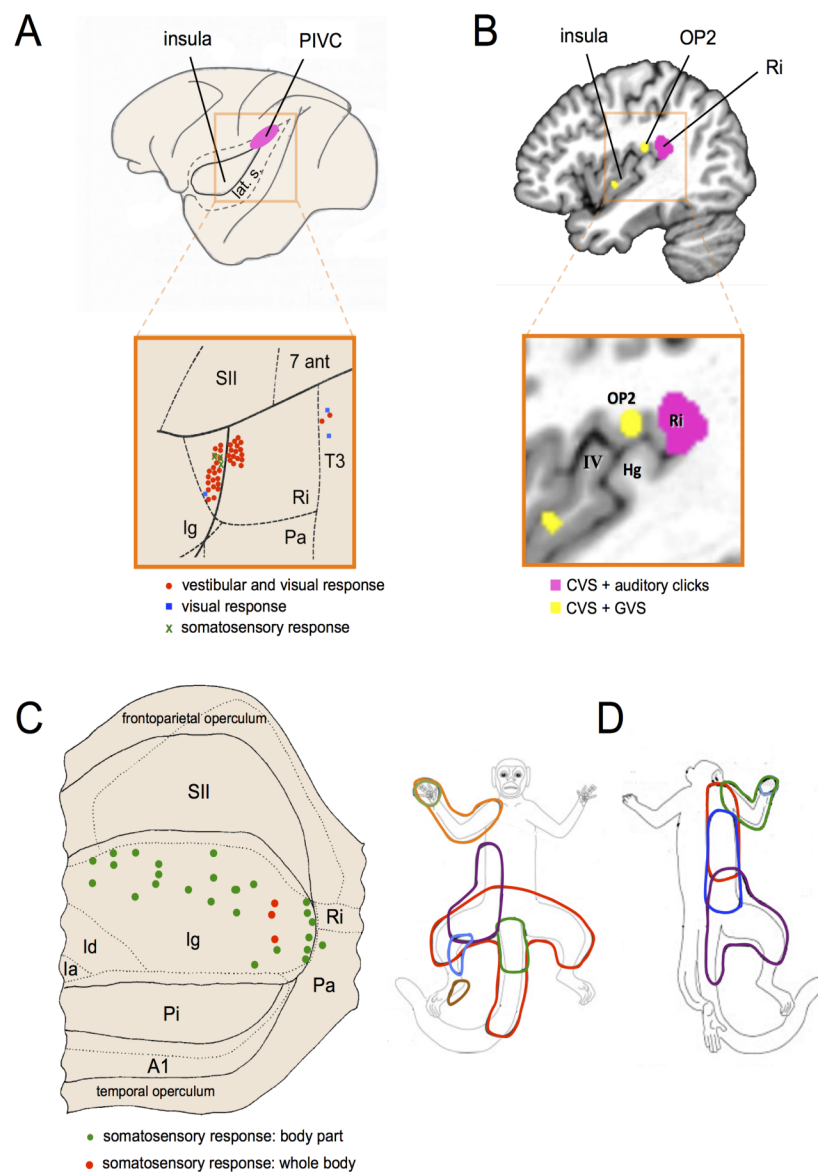


Figure 4: Anatomical location and functional properties of the parieto-insular vestibular cortex (PIVC). (A) Schematic representation of the macaque brain showing the location of the PIVC. For the purpose of illustration, the lateral sulcus (lat. s.) is shown unfolded. The macaque PIVC is located in 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 stimulation 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

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 & Hag-gard 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-

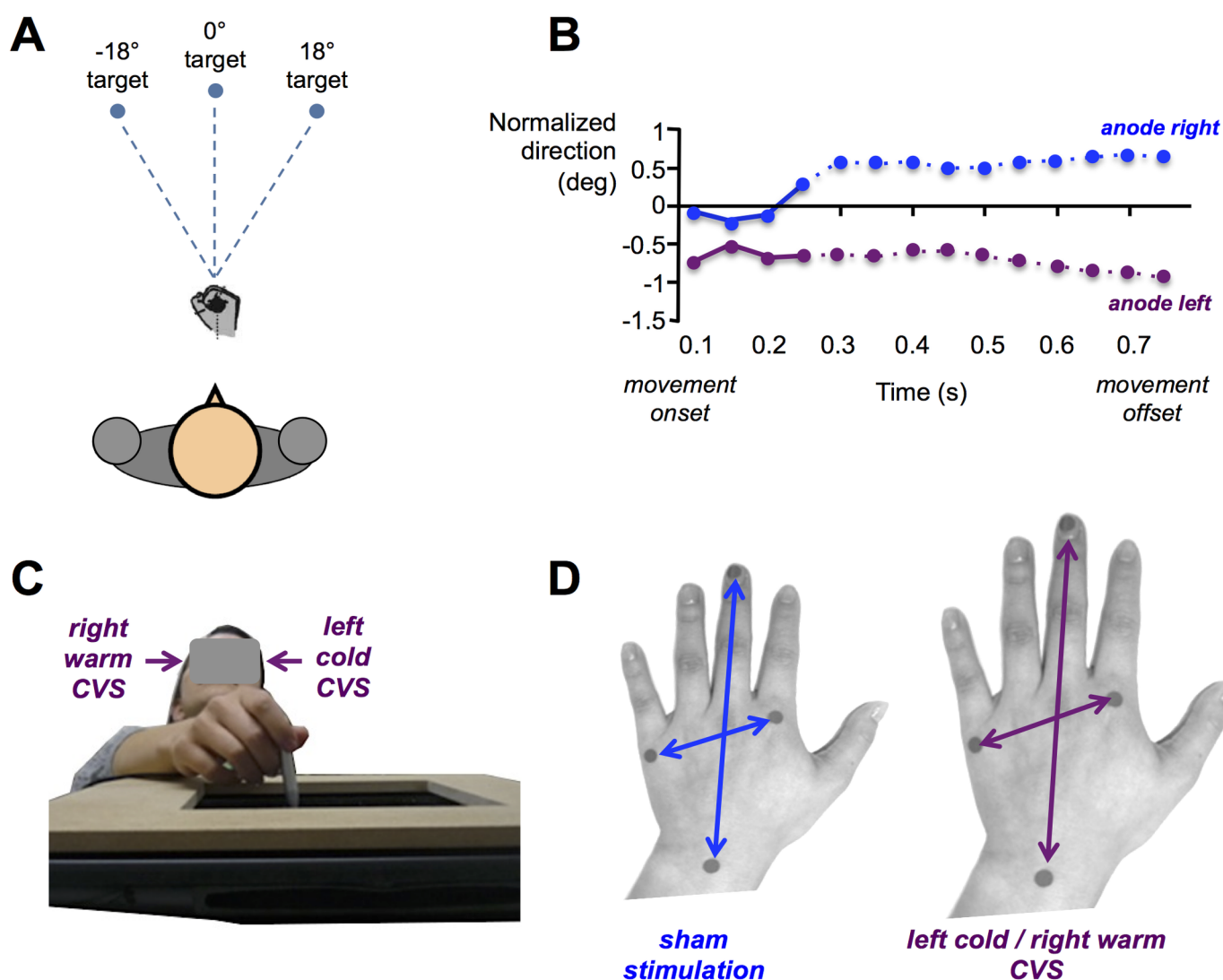


Figure 5: Influence of vestibular signals on motor control and perceived body size. (A) Pointing task toward memorized targets. Participants received binaural galvanic vestibular stimulation as soon as they initiated the hand movement (with eyes closed). (B) Deviation of the hand trajectory towards the 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 held 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 judg-

ment 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 (Fournieret & 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

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-location¹³ (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-

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 trans-

formation 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

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 hip-

pocampus 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 world 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 world 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.

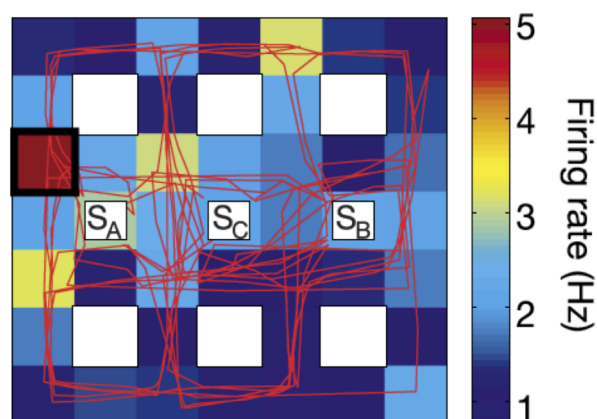


Figure 6: Map illustrating the firing rate of one cell in the right hippocampal showing a pattern of place selectivity. The rectangular map represents the virtual town explored by the participant using key presses on a keyboard and the red line represents the participant's trajectory within the virtual 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).

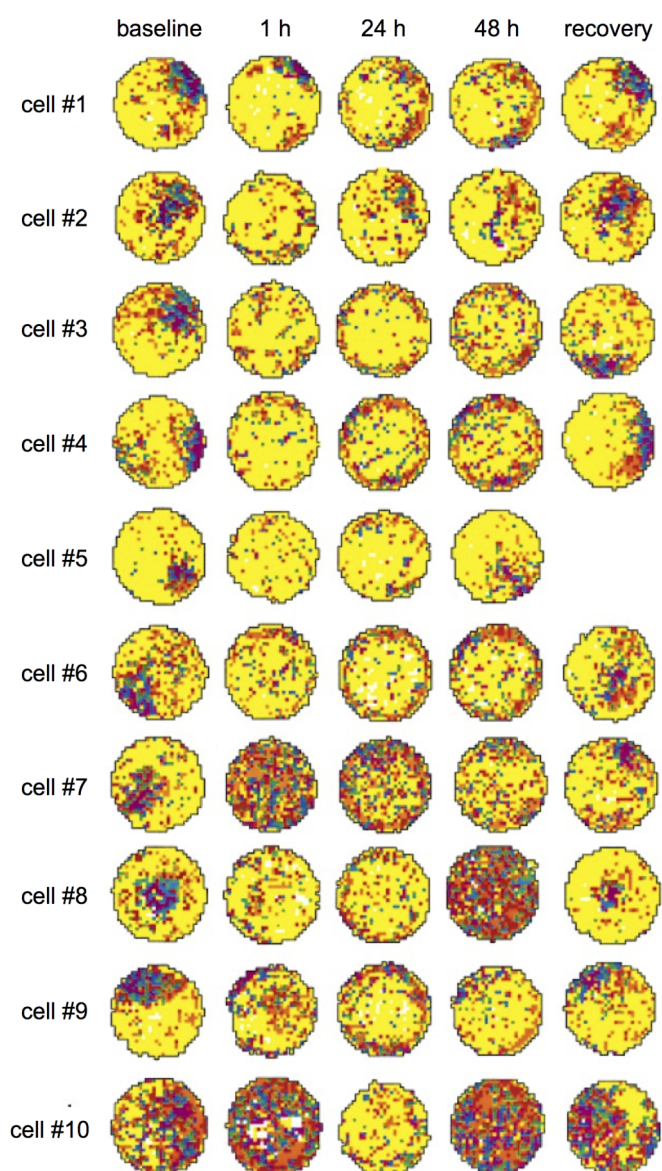


Figure 7: Modification of spatial selectivity of ten hippocampal place cells before and after inactivation of the vestibular apparatus with TTX injection. The colors ranging from yellow to purple represent the increase in firing rate of the place cells as a function of the location of the rat in the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

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](#)).

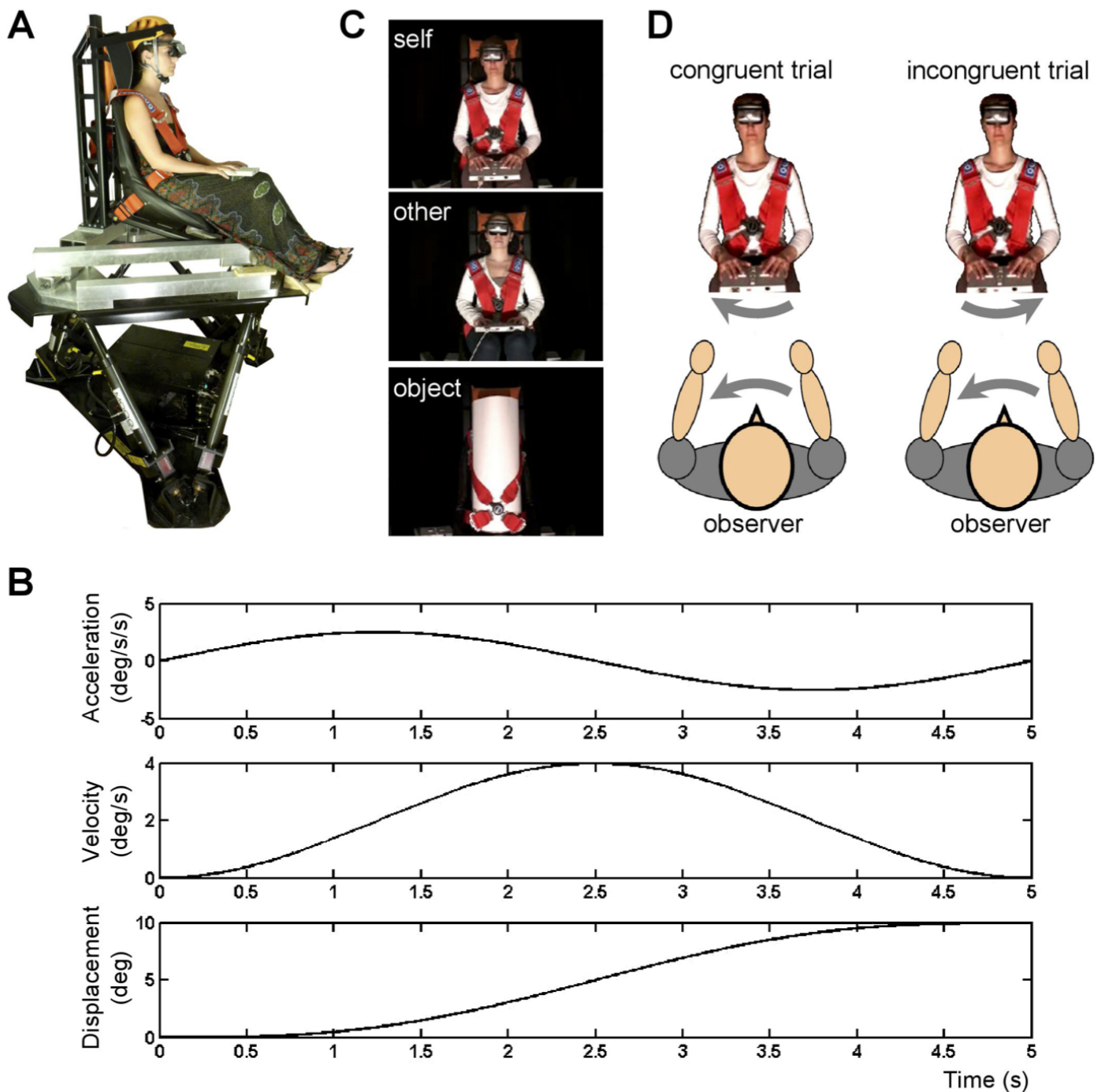


Figure 8: Experimental setup used to measure the influence of body movement observation on whole body self-motion perception. (A) Self-motion perception was tested in twenty-one observers seated on a motion platform. Motion stimuli were yaw rotations lasting for 5s with peak velocity of $0.1^\circ/\text{s}$, $0.6^\circ/\text{s}$, $1.1^\circ/\text{s}$, and $4^\circ/\text{s}$. (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 $4^\circ/\text{s}$. (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-grained 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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References

- Alsmith, A. (2012). What reason could there be to believe in pre-reflective bodily self-consciousness. In F. Paglieri (Ed.) *Consciousness in interaction: The role of the natural and social environment in shaping consciousness* (pp. 1-21). Amsterdam, NL: John Benjamins Publishing Company.
- André, J. M., Martinet, N., Paysant, J., Beis, J. M. & Le Chapelain, L. (2001). Temporary phantom limbs evoked by vestibular caloric stimulation in amputees. *Neuropsychiatry, Neuropsychology, and Behavioral Neurology*, 14 (3), 190-196.
- Angelaki, D. E. & Cullen, K. E. (2008). Vestibular system: The many facets of a multimodal sense. *Annual Review of Neuroscience*, 31, 125-150. [10.1146/annurev.neuro.31.060407.12555](https://doi.org/10.1146/annurev.neuro.31.060407.12555)
- Angelaki, D. E., Shaikh, A. G., Green, A. M. & Dickman, J. D. (2004). Neurons compute internal models of the physical laws of motion. *Nature*, 430 (6999), 560-564. [10.1038/nature02754](https://doi.org/10.1038/nature02754)
- Armell, K. C. & Ramachandran, V. S. (2003). Projecting sensations to external objects: Evidence from skin conductance response. *Proceedings of the Royal Society B: Biological Sciences*, 270 (1523), 1499-1506. [10.1098/rspb.2003.2364](https://doi.org/10.1098/rspb.2003.2364)
- Aspell, J. E., Heydrich, L., Marillier, G., Lavanchy, T., Herbelin, B. & Blanke, O. (2013). Turning body and self inside out: Visualized heartbeats alter bodily self-consciousness and tactile perception. *Psychological Science*, 24 (12), 2445-2453. [10.1177/0956797613498395](https://doi.org/10.1177/0956797613498395)
- Aspell, J. E., Lenggenhager, B. & Blanke, O. (2009). Keeping in touch with one's self: Multisensory mechanisms of self-consciousness. *PLoS One*, 4 (8), e6488-e6488. [10.1371/journal.pone.0006488](https://doi.org/10.1371/journal.pone.0006488)
- Bahrack, L. E. & Watson, J. S. (1985). Detection of intermodal proprioceptive-visual contingency as a potential basis of self-perception in infancy. *Developmental Psychology*, 21 (6), 963-973. [10.1037/0012-1649.21.6.963](https://doi.org/10.1037/0012-1649.21.6.963)
- Balaban, C. D. (1999). Vestibular autonomic regulation (including motion sickness and the mechanism of vomiting). *Current Opinion in Neurology*, 12 (1), 29-33.
- (2004). Projections from the parabrachial nucleus to the vestibular nuclei: Potential substrates for autonomic and limbic influences on vestibular responses. *Brain Research*, 996 (1), 126-137. [10.1016/j.brainres.2003.10.026](https://doi.org/10.1016/j.brainres.2003.10.026)
- (2011). Migraine, vertigo and migrainous vertigo: Links between vestibular and pain mechanisms. *Journal of Vestibular Research*, 21 (6), 315-321. [10.3233/VES-2011-0428](https://doi.org/10.3233/VES-2011-0428)

- Barmack, N. H. (2003). Central vestibular system: Vestibular nuclei and posterior cerebellum. *Brain Research Bulletin*, 60 (5-6), 511-541. [10.1016/S0361-9230\(03\)00055-8](https://doi.org/10.1016/S0361-9230(03)00055-8)
- Barnsley, N., McAuley, J. H., Mohan, R., Dey, A., Thomas, P. & Moseley, G. L. (2011). The rubber hand illusion increases histamine reactivity in the real arm. *Current Biology*, 21 (23), R945-R946. [10.1016/j.cub.2011.10.039](https://doi.org/10.1016/j.cub.2011.10.039)
- Barra, J., Marquer, A., Joassin, R., Reymond, C., Metge, L., Chauvineau, V. & Perennou, D. (2010). Humans use internal models to construct and update a sense of verticality. *Brain*, 133, 3552-3563. [10.1093/brain/awq311](https://doi.org/10.1093/brain/awq311)
- Barry, C. & Burgess, N. (2014). Neural mechanisms of self-location. *Current Biology*, 24 (8), R330-R339. [10.1016/j.cub.2014.02.049](https://doi.org/10.1016/j.cub.2014.02.049)
- Baumgartner, U., Iannetti, G. D., Zambreanu, L., Stoeter, P., Treede, R. D. & Tracey, I. (2010). Multiple somatotopic representations of heat and mechanical pain in the operculo-insular cortex: A high-resolution fMRI study. *Journal of Neurophysiology*, 104 (5), 2863-2872. [10.1152/jn.00253.2010](https://doi.org/10.1152/jn.00253.2010)
- Bekrater-Bodmann, R., Foell, J., Diers, M., Kamping, S., Rance, M., Kirsch, P. & Flor, H. (2014). The importance of synchrony and temporal order of visual and tactile input for illusory limb ownership experiences - An fMRI study applying virtual reality. *PLoS One*, 9 (1), e87013-e87013. [10.1371/journal.pone.0087013](https://doi.org/10.1371/journal.pone.0087013)
- Bense, S., Stephan, T., Yousry, T. A., Brandt, T. & Dieterich, M. (2001). Multisensory cortical signal increases and decreases during vestibular galvanic stimulation (fMRI). *Journal of Neurophysiology*, 85 (2), 886-899.
- Berlucchi, G. & Aglioti, S. M. (2010). The body in the brain revisited. *Experimental Brain Research*, 200 (1), 25-35. [10.1007/s00221-009-1970-7](https://doi.org/10.1007/s00221-009-1970-7)
- Bermúdez, J. L. (1998). *The paradox of self-consciousness*. Cambridge, MA: MIT Press.
- Berthoz, A. (1996). How does the cerebral cortex process and utilize vestibular signals? In R. W. Baloh & G. M. Halmagyi (Eds.) *Disorders of the vestibular system* (pp. 113-125). New York, NY: Oxford University Press.
- (2000). *The brain's sense of movement*. Cambridge, MA: Harvard University Press.
- Bester, H., Menendez, L., Besson, J. M. & Bernard, J. (1995). Spino (trigemino) parabrachiohypothalamic pathway: Electrophysiological evidence for an involvement in pain processes. *Journal of Neurophysiology*, 73 (2), 568-585.
- Bisiach, E., Rusconi, M. L. & Vallar, G. (1991). Remission of somatoparaphrenic delusion through vestibular stimulation. *Neuropsychologia*, 29 (10), 1029-1031. [10.1016/0028-3932\(91\)90066-H](https://doi.org/10.1016/0028-3932(91)90066-H)
- Blanke, O. & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Neuroscience*, 13 (1), 7-13. [10.1016/j.tics.2008.10.003](https://doi.org/10.1016/j.tics.2008.10.003)
- Blanke, O. & Mohr, C. (2005). Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin: Implications for neurocognitive mechanisms of corporeal awareness and self-consciousness. *Brain Research Reviews*, 50 (1), 184-199. [10.1016/j.brainresrev.2005.05.008](https://doi.org/10.1016/j.brainresrev.2005.05.008)
- Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, 13 (8), 556-571. [10.1038/nrn3292](https://doi.org/10.1038/nrn3292)
- Blanke, O., Landis, T., Spinelli, L. & Seeck, M. (2004). Out-of-body experience and autoscopia of neurological origin. *Brain*, 127 (2), 243-258. [10.1093/brain/awh040](https://doi.org/10.1093/brain/awh040)
- Blanke, O., Mohr, C., Michel, C. M., Pascual-Leone, A., Brugger, P., Seeck, M., Landis, T. & Thut, G. (2005). Linking out-of-body experience and self processing to mental own-body imagery at the temporoparietal junction. *Journal of Neuroscience*, 25 (3), 550-557. [10.1523/JNEUROSCI.2612-04.2005](https://doi.org/10.1523/JNEUROSCI.2612-04.2005)
- Blanke, O., Ortigue, S., Landis, T. & Seeck, M. (2002). Stimulating illusory own-body perceptions. *Nature*, 419 (6904), 269-270. [10.1038/419269a](https://doi.org/10.1038/419269a)
- Boccarda, C. N., Sargolini, F., Thoresen, V. H., Solstad, T., Witter, M., Moser, E. I. & Moser, M. B. (2010). Grid cells in pre- and parasubiculum. *Nature Neuroscience*, 13 (8), 987-994. [10.1038/nn.2602](https://doi.org/10.1038/nn.2602)
- Bonnier, P. (1905). L'Aschématie. *Revue Neurologique*, 13, 605-609.
- Bottini, G., Karnath, H. O., Vallar, G., Sterzi, R., Frith, C. D., Frackowiak, R. S. & Paulesu, E. (2001). Cerebral representations for egocentric space: Functional-anatomical evidence from caloric vestibular stimulation and neck vibration. *Brain*, 124 (6), 1182-1196. [10.1093/brain/124.6.1182](https://doi.org/10.1093/brain/124.6.1182)
- Bottini, G., Paulesu, E., Gandola, M., Loffredo, S., Scarpa, P., Sterzi, R., Santilli, I., Defanti, C., Scialfa, G., Fazio, F. & Vallar, G. (2005). Left caloric vestibular stimulation ameliorates right hemianesthesia. *Neurology*, 65 (8), 1278-1283. [10.1212/01.wnl.0000182398.14088.e8](https://doi.org/10.1212/01.wnl.0000182398.14088.e8)
- Bottini, G., Paulesu, E., Sterzi, R., Warburton, E., Wise, R. J., Vallar, G., Frackowiak, R. & Frith, C. D. (1995). Modulation of conscious experience by peripheral sens-

- ory stimuli. *Nature*, 376 (6543), 778-781. [10.1038/376778a0](#)
- Bottini, G., Sterzi, R., Paulesu, E., Vallar, G., Cappa, S. F., Erminio, F., Passingham, R., Frith, C. & Frackowiak, R. S. (1994). Identification of the central vestibular projections in man: A positron emission tomography activation study. *Experimental Brain Research*, 99 (1), 164-169. [10.1007/BF00241421](#)
- Botvinick, M. & Cohen, J. (1998). Rubber hands “feel” touch that eyes see. *Nature*, 391 (6669), 756-756. [10.1038/35784](#)
- Brandt, T., Schautzer, F., Hamilton, D. A., Bruning, R., Markowitsch, H. J., Kalla, R., Darlington, C., Smith, P. & Strupp, M. (2005). Vestibular loss causes hippocampal atrophy and impaired spatial memory in humans. *Brain*, 128 (11), 2732-2741. [10.1093/brain/awh617](#)
- Bremmer, F., Klam, F., Duhamel, J. R., Ben Hamed, S. & Graf, W. (2002). Visual-vestibular interactive responses in the macaque ventral intraparietal area (VIP). *European Journal of Neuroscience*, 16 (8), 1569-1586. [10.1046/j.1460-9568.2002.02206.x](#)
- Bremmer, F., Kubischik, M., Pekel, M., Lappe, M. & Hoffmann, K. P. (1999). Linear vestibular self-motion signals in monkey medial superior temporal area. *Annals of the New York Academy of Sciences*, 871 (1), 272-281. [10.1111/j.1749-6632.1999.tb09191.x](#)
- Bremmer, F., Schlack, A., Duhamel, J. R., Graf, W. & Fink, G. R. (2001). Space coding in primate posterior parietal cortex. *NeuroImage*, 14 (1), 46-51. [10.1006/nimg.2001.0817](#)
- Bresciani, J. P., Blouin, J., Popov, K., Bourdin, C., Sarlegna, F., Vercher, J. L. & Gauthier, G. M. (2002). Galvanic vestibular stimulation in humans produces online arm movement deviations when reaching towards memorized visual targets. *Neuroscience Letters*, 318 (1), 34-38. [10.1016/S0304-3940\(01\)02462-4](#)
- Brugger, P., Agosti, R., Regard, M., Wieser, H. G. & Landis, T. (1994). Heautoscopy, epilepsy, and suicide. *Journal of Neurology, Neurosurgery, and Psychiatry*, 57 (7), 838-839. [10.1136/jnnp.57.7.838](#)
- Bufalari, I., Lenggenhager, B., Porciello, G., Serra Holmes, B. & Aglioti, S. M. (2014). Enfacing others but only if they are nice to you. *Frontiers in Behavioral Neuroscience*, 8 (102), 1-12. [10.3389/fnbeh.2014.00102](#)
- Bunning, S. & Blanke, O. (2005). The out-of body experience: Precipitating factors and neural correlates. *Progress in Brain Research*, 150, 331-350. [10.1016/S0079-6123\(05\)50024-4](#)
- Burgess, N. & O’Keefe, J. (2003). Neural representations in human spatial memory. *Trends in Cognitive Sciences*, 7 (12), 517-519. [10.1016/j.tics.2003.10.014](#)
- Candidi, M., Micarelli, A., Viziano, A., Aglioti, S. M., Minio-Paluello, I. & Alessandrini, M. (2013). Impaired mental rotation in benign paroxysmal positional vertigo and acute vestibular neuritis. *Frontiers in Human Neuroscience*, 7, 1-11. [10.3389/fnhum.2013.00783](#)
- Capelari, E. D., Uribe, C. & Brasil-Neto, J. P. (2009). Feeling pain in the rubber hand: Integration of visual, proprioceptive, and painful stimuli. *Perception*, 38 (1), 92-99. [10.1068/p5892](#)
- Carruthers, G. (2008). Types of body representation and the sense of embodiment. *Consciousness and Cognition*, 17 (4), 1302-1316. [10.1016/j.concog.2008.02.001](#)
- Chen, A., DeAngelis, G. C. & Angelaki, D. E. (2010). Macaque parieto-insular vestibular cortex: Responses to self-motion and optic flow. *Journal of Neuroscience*, 30 (8), 3022-3042. [10.1523/JNEUROSCI.4029-09.2010](#)
- (2011). A comparison of vestibular spatiotemporal tuning in macaque parietoinsular vestibular cortex, ventral intraparietal area, and medial superior temporal area. *Journal of Neuroscience*, 31 (8), 3082-3094. [10.1523/JNEUROSCI.4476-10.2011](#)
- Cole, J. (2004). *Still lives*. Cambridge, MA: MIT Press.
- Coq, J. Q., Qi, H., Collins, C. E. & Kaas, J. H. (2004). Anatomical and functional organization of somatosensory areas of the lateral fissure of the new world titi monkey (*Callicebus moloch*). *The Journal of Comparative Neurology*, 476 (4), 363-387. [10.1002/cne.20237](#)
- Corradi-Dell’acqua, C., Ueno, K., Ogawa, A., Cheng, K., Rumiati, R. I. & Iriki, A. (2008). Effects of shifting perspective of the self: An fMRI study. *NeuroImage*, 40 (4), 1902-1911. [10.1016/j.neuroimage.2007.12.062](#)
- Courtial, E. & Wilson, D. A. (2014). Thalamic olfaction: Characterizing odor processing in the mediodorsal thalamus of the rat. *Journal of Neurophysiology*, 111 (6), 1274-1285. [10.1152/jn.00741.2013](#)
- Craig, A. D. (2009). How do you feel-now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, 10, 59-70. [10.1038/nrn2555](#)
- Cullen, K. E. (2011). The neural encoding of self-motion. *Current Opinion in Neurobiology*, 21 (4), 587-595. [10.1016/j.conb.2011.05.022](#)
- (2012). The vestibular system: Multimodal integration and encoding of self-motion for motor control.

- Trends in Neurosciences*, 35 (3), 185-196.
[10.1016/j.tins.2011.12.001](https://doi.org/10.1016/j.tins.2011.12.001)
- Cullen, K. E., Roy, J. E. & Sylvestre, P. A. (2003). Signal processing in vestibular nuclei: Dissociating sensory, motor, and cognitive influence. In L. Harris & M. Jenkin (Eds.) *Levels of perception* (pp. 285-309). Berlin, GER: Springer.
- David, N., Bewernick, B. H., Cohen, M. X., Newen, A., Lux, S., Fink, G. R. & Vogeley, K. (2006). Neural representations of self versus other: Visual-spatial perspective taking and agency in a virtual ball-tossing game. *Journal of Cognitive Neuroscience*, 18 (6), 898-910. [10.1162/jocn.2006.18.6.898](https://doi.org/10.1162/jocn.2006.18.6.898)
- David, N., Fiori, F. & Aglioti, S. M. (2014). Susceptibility to the rubber hand illusion does not tell the whole body-awareness story. *Cognitive, Affective & Behavioral Neuroscience*, 14 (1), 297-306.
[10.3758/s13415-013-0190-6](https://doi.org/10.3758/s13415-013-0190-6)
- Day, B. L. & Fitzpatrick, R. C. (2005). The vestibular system. *Current Biology*, 15 (15), R583-R586.
[10.1016/j.cub.2005.07.053](https://doi.org/10.1016/j.cub.2005.07.053)
- De Vignemont, F. (2010). Body schema and body image-pros and cons. *Neuropsychologia*, 48 (3), 669-680.
[10.1016/j.neuropsychologia.2009.09.022](https://doi.org/10.1016/j.neuropsychologia.2009.09.022)
- Deroualle, D. & Lopez, C. (2014). Toward a vestibular contribution to social cognition. *Frontiers in Integrative Neuroscience*, 8, 1-4. [10.3389/fnint.2014.00016](https://doi.org/10.3389/fnint.2014.00016)
- Dichgans, J. & Brandt, T. (1978). Visual-vestibular interaction: Effects on self-motion perception and postural control. In H. Autrum, R. Jung, W. R. Loewenstein, D. M. MacKay & H. L. Teuber (Eds.) *Handbook of sensory physiology* (pp. 755-804). Berlin, GER: Springer.
- Dieterich, M., Bense, S., Lutz, S., Drzezga, A., Stephan, T., Bartenstein, P. & Brandt, T. (2003). Dominance for vestibular cortical function in the non-dominant hemisphere. *Cerebral Cortex*, 13 (9), 994-1007.
[10.1093/cercor/13.9.994](https://doi.org/10.1093/cercor/13.9.994)
- Dilda, V., MacDougall, H. G., Curthoys, I. S. & Moore, S. T. (2012). Effects of galvanic vestibular stimulation on cognitive function. *Experimental Brain Research*, 216 (2), 275-285. [10.1007/s00221-011-2929-z](https://doi.org/10.1007/s00221-011-2929-z)
- Dobricki, M. & de la Rosa, S. (2013). The structure of conscious bodily self-perception during full-body illusions. *PLoS One*, 8 (12), e83840-e83840.
[10.1371/journal.pone.0083840](https://doi.org/10.1371/journal.pone.0083840)
- Doeller, C. F., Barry, C. & Burgess, N. (2010). Evidence for grid cells in a human memory network. *Nature*, 463 (7281), 657-661. [10.1038/nature08704](https://doi.org/10.1038/nature08704)
- Ebata, S., Sugiuchi, Y., Izawa, Y., Shinomiya, K. & Shinoda, Y. (2004). Vestibular projection to the periaudate cortex in the monkey. *Neuroscience Research*, 49 (1), 55-68. [10.1016/j.neures.2004.01.012](https://doi.org/10.1016/j.neures.2004.01.012)
- Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science*, 317 (5841), 1048-1048. [10.1126/science.1142175](https://doi.org/10.1126/science.1142175)
- Ehrsson, H. H., Spence, C. & Passingham, R. E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science*, 305 (5685), 875-877. [10.1126/science.1097011](https://doi.org/10.1126/science.1097011)
- Ehrsson, H. H., Wiech, K., Weiskopf, N., Dolan, R. J. & Passingham, R. E. (2007). Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proceedings of the National Academy of Sciences of the United States of America*, 104 (23), 9828-9833.
[10.1073/pnas.0610011104](https://doi.org/10.1073/pnas.0610011104)
- Eickhoff, S. B., Weiss, P. H., Amunts, K., Fink, G. R. & Zilles, K. (2006). Identifying human parieto-insular vestibular cortex using fMRI and cytoarchitectonic mapping. *Human Brain Mapping*, 27 (7), 611-621.
[10.1002/hbm.20205](https://doi.org/10.1002/hbm.20205)
- Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L. & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature*, 425 (6954), 184-188.
[10.1038/nature01964](https://doi.org/10.1038/nature01964)
- Falconer, C. J. & Mast, F. W. (2012). Balancing the mind: Vestibular induced facilitation of egocentric mental transformations. *Experimental Psychology*, 59 (6), 332-339. [10.1027/1618-3169/a000161](https://doi.org/10.1027/1618-3169/a000161)
- Farrer, C., Franck, N., Georgieff, N., Frith, C. D., Decety, J. & Jeannerod, M. (2003a). Modulating the experience of agency: A positron emission tomography study. *NeuroImage*, 18 (2), 324-333.
[10.1016/S1053-8119\(02\)00041-1](https://doi.org/10.1016/S1053-8119(02)00041-1)
- Farrer, C., Franck, N., Paillard, J. & Jeannerod, M. (2003b). The role of proprioception in action recognition. *Consciousness and Cognition*, 12 (4), 609-619.
[10.1016/S1053-8100\(03\)00047-3](https://doi.org/10.1016/S1053-8100(03)00047-3)
- Farrer, C., Frey, S. H., Van Horn, J. D., Tunik, E., Turk, D., Inati, S. & Grafton, S. T. (2008). The angular gyrus computes action awareness representations. *Cerebral Cortex*, 18, 254-261.
[10.1016/S1053-8100\(03\)00047-3](https://doi.org/10.1016/S1053-8100(03)00047-3)
- Fasold, O., von Brevern, M., Kuhberg, M., Ploner, C. J., Villringer, A., Lempert, T. & Wenzel, R. (2002). Human vestibular cortex as identified with caloric stimulation in functional magnetic resonance imaging.

- NeuroImage*, 17 (3), 1384-1393.
[10.1006/nimg.2002.1241](https://doi.org/10.1006/nimg.2002.1241)
- Feil, K. & Herbert, H. (1995). Topographic organization of spinal and trigeminal somatosensory pathways to the rat parabrachial and Kölliker-Fuse nuclei. *The Journal of Comparative Neurology*, 353 (4), 506-528.
[10.1002/cne.903530404](https://doi.org/10.1002/cne.903530404)
- Fernández, C. & Goldberg, J. (1976). Physiology of peripheral neurons innervating otolith organs of the squirrel monkey. I. Response to static tilts and to long-duration centrifugal force. *Journal of Neurophysiology*, 39 (5), 970-984.
- Ferrè, E. R., Bottini, G. & Haggard, P. (2011). Vestibular modulation of somatosensory perception. *The European Journal of Neuroscience*, 34 (8), 1337-1344.
[10.1111/j.1460-9568.2011.07859.x](https://doi.org/10.1111/j.1460-9568.2011.07859.x)
- (2012). Vestibular inputs modulate somatosensory cortical processing. *Brain Structure & Function*, 217 (4), 859-864. [10.1007/s00429-012-0404-7](https://doi.org/10.1007/s00429-012-0404-7)
- Ferrè, E. R., Vagnoni, E. & Haggard, P. (2013). Vestibular contributions to bodily awareness. *Neuropsychologia*, 51 (8), 1445-1452.
[10.1016/j.neuropsychologia.2013.04.006](https://doi.org/10.1016/j.neuropsychologia.2013.04.006)
- Filippetti, M. L., Johnson, M. H., Lloyd-Fox, S., Dragovic, D. & Farroni, T. (2013). Body perception in newborns. *Current Biology*, 23 (23), 2413-2416.
[10.1016/j.cub.2013.10.017](https://doi.org/10.1016/j.cub.2013.10.017)
- Fitzpatrick, R. C. & Day, B. L. (2004). Probing the human vestibular system with galvanic stimulation. *Journal of Applied Physiology*, 96 (6), 2301-2316.
[10.1152/jappphysiol.00008.2004](https://doi.org/10.1152/jappphysiol.00008.2004)
- Fitzpatrick, R. C., Marsden, J., Lord, S. R. & Day, B. L. (2002). Galvanic vestibular stimulation evokes sensations of body rotation. *Neuroreport*, 13 (18), 2379-2383.
[10.1097/01.wnr.0000048002.96487.de](https://doi.org/10.1097/01.wnr.0000048002.96487.de)
- Fourneret, P. & Jeannerod, M. (1998). Limited conscious monitoring of motor performance in normal subjects. *Neuropsychologia*, 36 (11), 1133-1140.
[10.1016/S0028-3932\(98\)00006-2](https://doi.org/10.1016/S0028-3932(98)00006-2)
- Fourneret, P., Franck, N., Slachevsky, A. & Jeannerod, M. (2001). Self-monitoring in schizophrenia revisited. *NeuroReport*, 12 (6), 1203-1208.
[10.1097/00001756-200105080-00030](https://doi.org/10.1097/00001756-200105080-00030)
- Friston, K. (2012). Predictive coding, precision and synchrony. *Cognitive Neuroscience*, 3 (3-4), 238-239.
[10.1080/17588928.2012.691277](https://doi.org/10.1080/17588928.2012.691277)
- Fukushima, K. (1997). Cortico-vestibular interactions: Anatomy, electrophysiology, and functional considerations. *Experimental Brain Research*, 117 (1), 1-16.
[10.1007/PL00005786](https://doi.org/10.1007/PL00005786)
- Fukushima, J., Akao, T., Kurkin, S., Kaneko, C. R. & Fukushima, K. (2006). The vestibular-related frontal cortex and its role in smooth-pursuit eye movements and vestibular-pursuit interactions. *Journal of Vestibular Research*, 16 (1-2), 1-22.
- Furlanetto, T., Bertone, C. & Becchio, C. (2013). The bi-located mind: New perspectives on self-localization and self-identification. *Frontiers in Human Neuroscience*, 7, 1-6. [10.3389/fnhum.2013.00071](https://doi.org/10.3389/fnhum.2013.00071)
- Furman, D. J., Waugh, C. E., Bhattacharjee, K., Thompson, R. J. & Gotlib, I. H. (2013). Interoceptive awareness, positive affect, and decision making in Major Depressive Disorder. *Journal of Affective Disorders*, 151 (2), 780-785. [10.1016/j.jad.2013.06.044](https://doi.org/10.1016/j.jad.2013.06.044)
- Furuya, Y., Matsumoto, J., Hori, E., Boas, C. V., Tran, A. H., Shimada, Y. & Nishijo, H. (2014). Place-related neuronal activity in the monkey parahippocampal gyrus and hippocampal formation during virtual navigation. *Hippocampus*, 24 (1), 113-130.
[10.1002/hipo.22209](https://doi.org/10.1002/hipo.22209)
- Fyhn, M., Hafting, T., Witter, M. P., Moser, E. & Moser, M. B. (2008). Grid cells in mice. *Hippocampus*, 18 (12), 1230-1238. [10.1002/hipo.20472](https://doi.org/10.1002/hipo.20472)
- Gallagher, S. (2000). Philosophical conceptions of the self: Implications for cognitive science. *Trends in Cognitive Neuroscience*, 4 (1), 14-21.
[10.1016/S1364-6613\(99\)01417-5](https://doi.org/10.1016/S1364-6613(99)01417-5)
- (2005). *How the body shapes the mind*. New York, NY: Oxford University Press.
- Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119 (2), 593-609. [10.1093/brain/119.2.593](https://doi.org/10.1093/brain/119.2.593)
- Ganesh, S., van Schie, H. T., de Lange, F. P., Thompson, E. & Wigboldus, D. H. J. (2012). How the human brain goes virtual: Distinct cortical regions of the person-processing network are involved in self-identification with virtual agents. *Cerebral Cortex*, 22 (7), 1577-1585. [10.1093/cercor/bhr227](https://doi.org/10.1093/cercor/bhr227)
- Gentsch, A. & Schütz-Bosbach, S. (2011). I did it: Unconscious expectation of sensory consequences modulates the experience of self-agency and its functional signature. *Journal of Cognitive Neuroscience*, 23 (12), 3817-3828. [10.1162/jocn_a_00012](https://doi.org/10.1162/jocn_a_00012)
- Gilbert, J. W., Vogt, M., Windsor, R. E., Mick, G. E., Richardson, G. B., Storey, B. B. & Maddox, M. L. (2014). Vestibular dysfunction in patients with chronic pain or underlying neurologic disorders. *The Journal of the American Osteopathic Association*, 114 (3), 172-178. [10.7556/jaoa.2014.034](https://doi.org/10.7556/jaoa.2014.034)

- Glasauer, S., Amorim, M. A., Vitte, E. & Berthoz, A. (1994). Goal-directed linear locomotion in normal and labyrinthine-defective subjects. *Experimental Brain Research*, 98 (2), 323-335. [10.1007/BF00228420](https://doi.org/10.1007/BF00228420)
- Green, C. (1968). *Out-of-body experiences*. Oxford, UK: Institute of Psychophysical Research.
- Grüsser, O. J., Guldin, W. O., Mirring, S. & Salah-Eldin, A. (1994). Comparative physiological and anatomical studies of the primate vestibular cortex. In B. Al-bowitz, K. Albus, U. Kuhnt, H. C. Nothdurf & P. Wahle (Eds.) *Structural and functional organization of the neocortex* (pp. 358-371). Berlin, GER: Springer.
- Grüsser, O. J., Pause, M. & Schreier, U. (1990a). Localization and responses of neurones in the parieto-insular vestibular cortex of awake monkeys (*Macaca fascicularis*). *Journal of Physiology*, 430, 537-557.
- (1990b). Vestibular neurones in the parieto-insular cortex of monkeys (*Macaca fascicularis*): Visual and neck receptor responses. *Journal of Physiology*, 430, 559-583.
- Gu, Y., DeAngelis, G. C. & Angelaki, D. E. (2007). A functional link between area MSTd and heading perception based on vestibular signals. *Nature Neuroscience*, 10 (8), 1038-1047. [10.1038/nn1935](https://doi.org/10.1038/nn1935)
- Guillaud, E., Simoneau, M. & Blouin, J. (2011). Prediction of the body rotation-induced torques on the arm during reaching movements: Evidence from a proprioceptively deafferented subject. *Neuropsychologia*, 49 (7), 2055-2059. [10.1016/j.neuropsychologia.2011.03.035](https://doi.org/10.1016/j.neuropsychologia.2011.03.035)
- Guldin, W. O. & Grüsser, O. J. (1998). Is there a vestibular cortex? *Trends in Neuroscience*, 21 (6), 254-359. [10.1016/S0166-2236\(97\)01211-3](https://doi.org/10.1016/S0166-2236(97)01211-3)
- Guldin, W. O., Akbarian, S. & Grüsser, O. J. (1992). Cortico-cortical connections and cytoarchitectonics of the primate vestibular cortex: A study in squirrel monkeys (*Saimiri sciureus*). *Journal of Comparative Neurology*, 326 (3), 375-401. [10.1002/cne.903260306](https://doi.org/10.1002/cne.903260306)
- Gutiérrez-Martínez, O., Gutiérrez-Maldonado, J. & Loreto-Quijada, D. (2011). Control over the virtual environment influences the presence and efficacy of a virtual reality intervention on pain. *Studies in Health Technology and Informatics*, 167, 111-115. [10.3233/978-1-60750-766-6-111](https://doi.org/10.3233/978-1-60750-766-6-111)
- Hänsel, A., Lenggenhager, B., von Känel, R., Curatolo, M. & Blanke, O. (2011). Seeing and identifying with a virtual body decreases pain perception. *European Journal of Pain*, 15 (8), 874-879. [10.1016/j.ejpain.2011.03.013](https://doi.org/10.1016/j.ejpain.2011.03.013)
- Herbert, H., Moga, M. M. & Saper, C. B. (1990). Connections of the parabrachial nucleus with the nucleus of the solitary tract and the medullary reticular formation in the rat. *The Journal of Comparative Neurology*, 293 (4), 540-580. [10.1002/cne.902930404](https://doi.org/10.1002/cne.902930404)
- Heydrich, L. & Blanke, O. (2013). Distinct illusory own-body perceptions caused by damage to posterior insula and extrastriate cortex. *Brain*, 136 (3), 790-803. [10.1093/brain/aws364](https://doi.org/10.1093/brain/aws364)
- Hoffman, H. G., Sharar, S. R., Coda, B., Everett, J. J., Ciol, M., Richards, T. & Patterson, D. R. (2004). Manipulating presence influences the magnitude of virtual reality analgesia. *Pain*, 111 (1-2), 162-168. [10.1016/j.pain.2004.06.013](https://doi.org/10.1016/j.pain.2004.06.013)
- Hüfner, K., Hamilton, D. A., Kalla, R., Stephan, T., Glasauer, S., Ma, J. & Brandt, T. (2007). Spatial memory and hippocampal volume in humans with unilateral vestibular deafferentation. *Hippocampus*, 17 (6), 471-485. [10.1002/hipo.20283](https://doi.org/10.1002/hipo.20283)
- Indovina, I., Maffei, V., Bosco, G., Zago, M., Macaluso, E. & Lacquaniti, F. (2005). Representation of visual gravitational motion in the human vestibular cortex. *Science*, 308 (5720), 416-419. [10.1126/science.1107961](https://doi.org/10.1126/science.1107961)
- Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D. & Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron*, 70 (2), 363-374. [10.1016/j.neuron.2011.03.009](https://doi.org/10.1016/j.neuron.2011.03.009)
- Ionta, S., Perruchoud, D., Draganski, B. & Blanke, O. (2012). Body context and posture affect mental imagery of hands. *PLoS One*, 7 (3), e34382-e34382. [10.1371/journal.pone.0034382](https://doi.org/10.1371/journal.pone.0034382)
- Jacobs, J., Weidemann, C. T., Miller, J. F., Solway, A., Burke, J. F., Wei, X. X. & Kahana, M. J. (2013). Direct recordings of grid-like neuronal activity in human spatial navigation. *Nature Neuroscience*, 16 (9), 1188-1190. [10.1038/nn.3466](https://doi.org/10.1038/nn.3466)
- Jasmin, L., Burke, A. R., Card, J. P. & Basbaum, A. I. (1997). Transneuronal labeling of a nociceptive pathway, the spino-(trigemino-)parabrachio-amygdaloid, in the rat. *Journal of Neuroscience*, 17 (10), 3751-3765.
- Jauregui-Renaud, K., Villanueva, P. L. & del Castillo, M. S. (2005). Influence of acute unilateral vestibular lesions on the respiratory rhythm after active change of posture in human subjects. *Journal of Vestibular Research*, 15 (1), 41-48.
- Jeannerod, M. (2003). The mechanism of self-recognition in humans. *Behavioural Brain Research*, 142 (1-2), 1-15. [10.1016/S0166-4328\(02\)00384-4](https://doi.org/10.1016/S0166-4328(02)00384-4)

- (2006). *Motor cognition: What actions tell to the self*. Oxford, UK: Oxford University Press.
- Kannape, O. A., Schwabe, L., Tadi, T. & Blanke, O. (2010). The limits of agency in walking humans. *Neuropsychologia*, 48 (6), 1628-1636. [10.1016/j.neuropsychologia.2010.02.005](https://doi.org/10.1016/j.neuropsychologia.2010.02.005)
- Kavounoudias, A., Roll, R. & Roll, J. P. (1998). The plantar sole is a “dynamometric map” for human balance control. *NeuroReport*, 9 (14), 3247-3252.
- Kerkhoff, G., Hildebrandt, H., Reinhart, S., Kardinal, M., Dimova, V. & Utz, K. S. (2011). A long-lasting improvement of tactile extinction after galvanic vestibular stimulation: Two Sham-stimulation controlled case studies. *Neuropsychologia*, 49 (2), 186-195. [10.1016/j.neuropsychologia.2010.11.014](https://doi.org/10.1016/j.neuropsychologia.2010.11.014)
- Kessler, K. & Thomson, L. A. (2010). The embodied nature of spatial perspective taking: Embodied transformation versus sensorimotor interference. *Cognition*, 114 (1), 72-88. [10.1016/j.cognition.2009.08.015](https://doi.org/10.1016/j.cognition.2009.08.015)
- Keysers, C., Wicker, B., Gazzola, V., Anton, J. L., Fogassi, L. & Gallese, V. (2004). A touching sight: SII/PV activation during the observation and experience of touch. *Neuron*, 42 (2), 335-346. [10.1016/S0896-6273\(04\)00156-4](https://doi.org/10.1016/S0896-6273(04)00156-4)
- Killian, N. J., Jutras, M. J. & Buffalo, E. A. (2012). A map of visual space in the primate entorhinal cortex. *Nature*, 491 (7426), 761-764. [10.1038/nature11587](https://doi.org/10.1038/nature11587)
- Kim, Y. R., Son, J. W., Lee, S. I., Shin, C. J., Kim, S. K., Ju, G. & Ha, T. H. (2012). Abnormal brain activation of adolescent internet addict in a ball-throwing animation task: Possible neural correlates of disembodiment revealed by fMRI. *Progress in Neuro-Psychopharmacology & Biological Psychiatry*, 39 (1), 88-95. [10.1016/j.pnpbp.2012.05.013](https://doi.org/10.1016/j.pnpbp.2012.05.013)
- Klam, F. & Graf, W. (2003). Vestibular signals of posterior parietal cortex neurons during active and passive head movements in macaque monkeys. *Annals of the New York Academy of Sciences*, 1004, 271-282. [10.1196/annals.1303.024](https://doi.org/10.1196/annals.1303.024)
- (2006). Discrimination between active and passive head movements by macaque ventral and medial intraparietal cortex neurons. *Journal of Physiology*, 574 (2), 367-386. [10.1113/jphysiol.2005.103697](https://doi.org/10.1113/jphysiol.2005.103697)
- Kotchabhakdi, N., Rinvik, E., Walberg, F. & Yingchareon, K. (1980). The vestibulo-thalamic projections in the cat studied by retrograde axonal transport of horseradish peroxidase. *Experimental Brain Research*, 40 (4), 405-418. [10.1007/BF00236149](https://doi.org/10.1007/BF00236149)
- Kurth, F., Zilles, K., Fox, P. T., Laird, A. R. & Eickhoff, S. B. (2010). A link between the systems: Functional differentiation and integration within the human insula revealed by meta-analysis. *Brain Structure and Function*, 214 (5-6), 519-534. [10.1007/s00429-010-0255-z](https://doi.org/10.1007/s00429-010-0255-z)
- Lackner, J. R. & DiZio, P. (2005). Vestibular, proprioceptive, and haptic contributions to spatial orientation. *Annual Reviews of Psychology*, 56, 115-147. [10.1146/annurev.psych.55.090902.142023](https://doi.org/10.1146/annurev.psych.55.090902.142023)
- Lackner, J. R. (1992). Spatial orientation in weightless environments. *Perception*, 21 (6), 803-812. [10.1068/p210803](https://doi.org/10.1068/p210803)
- Lacquaniti, F., Bosco, G., Indovina, I., La Scaleia, B., Maffei, V., Moscatelli, A. & Zago, M. (2013). Visual gravitational motion and the vestibular system in humans. *Frontiers in Integrative Neuroscience*, 7, 1-12. [10.3389/fnint.2013.00101](https://doi.org/10.3389/fnint.2013.00101)
- Lai, H., Tsumori, T., Shiroyama, T., Yokota, S., Nakano, K. & Yasui, Y. (2000). Morphological evidence for a vestibulo-thalamo-striatal pathway via the parafascicular nucleus in the rat. *Brain Research*, 872 (1-2), 208-214. [10.1016/S0006-8993\(00\)02457-4](https://doi.org/10.1016/S0006-8993(00)02457-4)
- Lambrey, S., Doeller, C., Berthoz, A. & Burgess, N. (2012). Imagining being somewhere else: Neural basis of changing perspective in space. *Cerebral Cortex*, 22 (1), 166-174. [10.1093/cercor/bhr101](https://doi.org/10.1093/cercor/bhr101)
- Lamm, C., Decety, J. & Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *NeuroImage*, 54 (3), 2492-2502. [10.1016/j.neuroimage.2010.10.014](https://doi.org/10.1016/j.neuroimage.2010.10.014)
- Legrand, D. (2007). Pre-reflective self-consciousness: On being bodily in the world. *Janus Head*, 9 (2), 493-519.
- Lenggenhager, B., Azevedo, R. T., Mancini, A. & Aglioti, S. M. (2013). Listening to your heart and feeling yourself: Effects of exposure to interoceptive signals during the ultimatum game. *Experimental Brain Research*, 230 (2), 233-241. [10.1007/s00221-013-3647-5](https://doi.org/10.1007/s00221-013-3647-5)
- Lenggenhager, B., Halje, P. & Blanke, O. (2011). Alpha band oscillations correlate with illusory self-location induced by virtual reality. *European Journal of Neuroscience*, 33 (10), 1935-1943. [10.1111/j.1460-9568.2011.07647.x](https://doi.org/10.1111/j.1460-9568.2011.07647.x)
- Lenggenhager, B., Lopez, C. & Blanke, O. (2008). Influence of galvanic vestibular stimulation on egocentric and object-based mental transformations. *Experimental Brain Research*, 184 (2), 211-221. [10.1007/s00221-007-1095-9](https://doi.org/10.1007/s00221-007-1095-9)

- Lenggenhager, B., Mouthon, M. & Blanke, O. (2009). Spatial aspects of bodily self-consciousness. *Consciousness and Cognition*, 18 (1), 110-117. [10.1016/j.concog.2008.11.003](https://doi.org/10.1016/j.concog.2008.11.003)
- Lenggenhager, B., Pazzaglia, M., Scivoletto, G., Molinari, M. & Aglioti, S. . (2012). The sense of the body in individuals with spinal cord injury. *PLoS ONE*, 7 (11), e50757-e50757. [10.1371/journal.pone.0050757](https://doi.org/10.1371/journal.pone.0050757)
- Lenggenhager, B., Tadi, T., Metzinger, T. & Blanke, O. (2007). Video ergo sum: Manipulating bodily self-consciousness. *Science*, 317 (5841), 1096-1099. [10.1126/science.1143439](https://doi.org/10.1126/science.1143439)
- Limanowski, J., Lutti, A. & Blankenburg, F. (2014). The extrastriate body area is involved in illusory limb ownership. *NeuroImage*, 86, 514-524. [10.1016/j.neuroimage.2013.10.035](https://doi.org/10.1016/j.neuroimage.2013.10.035)
- Liu, S., Dickman, J. D. & Angelaki, D. E. (2011). Response dynamics and tilt versus translation discrimination in parietoinsular vestibular cortex. *Cerebral Cortex*, 21 (3), 563-573. [10.1093/cercor/bhq123](https://doi.org/10.1093/cercor/bhq123)
- Lobel, E., Kleine, J. F., Le Bihan, D., Leroy-Willig, A. & Berthoz, A. (1998). Functional MRI of galvanic vestibular stimulation. *Journal of Neurophysiology*, 80 (5), 2699-2709.
- Longo, M. R. & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences of the United States of America*, 107 (26), 11727-11732. [10.1073/pnas.1003483107](https://doi.org/10.1073/pnas.1003483107)
- Longo, M. R., Schuur, F., Kammers, M. P., Tsakiris, M. & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition*, 107 (3), 978-998. [10.1016/j.cognition.2007.12.004](https://doi.org/10.1016/j.cognition.2007.12.004)
- Lopez, C. & Blanke, O. (2011). The thalamocortical vestibular system in animals and humans. *Brain Research Reviews*, 67 (1-2), 119-146. [10.1016/j.brainresrev.2010.12.002](https://doi.org/10.1016/j.brainresrev.2010.12.002)
- Lopez, C. (2013). A neuroscientific account of how vestibular disorders impair bodily self-consciousness. *Frontiers in Integrative Neuroscience*, 7, 1-8. [10.3389/fnint.2013.00091](https://doi.org/10.3389/fnint.2013.00091)
- Lopez, C., Blanke, O. & Mast, F. W. (2012). The vestibular cortex in the human brain revealed by coordinate-based activation likelihood estimation meta-analysis. *Neuroscience*, 212, 159-179. [10.1016/j.neuroscience.2012.03.028](https://doi.org/10.1016/j.neuroscience.2012.03.028)
- Lopez, C., Falconer, C. J. & Mast, F. W. (2013). Being moved by the self and others: Influence of empathy on self-motion perception. *PLoS One*, 8 (1), e48293-e48293. [10.1371/journal.pone.0048293](https://doi.org/10.1371/journal.pone.0048293)
- Lopez, C., Halje, P. & Blanke, O. (2008). Body ownership and embodiment: Vestibular and multisensory mechanisms. *Clinical Neurophysiology*, 38 (3), 149-161. [10.1016/j.neucli.2007.12.006](https://doi.org/10.1016/j.neucli.2007.12.006)
- Lopez, C., Lenggenhager, B. & Blanke, O. (2010). How vestibular stimulation interacts with illusory hand ownership. *Consciousness and Cognition*, 19 (1), 33-47. [10.1016/j.concog.2009.12.003](https://doi.org/10.1016/j.concog.2009.12.003)
- Lopez, C., Schreyer, H. M., Preuss, N. & Mast, F. W. (2012). Vestibular stimulation modifies the body schema. *Neuropsychologia*, 50 (8), 1830-1837. [10.1016/j.neuropsychologia.2012.04.008](https://doi.org/10.1016/j.neuropsychologia.2012.04.008)
- Ludvig, N., Tang, H. M., Gohil, B. C. & Botero, J. M. (2004). Detecting location-specific neuronal firing rate increases in the hippocampus of freely-moving monkeys. *Brain Research*, 1014 (1-2), 97-109. [10.1016/j.brainres.2004.03.071](https://doi.org/10.1016/j.brainres.2004.03.071)
- Macpherson, F. (2011). *The senses: Classic and contemporary philosophical perspectives*. Oxford, UK: Oxford University Press.
- Maister, L. & Tsakiris, M. (2014). My face, my heart: Cultural differences in integrated bodily self-awareness. *Cognitive Neuroscience*, 5 (1), 10-16. [10.1080/17588928.2013.808613](https://doi.org/10.1080/17588928.2013.808613)
- Makin, T. R., Holmes, N. P. & Ehrsson, H. H. (2008). On the other hand: Dummy hands and peripersonal space. *Behavioural Brain Research*, 191 (1), 1-10. [10.1016/j.bbr.2008.02.041](https://doi.org/10.1016/j.bbr.2008.02.041)
- Marlinski, V. & McCrea, R. A. (2008a). Activity of ventroposterior thalamus neurons during rotation and translation in the horizontal plane in the alert squirrel monkey. *Journal of Neurophysiology*, 99 (5), 2533-2545. [10.1152/jn.00761.2007](https://doi.org/10.1152/jn.00761.2007)
- (2008b). Coding of self-motion signals in ventroposterior thalamus neurons in the alert squirrel monkey. *Experimental Brain Research*, 189 (4), 463-472. [10.1007/s00221-008-1442-5](https://doi.org/10.1007/s00221-008-1442-5)
- Matsumura, N., Nishijo, H., Tamura, R., Eifuku, S., Endo, S. & Ono, T. (1999). Spatial- and task-dependent neuronal responses during real and virtual translocation in the monkey hippocampal formation. *Journal of Neuroscience*, 19 (6), 2381-2393.
- Mazzola, L., Faillenot, I., Barral, F. G., Mauguière, F. & Peyron, R. (2012). Spatial segregation of somato-sensory and pain activations in the human operculo-insular cortex. *NeuroImage*, 60 (1), 409-418. [10.1016/j.neuroimage.2011.12.072](https://doi.org/10.1016/j.neuroimage.2011.12.072)
- Mazzola, L., Isnard, J., Peyron, R., Guénot, M. & Mauguière, F. (2009). Somatotopic organization of pain

- responses to direct electrical stimulation of the human insular cortex. *Pain*, 146 (12), 99-104.
[10.1016/j.pain.2009.07.014](https://doi.org/10.1016/j.pain.2009.07.014)
- McCandless, C. H. & Balaban, C. D. (2010). Parabrachial nucleus neuronal responses to off-vertical axis rotation in macaques. *Experimental Brain Research*, 202 (2), 271-290. [10.1007/s00221-009-2130-9](https://doi.org/10.1007/s00221-009-2130-9)
- McGeoch, P. D., Williams, L. E., Lee, R. R. & Ramachandran, V. S. (2008). Behavioural evidence for vestibular stimulation as a treatment for central post-stroke pain. *Journal of Neurology, Neurosurgery and Psychiatry*, 79 (11), 1298-1301.
[10.1136/jnmp.2008.146738](https://doi.org/10.1136/jnmp.2008.146738)
- McHugh, T. J., Blum, K. I., Tsien, J. Z., Tonegawa, S. & Wilson, M. A. (1996). Impaired hippocampal representation of space in CA1-specific NMDAR1 knockout mice. *Cell*, 87 (7), 1339-1349.
[10.1016/S0092-8674\(00\)81828-0](https://doi.org/10.1016/S0092-8674(00)81828-0)
- McIntyre, J., Zago, M., Berthoz, A. & Lacquaniti, F. (2001). Does the brain model Newton's laws? *Nature Neuroscience*, 4 (7), 693-694. [10.1038/89477](https://doi.org/10.1038/89477)
- Meng, H., Bai, R. S., Sato, H., Imagawa, M., Sasaki, M. & Uchino, Y. (2001). Otolith-activated vestibulothalamic neurons in cats. *Experimental Brain Research*, 141 (4), 415-424. [10.1007/s00221-001-0902-y](https://doi.org/10.1007/s00221-001-0902-y)
- Meng, H., May, P. J., Dickman, J. D. & Angelaki, D. E. (2007). Vestibular signals in primate thalamus: Properties and origins. *Journal of Neuroscience*, 27 (50), 13590-13602. [10.1523/JNEUROSCI.3931-07.2007](https://doi.org/10.1523/JNEUROSCI.3931-07.2007)
- Metzinger, T. (2003). *Being no one. The self-model theory of subjectivity*. Cambridge, MA: Bradford Books.
- (2007). Empirical perspectives from the self-model theory of subjectivity: A brief summary with examples. *Progress in Brain Research*, 168, 215-278.
[10.1016/S0079-6123\(07\)68018-2](https://doi.org/10.1016/S0079-6123(07)68018-2)
- (2013). Why are dreams interesting for philosophers? The example of minimal phenomenal selfhood, plus an agenda for future research. *Frontiers in Psychology*, 4, 1-17. [10.3389/fpsyg.2013.00746](https://doi.org/10.3389/fpsyg.2013.00746)
- (2014). First-order embodiment, second-order embodiment, third-order embodiment. In L. Shapiro (Ed.) *The Routledge Handbook of Embodied Cognition*. London, UK: Routledge.
- Michal, M., Reuchlein, B., Adler, J., Reiner, I., Beutel, M. E., Vögele, C. & Schulz, A. (2014). Striking discrepancy of anomalous body experiences with normal interoceptive accuracy in depersonalization-derealization disorder. *PLoS One*, 9 (2), e89823-e89823.
[10.1371/journal.pone.0089823](https://doi.org/10.1371/journal.pone.0089823)
- Miller, J. F., Neufang, M., Solway, A., Brandt, A., Trippe, M., Mader, I. & Schulze-Bonhage, A. (2013). Neural activity in human hippocampal formation reveals the spatial context of retrieved memories. *Science*, 342 (6162), 1111-1114.
[10.1126/science.1244056](https://doi.org/10.1126/science.1244056)
- Mittelstaedt, H. (1992). Somatic versus vestibular gravity reception in man. *Annals of the New York Academy of Sciences*, 656, 124-139.
[10.1111/j.1749-6632.1992.tb25204.x](https://doi.org/10.1111/j.1749-6632.1992.tb25204.x)
- (1996). Somatic graviception. *Biological Psychology*, 42 (1-2), 53-74. [10.1016/0301-0511\(95\)05146-5](https://doi.org/10.1016/0301-0511(95)05146-5)
- Moga, M. M., Herbert, H., Hurley, K. M., Yasui, Y., Gray, T. S. & Saper, C. B. (1990). Organization of cortical, basal forebrain, and hypothalamic afferents to the parabrachial nucleus in the rat. *The Journal of Comparative Neurology*, 295 (4), 624-661.
[10.1002/cne.902950408](https://doi.org/10.1002/cne.902950408)
- Mohan, R., Jensen, K. B., Petkova, V. I., Dey, A., Barnsley, N., Ingvar, M. & Ehrsson, H. H. (2012). No pain relief with the rubber hand illusion. *PLoS One*, 7, e52400-e52400. [10.1371/journal.pone.0052400](https://doi.org/10.1371/journal.pone.0052400)
- Moseley, G. L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A. & Spence, C. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proceedings of the National Academy of Sciences of the United States of America*, 105 (35), 13169-13171.
[10.1073/pnas.0803768105](https://doi.org/10.1073/pnas.0803768105)
- Nielsen, T. I. (1963). Volition - An new experimental approach. *Scandinavian Journal of Psychology*, 4 (1), 225-230. [10.1111/j.1467-9450.1963.tb01326.x](https://doi.org/10.1111/j.1467-9450.1963.tb01326.x)
- O'Keefe, J. & Conway, D. H. (1978). Hippocampal place units in the freely moving rat: Why they fire where they fire. *Experimental Brain Research*, 31 (4), 573-590. [10.1007/BF00239813](https://doi.org/10.1007/BF00239813)
- O'Keefe, J. & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, 34 (1), 171-175. [10.1016/0006-8993\(71\)90358-1](https://doi.org/10.1016/0006-8993(71)90358-1)
- O'Mara, S., Rolls, E. T., Berthoz, A. & Kesner, R. P. (1994). Neurons responding to whole-body motion in the primate hippocampus. *Journal of Neuroscience*, 14 (11), 6511-6523. [10.1.1.64.9583](https://doi.org/10.1.1.64.9583)
- Ödkvist, L. M., Schwarz, D. W. F., Fredrickson, J. M. & Hassler, R. (1974). Projection of the vestibular nerve to the area 3a arm field in the squirrel monkey (*Saimiri sciureus*). *Experimental Brain Research*, 21 (1), 97-105.
[10.1007/BF00234260](https://doi.org/10.1007/BF00234260)

- Ono, T., Nakamura, K., Nishijo, H. & Eifuku, S. (1993). Monkey hippocampal neurons related to spatial and nonspatial functions. *Journal of Neurophysiology*, 70 (4), 1516-1529.
- Ostrowsky, K., Magnin, M., Ryvlin, P., Isnard, J., Guenot, M. & Mauguiere, F. (2002). Representation of pain and somatic sensation in the human insula: A study of responses to direct electrical cortical stimulation. *Cerebral Cortex*, 12 (4), 376-385. [10.1093/cercor/12.4.376](https://doi.org/10.1093/cercor/12.4.376)
- Paillard, J. (1991). Knowing where and knowing how to get there. In J. Paillard (Ed.) *Brain and Space* (pp. 461-481). New York, NY: Oxford University Press.
- Paladino, M. P., Mazzurega, M., Pavani, F. & Schubert, T. W. (2010). Synchronous multisensory stimulation blurs self-other boundaries. *Psychological Science*, 21 (9), 1202-1207. [10.1177/0956797610379234](https://doi.org/10.1177/0956797610379234)
- Parsons, L. M. (1987). Imagined spatial transformation of one's body. *Journal of Experimental Psychology: General*, 116 (2), 172-191. [10.1037/0096-3445.116.2.172](https://doi.org/10.1037/0096-3445.116.2.172)
- Patterson, D. R. & Jensen, M. P. (2003). Hypnosis and clinical pain. *Psychological Bulletin*, 129 (4), 495-521. [10.1037/0033-2909.129.4.495](https://doi.org/10.1037/0033-2909.129.4.495)
- Petkova, V. I. & Ehrsson, H. H. (2008). If I were you: Perceptual illusion of body swapping. *PLoS One*, 3 (12), e3832-e3832. [10.1371/journal.pone.0003832](https://doi.org/10.1371/journal.pone.0003832)
- Petkova, V. I., Bjornsdotter, M., Gentile, G., Jonsson, T., Li, T. Q. & Ehrsson, H. H. (2011). From part- to whole-body ownership in the multisensory brain. *Current Biology*, 21 (13), 1118-1122. [10.1016/j.cub.2011.05.022](https://doi.org/10.1016/j.cub.2011.05.022)
- Pfeiffer, C., Lopez, C., Schmutz, V., Duenas, J. A., Martuzzi, R. & Blanke, O. (2013). Multisensory origin of the subjective first-person perspective: Visual, tactile, and vestibular mechanisms. *PLoS One*, 8 (4), e61751-e61751. [10.1371/journal.pone.0061751](https://doi.org/10.1371/journal.pone.0061751)
- Poucet, B., Lenck-Santini, P. P., Paz-Villagran, V. & Save, E. (2003). Place cells, neocortex and spatial navigation: A short review. *Journal of Physiology*, 97 (4-6), 537-546. [10.1016/j.jphysparis.2004.01.011](https://doi.org/10.1016/j.jphysparis.2004.01.011)
- Péruch, P., Borel, L., Gaunet, F., Thinus-Blanc, G., Magan, J. & Lacour, M. (1999). Spatial performance of unilateral vestibular defective patients in nonvisual versus visual navigation. *Journal of Vestibular Research*, 9 (1), 37-47.
- Ramachandran, V. S., McGeoch, P. D. & Williams, L. (2007). Can vestibular caloric stimulation be used to treat Dejerine-Roussy Syndrome? *Medical Hypotheses*, 69 (3), 486-488. [10.1016/j.mehy.2006.12.036](https://doi.org/10.1016/j.mehy.2006.12.036)
- Ramachandran, V. S., McGeoch, P. D., Williams, L. & Arcilla, G. (2007). Rapid relief of thalamic pain syndrome induced by vestibular caloric stimulation. *Neurocase*, 13 (3), 185-188. [10.1080/13554790701450446](https://doi.org/10.1080/13554790701450446)
- Riva, G., Waterworth, J., Waterworth, E. L. & Mantovani, F. (2011). From intention to action: The role of presence. *New Ideas in Psychology*, 29 (1), 24-37. [10.1016/j.newideapsych.2009.11.002](https://doi.org/10.1016/j.newideapsych.2009.11.002)
- Rizzolatti, G. & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169-192. [10.1146/annurev.neuro.27.070203.144230](https://doi.org/10.1146/annurev.neuro.27.070203.144230)
- Rizzolatti, G., Fadiga, L., Gallese, V. & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Research*, 3 (2), 131-141. [10.1016/0926-6410\(95\)00038-0](https://doi.org/10.1016/0926-6410(95)00038-0)
- Robertson, R. G., Rolls, E. T., Georges-François, P. & Panzeri, S. (1999). Head direction cells in the primate pre-subiculum. *Hippocampus*, 9 (3), 206-219. [10.1002/\(SICI\)1098-1063\(1999\)9:3<206::AID-HIPO2>3.0.CO;2-H](https://doi.org/10.1002/(SICI)1098-1063(1999)9:3<206::AID-HIPO2>3.0.CO;2-H)
- Rochat, P. (1998). Self-perception and action in infancy. *Experimental Brain Research*, 123 (1-2), 102-109. [10.1007/s002210050550](https://doi.org/10.1007/s002210050550)
- Röder, C. H., Michal, M., Overbeck, G., van de Ven, V. G. & Linden, D. E. J. (2007). Pain response in depersonalization: A functional imaging study using hypnosis in healthy subjects. *Psychotherapy and Psychosomatics*, 76 (2), 115-121. [10.1159/000097970](https://doi.org/10.1159/000097970)
- Romano, D., Pfeiffer, C., Maravita, A. & Blanke, O. (2014). Illusory self-identification with an avatar reduces arousal responses to painful stimuli. *Behavioural Brain Research*, 261, 275-281. [10.1016/j.bbr.2013.12.049](https://doi.org/10.1016/j.bbr.2013.12.049)
- Roy, J. E. & Cullen, K. E. (2004). Dissociating self-generated from passively applied head motion: Neural mechanisms in the vestibular nuclei. *Journal of Neuroscience*, 24 (9), 2102-2111. [10.1523/JNEUROSCI.3988-03.2004](https://doi.org/10.1523/JNEUROSCI.3988-03.2004)
- Salomon, R., Lim, M., Pfeiffer, C., Gassert, R. & Blanke, O. (2013). Full body illusion is associated with widespread skin temperature reduction. *Frontiers in Behavioral Neuroscience*, 7, 1-11. [10.3389/fnbeh.2013.00065](https://doi.org/10.3389/fnbeh.2013.00065)
- Sanchez-Vives, M. V. & Slater, M. (2005). From presence to consciousness through virtual reality. *Nature Reviews in Neuroscience*, 6 (4), 332-339. [10.1038/nrn1651](https://doi.org/10.1038/nrn1651)
- Sang, F. Y., Jauregui-Renaud, K., Green, D. A., Bronstein, A. M. & Gresty, M. A. (2006). Depersonalisation/derealisation symptoms in vestibular disease. *Journal of Neurology Neurosurgery and Psychiatry*, 77

- (3), 760-766.
[10.1136/jnnp.2007.122119](https://doi.org/10.1136/jnnp.2007.122119)
- Sargolini, F., Fyhn, M., Hafting, T., McNaughton, B. L., Witter, M. P., Moser, M. B. & Moser, E. I. (2006). Conjunctive representation of position, direction, and velocity in entorhinal cortex. *Science*, 312 (5774), 758-762. [10.1126/science.1125572](https://doi.org/10.1126/science.1125572)
- Schilder, P. (1935). *The image and appearance of the human body*. New York, NY: International Universities Press.
- Schlack, A., Sterbing-D'Angelo, S. J., Hartung, K., Hoffmann, K. P. & Bremmer, F. (2005). Multisensory space representations in the macaque ventral intraparietal area. *Journal of Neuroscience*, 25 (18), 4616-4625.
[10.1523/JNEUROSCI.0455-05.2005](https://doi.org/10.1523/JNEUROSCI.0455-05.2005)
- Schneider, R. J., Friedman, D. P. & Mishkin, M. (1993). A modality-specific somatosensory area within the insula of the rhesus monkey. *Brain Research*, 621 (1), 116-120. [10.1016/0006-8993\(93\)90305-7](https://doi.org/10.1016/0006-8993(93)90305-7)
- Schwabe, L., Lenggenhager, B. & Blanke, O. (2009). The timing of temporoparietal and frontal activations during mental own body transformations from different visuospatial perspectives. *Human Brain Mapping*, 30 (6), 1801-1812. [10.1002/hbm.20764](https://doi.org/10.1002/hbm.20764)
- Schwarz, D. W. F. & Fredrickson, J. M. (1971). Rhesus monkey vestibular cortex: A bimodal primary projection field. *Science*, 172 (3980), 280-281.
[10.1126/science.172.3980.280](https://doi.org/10.1126/science.172.3980.280)
- Schwarz, D. W. F., Deecke, L. & Fredrickson, J. M. (1973). Cortical projection of group I muscle afferents to areas 2, 3a, and the vestibular field in the rhesus monkey. *Experimental Brain Research*, 17 (5), 516-526.
[10.1007/BF00234865](https://doi.org/10.1007/BF00234865)
- Serino, A., Alsmith, A., Costantini, M., Mandrigin, A., Tajadura-Jimenez, A. & Lopez, C. (2013). Bodily ownership and self-location: Components of bodily self-consciousness. *Consciousness and Cognition*, 22 (4), 1239-1252. [10.1016/j.concog.2013.08.013](https://doi.org/10.1016/j.concog.2013.08.013)
- Serino, A., Giovagnoli, G. & Ladavas, E. (2009). I feel what you feel if you are similar to me. *PLoS One*, 4 (3), e4930-e4930. [10.1371/journal.pone.0004930](https://doi.org/10.1371/journal.pone.0004930)
- Serino, A., Pizzoferrato, F. & Ladavas, E. (2008). Viewing a face (especially one's own face) being touched enhances tactile perception on the face. *Psychological Science*, 19 (5), 434-438.
[10.1111/j.1467-9280.2008.02105.x](https://doi.org/10.1111/j.1467-9280.2008.02105.x)
- Seth, A. K. (2013). Interoceptive inference, emotion, and the embodied self. *Trends of Cognitive Sciences*, 17 (11), 565-573. [10.1016/j.tics.2013.09.007](https://doi.org/10.1016/j.tics.2013.09.007)
- Smith, A. J. T. (2010). Comment: Minimal conditions for the simplest form of self-consciousness. In H. C. Fuchs, C. Sattel & P. Henningsen (Eds.) *The embodied self: Dimensions, coherence, disorders*. Stuttgart, GER: Schattauer.
- Stackman, R. W. & Taube, J. S. (1997). Firing properties of head direction cells in the rat anterior thalamic nucleus: Dependence on vestibular input. *Journal of Neuroscience*, 17 (11), 4349-4358.
- Stackman, R. W., Clark, A. S. & Taube, J. S. (2002). Hippocampal spatial representations require vestibular input. *Hippocampus*, 12 (3), 291-303.
[10.1002/hipo.1112](https://doi.org/10.1002/hipo.1112)
- Stratton, G. M. (1899). The spatial harmony of touch and sight. *Mind*, 8 (32), 492-505.
- Sugiuchi, Y., Izawa, Y., Ebata, S. & Shinoda, Y. (2005). Vestibular cortical area in the periarculate cortex: Its afferent and efferent projections. *Annals of the New York Academy of Sciences*, 1039 (2005), 111-123.
[10.1196/annals.1325.011](https://doi.org/10.1196/annals.1325.011)
- Suzuki, K., Garfinkel, S. N., Critchley, H. D. & Seth, A. K. (2013). Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion. *Neuropsychologia*, 51 (13), 2909-2917.
[10.1016/j.neuropsychologia.2013.08.014](https://doi.org/10.1016/j.neuropsychologia.2013.08.014)
- Suzuki, M., Kitano, H., Ito, R., Kitanishi, T., Yazawa, Y., Ogawa, T. & Kitajima, K. (2001). Cortical and subcortical vestibular response to caloric stimulation detected by functional magnetic resonance imaging. *Cognitive Brain Research*, 12 (3), 441-449.
[10.1016/S0926-6410\(01\)00080-5](https://doi.org/10.1016/S0926-6410(01)00080-5)
- Tajadura-Jiménez, A., Longo, M., Coleman, R. & Tsakiris, M. (2012). The person in the mirror: Using the enfacement illusion to investigate the experiential structure of self-identification. *Consciousness and Cognition*, 21 (4), 1725-1738.
[doi:10.1016/j.concog.2012.10.004](https://doi.org/10.1016/j.concog.2012.10.004)
- Taube, J. S. (2007). The head direction signal: Origins and sensory-motor integration. *Annual Review of Neuroscience*, 30, 181-207.
[10.1146/annurev.neuro.29.051605.112854](https://doi.org/10.1146/annurev.neuro.29.051605.112854)
- Tomlinson, R. D. & Robinson, D. A. (1984). Signals in vestibular nucleus mediating vertical eye movements in the monkey. *Journal of Neurophysiology*, 51 (6), 1121-1136.
- Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia*, 48 (3), 703-712. [10.1016/j.neuropsychologia.2009.09.034](https://doi.org/10.1016/j.neuropsychologia.2009.09.034)

- Tsakiris, M., Hesse, M. D., Boy, C., Haggard, P. & Fink, G. R. (2007). Neural signatures of body ownership: A sensory network for bodily self-consciousness. *Cerebral Cortex*, 17 (10), 2235-2244. [10.1093/cercor/bhl131](https://doi.org/10.1093/cercor/bhl131)
- Tsakiris, M., Prabhu, G. & Haggard, P. (2006). Having a body versus moving your body: How agency structures body-ownership. *Consciousness and Cognition*, 15 (2), 423-432. [10.1016/j.concog.2005.09.004](https://doi.org/10.1016/j.concog.2005.09.004)
- Tsakiris, M., Schutz-Bosbach, S. & Gallagher, S. (2007). On agency and body-ownership: Phenomenological and neurocognitive reflections. *Consciousness and Cognition*, 16 (3), 645-660. [10.1016/j.concog.2007.05.012](https://doi.org/10.1016/j.concog.2007.05.012)
- Tsakiris, M., Tajadura-Jimenez, A. & Costantini, M. (2011). Just a heartbeat away from one's body: Interoceptive sensitivity predicts malleability of body-representations. *Proceedings of the Royal Society B: Biological Sciences*, 278 (1717), 2470-2476. [10.1098/rspb.2010.2547](https://doi.org/10.1098/rspb.2010.2547)
- Ulanovsky, N. & Moss, C. F. (2007). Hippocampal cellular and network activity in freely moving echolocating bats. *Nature Neuroscience*, 10 (2), 224-233. [10.1038/nm1829](https://doi.org/10.1038/nm1829)
- Väljamäe, A. (2009). Auditorily-induced illusory self-motion: A review. *Brain Research Reviews*, 61 (2), 240-255. [10.1016/j.brainresrev.2009.07.001](https://doi.org/10.1016/j.brainresrev.2009.07.001)
- Vaitl, D., Mittelstaedt, H., Saborowski, R., Stark, R. & Baisch, F. (2002). Shifts in blood volume alter the perception of posture: Further evidence for somatic graviception. *International Journal of Psychophysiology*, 44 (1), 1-11. [10.1016/S0167-8760\(01\)00184-2](https://doi.org/10.1016/S0167-8760(01)00184-2)
- Vallar, G., Sterzi, R., Bottini, G., Cappa, S. & Rusconi, M. L. (1990). Temporary remission of left hemianesthesia after vestibular stimulation. A sensory neglect phenomenon. *Cortex*, 26 (1), 123-131. [10.1016/S0010-9452\(13\)80078-0](https://doi.org/10.1016/S0010-9452(13)80078-0)
- Van Elk, M. & Blanke, O. (2014). Imagined own-body transformations during passive self-motion. *Psychological Research*, 78 (1), 18-27. [10.1007/s00426-013-0486-8](https://doi.org/10.1007/s00426-013-0486-8)
- Van Elk, M., Lenggenhager, B., Heydrich, L. & Blanke, O. (2014). Suppression of the auditory N1-component for heartbeat-related sounds reflects interoceptive predictive coding. *Biological Psychology*, 99, 172-182. [10.1016/j.biopsycho.2014.03.004](https://doi.org/10.1016/j.biopsycho.2014.03.004)
- van Essen, D. C., Drury, H. A., Dickson, J., Harwell, J., Hanlon, D. & Anderson, C. H. (2001). An integrated software suite for surface-based analyses of cerebral cortex. *Journal of the American Medical Informatics Association*, 8 (5), 443-459. [10.1098/rspb.2010.2547](https://doi.org/10.1098/rspb.2010.2547)
- Vogele, K. & Fink, G. R. (2003). Neural correlates of the first-person-perspective. *Trends in Cognitive Science*, 7 (1), 38-42. [10.1016/S1364-6613\(02\)00003-7](https://doi.org/10.1016/S1364-6613(02)00003-7)
- Waespe, W. & Henn, V. (1978). Conflicting visual-vestibular stimulation and vestibular nucleus activity in alert monkeys. *Experimental Brain Research*, 33 (2), 203-211. [10.1007/BF00238060](https://doi.org/10.1007/BF00238060)
- Werner, N. S., Mannhart, T., Reyes Del Paso, G. A. & Duschek, S. (2014). Attention interference for emotional stimuli in cardiac interoceptive awareness. *Psychophysiology*, 51 (6), 573-578. [10.1111/psyp.12200](https://doi.org/10.1111/psyp.12200)
- Wicker, B., Keysers, C., Plailly, J., Royet, J. P., Gallese, V. & Rizzolatti, G. (2003). Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron*, 40 (3), 655-664. [10.1016/S0896-6273\(03\)00679-2](https://doi.org/10.1016/S0896-6273(03)00679-2)
- Wiener, S. I., Berthoz, A. & Zugaro, M. B. (2002). Multi-sensory processing in the elaboration of place and head direction responses by limbic system neurons. *Brain Research Cognitive Brain Research*, 14 (1), 75-90. [10.1016/S0926-6410\(02\)00062-9](https://doi.org/10.1016/S0926-6410(02)00062-9)
- Windt, J. M. (2010). The immersive spatiotemporal hallucination model of dreaming. *Phenomenology and the Cognitive Sciences*, 9 (2), 295-316. [10.1007/s11097-010-9163-1](https://doi.org/10.1007/s11097-010-9163-1)
- Wissmath, B., Weibel, D., Schmutz, J. & Mast, F. W. (2011). Being present in more than one place at a time? Patterns of mental self-localization. *Consciousness and Cognition*, 20 (4), 1808-1815. [10.1016/j.concog.2011.05.008](https://doi.org/10.1016/j.concog.2011.05.008)
- Wolpert, D. M. & Miall, R. C. (1996). Forward models for physiological motor control. *Neural Networks*, 9 (8), 1265-1279. [10.1016/S0893-6080\(96\)00035-4](https://doi.org/10.1016/S0893-6080(96)00035-4)
- Yartsev, M. M., Witter, M. P. & Ulanovsky, N. (2011). Grid cells without theta oscillations in the entorhinal cortex of bats. *Nature*, 479 (7371), 103-107. [10.1038/nature10583](https://doi.org/10.1038/nature10583)
- Yates, B. J. & Bronstein, A. M. (2005). The effects of vestibular system lesions on autonomic regulation: Observations, mechanisms, and clinical implications. *Journal of Vestibular Research*, 15 (3), 119-129.
- Zennou-Azogui, Y., Bourgeon, S. & Xerri, C. (2011). Hypergravity experience during development alters forepaw somatosensory maps and influences cortical experience-dependent plasticity in adult rat. *Presented at the Conference on Development and Plasticity of Thalamocortical Systems*. Arolla, SUI.
- zu Eulenburg, P., Baumgärtner, U., Treede, R. D. & Dieterich, M. (2013). Interoceptive and multimodal func-

tions of the operculo-insular cortex: Tactile, nociceptive and vestibular representations. *NeuroImage*, 83, 75-86.

[10.1016/j.neuroimage.2013.06.057](https://doi.org/10.1016/j.neuroimage.2013.06.057)

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

Perspectival Structure and Vestibular Processing

A Commentary on Bigna Lenggenhager & Christophe Lopez

Adrian Alsmith

I begin by contrasting a taxonomic approach to the vestibular system with the structural approach I take in the bulk of this commentary. I provide an analysis of perspectival structure. Employing that analysis and following the structural approach, I propose three lines of empirical investigation to selectively manipulate and measure vestibular processing and perspectival structure. The hope is that this serves to indicate how interdisciplinary research on vestibular processing might advance our understanding of the structural features of conscious experience.

Keywords

Egocentric | Egomotion | First-person perspective | Galvanic vestibular stimulation (GVS) | GVS | Head-mounted display | Perspective | Phenomenal groove | Phenomenal grooves | Scalp EEG | Self-consciousness | Structural features of consciousness | Tendon vibration stimulation | The body-swap illusion | The full-body illusion | The senses | Vestibular | Vestibular evoked potentials

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1 Structural vs. taxonomic approaches to vestibular processes

Philosophical work on the senses has largely been concerned with taxonomic issues: What makes an event sensory? Under which sensory kind should that event be classified? Answering these questions requires criteria of individuation. These would enable us to determine

whether an event is the same as (or different to) sensory events in general and whether it is the same as (or different to) sensory events of a specific kind. A criterion of the first sort would allow us to identify vestibular events as sensory events. This would justify the belief that vesti-

bular processes are sensory processes. A criterion of the second sort would allow us to identify vestibular sensory events as being of a specific kind, i.e., distinctively vestibular sensory events. This would justify the belief that there is such a thing as a vestibular sense. Failing to provide a criterion of the first sort would force one to classify vestibular events as non-sensory. But even if one were able to determine that vestibular events are sensory, one would still require a criterion of the second sort to classify vestibular events as sensory events of a kind that is distinct from, e.g., visual or haptic events.

To expand on this last point: as Lenggenhager and Lopez so masterfully describe, central vestibular processes are inherently multisensory, and as a consequence there is scarcely a part of our sensory and cognitive life that vestibular processes leave untouched (see especially §2.2 of the target article). But then, if vestibular processes are implicated in so many sensory and cognitive processes, it may be most accurate to see vestibular processing as simply a common part of many processes, rather than as an independent sensory system. That is, one may begin to seriously consider the possibility that vestibular processing does not constitute a form of sensory processing of its own kind, but rather constitutes a form of processing common to various other processes that are themselves sensory. This is, in effect, an issue that arises from applying a criterion for individuating the senses that includes the physiology (and neurophysiology) of the entire system. One might not be forced to this conclusion if one used an alternative criterion (Macpherson 2011a, 2011b). But it seems that each of the criteria commonly discussed would generate their own problems. For instance, employing a more restrictive criterion that delimited sensory systems according to their peripheral sensory organs would face the issue of whether the sensory organs of the vestibular system ought to include or exclude the so-called “truncal” or “somatic” graviceptors (Mittelstaedt 1992, 1996; Vaitl et al. 2002). Similar issues would be faced when attempting to individuate the senses in terms of a distinctive proximal stimulus. Alternatively, one might

individuate the senses by means of certain distinctive experiences: vision distinctively represents the brightness, hue, and saturation of colours; audition represents the volume, pitch, and tone of sounds. The natural candidates for the vestibular system would be experiences that represent verticality, rotation, and translation. But whilst it is certain that the vestibular system typically contributes to experiences of verticality, rotation, and translation, these are all experiences of a kind that can be had through visual sensation alone, or through a combination of visual, somatic, and proprioceptive sensation. Moreover, although vertiginous experiences are the hallmark of vestibular dysfunction, these are either experiences of rotation, which brings us back to the aforementioned issue, or they are more vaguely classified as pseudo-vertiginous experiences of dizziness that may have any number of non-vestibular aetiologies. Suffice to say that it may be surprisingly difficult to find appropriate criteria to justify the claim that there is such a thing as a *distinctively* vestibular sensory process.

The foregoing characterises what would be the typical philosophical approach to the vestibular system, *qua* sensory system. This *taxonomic approach* captures certain philosophical interests, but it is completely inadequate for the task of bringing out the significance of the scope of the vestibular system’s influence. An alternative, *structural approach* focuses on the role played by vestibular events in processes that exhibit a certain kind of structure, to determine the contribution of those events to that structure. Note that the structural and taxonomic approaches are independent, insofar as they have different epistemic goals. They aim to further our knowledge in different ways. The goal of the taxonomic approach is to determine whether, and if so why, there is a distinctive sensory system of a certain kind. The goal of the structural approach is to determine whether, and if so how, a certain kind of process contributes to a certain kind of structure. By assuming that one can identify processes as objects of study without first employing an exhaustive taxonomy, a structural approach can assume that there are such things as vestibular

processes without any commitment to these processes being wholly distinct from others. And by tracking the varied yet systematic effects of vestibular processes, one can determine whether vestibular processes contribute to a certain kind of structure, irrespective of, whether or not the vestibular system is a distinctive sensory system. As vestibular processes are implicated in so many and various sensory and cognitive processes, the structural approach seems to be the most fruitful in terms of the amount we might learn. It also seems more fruitful in terms of the kind of knowledge we might gain. For we may learn nothing about how vestibular processes affect our experiential life by learning that vestibular processes may not be, in the final analysis, of a distinctive sensory kind. But we will certainly learn something about how vestibular processes affect our experiential life by learning that vestibular processes contribute to a certain experiential structure. Accordingly, I leave aside taxonomic issues in the rest of this commentary and focus on structural issues. Specifically, I focus on issues concerning the role of the vestibular system in providing a particular kind of structure to our experience of the body and the world, namely a perspectival structure.

To begin with, we need a preliminary analysis of experiential phenomena that exhibit perspectival structure. I will call these *perspectival phenomena*. In the next section, I offer a rudimentary analysis of perspectival structure, the aim of which is to show that perspectival phenomena are more differentiated than commonly recognised. In the following three sections, I propose three lines of empirical investigation. Each would attempt to selectively study perspectival phenomena through measurement and manipulation of vestibular processes. If the experiments proposed yielded interesting results, they would further our knowledge of how vestibular processes affect the perspectival structure of our experiential life. Accordingly, the overall aim is to demonstrate how an analysis of perspectival structure might fruitfully interface with empirical research and facilitate understanding of structural features of conscious experience that would otherwise be obscured.

2 The differentiation of perspectival phenomena

The notion of a subjective perspective (sometimes described as a *first-person perspective*) is at the core of contemporary research on bodily self-consciousness (Blanke & Metzinger 2009; Metzinger 2003, 2009). However, its role has often been merely facilitative, serving as a means to study *other* components of bodily self-consciousness, such as the experience of bodily agency, ownership, and self-location (Ehrsson 2007; Lenggenhager et al. 2007; Petkova et al. 2011a, see Serino et al. 2013 for review). Consequently, the fact that the very notion of perspective covers a range of distinct phenomena has tended to be overlooked.¹ Referring to someone's perceptual experience as having a perspectival structure may mean any one of several distinct things. It may mean that there is an *origin* to her sensory field, relative to which certain things (or parts of things) are perceptible and perceived from a particular direction and relative to which certain other things (or parts of things) are not perceptible or noticeably occluded.² Alternatively, it may mean that her experience is organised according to an *egocentric* frame of reference centred upon her body, according to which she experiences locations as situated relative to a particular point at the intersection of three orthogonal axes. Or it may be that, thanks to *egomotion*, the flow of her sensory experience is such that she can see where she is headed as she moves. Taking *another individual's* perspective into account in social interactions can involve either of the first two forms of perspective (Moll & Meltzoff 2011).

¹ My discussion is restricted to spatial perspectival phenomena; I omit discussion of the respects in which temporal experience may be perspectival. This is mostly for the sake of simplicity. However, there is good reason to think that we represent time in a manner that is asymmetrically dependent upon the ways in which we represent space (Boroditsky 2000; Casasanto & Boroditsky 2008). Addressing issues concerning the structure of spatial experience first may thus be prudent.

² This notion is intended to capture the idea that there is a point of "origin" to the so-called line of sight (which is not so much a line as an angle). This corresponds to perhaps the earliest documented notion of perceptual perspective, associated with what Euclid and Ptolemy respectively called the "visual pyramid" and "visual cone", where the apex (origin) of the pyramid or cone is at the eye and the base at the object (Howard 2012).

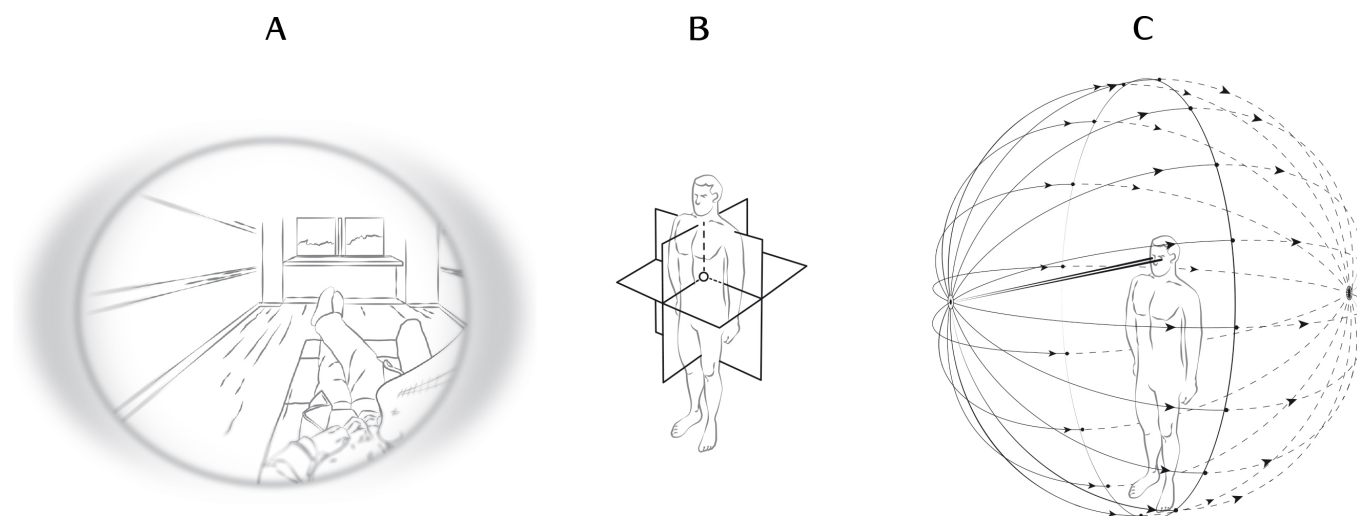


Figure 1: Three forms of perspectival structure. **A.** An artistic rendition of a human monocular visual field. After Mach 1959, p.18. **B.** An egocentric frame of reference centred upon a human torso. **C.** The directions of deformations in the visual field specifying egomotion. Cf. Gibson 1950, p. 123.

Moreover, the perspective of the subject need not figure explicitly in the experience for it to be perspectival; perspective can structure perceptual experience implicitly, by determining the way in which objects are experienced, without itself being part of the content of the *experience* (Campbell 1994; Merleau-Ponty 2002; Perry 1993; Zahavi 2005).

We can summarise these remarks by saying that perspectival phenomena in spatial experience vary along three dimensions.³ First, perspectival structure can take at least three forms:⁴

- Origin of a sensory field (*origin*)
- Centre of an egocentric frame of reference (*egocentric*)
- Focal point of a sensory flow field in action (*egomotion*)

³ I do not intend the following to be exhaustive. Moreover, although all of the perspectival phenomena that I discuss are visual, I do believe that each of the forms of perspectival structure that I describe also characterises perspectival experience in haptic perception.

⁴ The most I intend to claim here is that these forms of perspectival structure are non-identical. Perhaps the origin of a given sensory field, the centre of a given egocentric frame of reference, and the focal point of a given sensory flow field could occupy the same location under some description. However, this certainly need not always be the case. Moreover, each form of perspectival structure will present the objects of perceptual experience as related to the subject of experience in different ways, e.g., as only partially visible, as straight ahead, or as in one's way. Below I will suggest various ways in which these might be selectively manipulated, but I do not intend to make the case that forms of perspectival structure can be dissociated from one another.

Perspectival phenomena that exhibit any of these forms of perspectival structure can vary along two further dimensions: the perspective of a given perspectival experience may be either *implicit* or *explicit*, and may be attributed to the subject or to another individual. A perspective is *explicit* in a perspectival experience if the subject is consciously aware of the location of the origin, centre, or focal point in question; it is *implicit* if the subject is not.⁵ The perspective in question may belong to the subject, a *first-person perspective*, or it may belong to another individual, a *third-person perspective*.

This simple framework enables one to study perspectival phenomena selectively, rather than studying an undifferentiated cluster of perspectival phenomena simultaneously. In the sections that follow, I shall suggest a number of ways in which one might engage in such a selective study of perspectival phenomena by in-

⁵ When a perspective is explicit, the location of the origin, centre, or focal point is part of the content of the experience. Any beliefs that the subject has about the location in question do not go beyond the content of that experience (cf. Peacocke 1999, p. 265). The experience may represent the location in question in an imprecise or wholly incorrect manner; the subject's beliefs will be correspondingly imprecise or incorrect. Implicit perspectives structure experience without being part of the content of experience. I leave it open whether implicit perspectives are nevertheless experienced *qua* structural feature, or whether, for example, they are merely formal structures that determine the ways in which things are experienced, without themselves being experienced. Issues like this are difficult to evaluate, but for discussion see Alsmith (2012).

tervening upon and registering the activation of vestibular processes.

3 Perspectival variation in multisensory stimulation

One consequence of not distinguishing between perspectival phenomena is that the notion of a *first-person perspective* becomes ambiguous. One can clearly see this ambiguity in descriptions of the role of *first-person perspective* in the multisensory stimulation protocols developed in recent work on the neuroscience of bodily self-consciousness. These protocols all involve participants being touched on their torso whilst visually observing a body-shape (either the body of another person, a mannequin, or a virtual body) being touched on its torso. The protocols differ along two dimensions: the side of the torso stimulated and the location of the origin of the participants' line of sight with respect to the body being observed. In one protocol, the body-swap illusion, participants are stroked on their chest whilst they look at a body being stroked on its chest from a position located where its head would be (cf. Ehrsson 2007; see Petkova et al. 2011b; Petkova & Ehrsson 2008; Petkova et al. 2011a). In another protocol, the full-body illusion, participants are stroked on their back, whilst they observe a body from behind being stroked on its back from a position entirely removed from its location (Ionta et al. 2011; Lenggenhager et al. 2007; Pfeiffer et al. 2013). The body-swap illusion protocol is often distinguished from the full-body illusion protocol as involving first-person perspective as an independent variable (Petkova et al. 2011a). However, recent work on the full-body illusion has demonstrated effects that the authors describe as changes in first-person perspective (Pfeiffer et al. 2014): Participants lain prone whilst feeling and observing strokes on the back report experiences of either looking up or down at the body they observe (Ionta et al. 2011). These variations in report seem to depend upon the individual's relative weighting of vestibular and visual gravitational cues (Pfeiffer et al. 2013).

Admitting the differentiation of perspectival phenomena allows us to make sense of the differences in use of the term *first-person*

perspective. In the terms introduced in the previous section, the *first-person perspective* in the body-swap illusion is an *origin* perspective. It presents the typical view of one's own body with a line of sight originating in the head. The *first-person perspective* in the full-body illusion is an *egocentric* perspective. It forms the centre of an egocentric frame of reference, according to which the observed body occupies a location in a particular egocentric direction (up or down). Distinguishing these forms of first-person perspectival experience reveals that each of these protocols facilitates manipulation of a distinct form of perspectival experience. It also sheds light on the fact that the differences in vestibular and somatosensory processing between these forms of perspectival experience have yet to be compared.

One way of conducting such a comparison would be to use virtual reality display techniques to present an individual with two avatars in series, whilst measuring time-locked vestibular evoked potentials via scalp EEG.

Experiment 1: Participants are stroked on *both* their chest *and* their back whilst supine, whilst wearing a head-mounted display. In the meantime, participants observe either the chest of Avatar 1 being stroked on its chest, presented from a position corresponding to the avatar's head, as in the body-swap illusion, or they observe Avatar 2 being stroked on its back, as in the full-body illusion. Ideally, the two avatars are presented in the same viewing, such that the participant views one avatar and then in a continuous movement shifts their gaze to view the other.⁶

I have claimed that each of the two protocols conjoined in this proposed experiment facilitates manipulation of different forms of perspectival experience. If this is correct, then finding significant differences in vestibularly-evoked potentials between observation of Avatar 1 and Avatar 2 would be a first step in determining differences in vestibular processing between these forms of perspectival experience.

⁶ This would be, I take it, as close as practically possible to viewing the two avatars at the same time, given limitations in the field of view.

As noted earlier, there do seem to be individual differences in the contents of *egocentric* perspectival experience in the full-body illusion. This would suggest that some individuals, those who are more heavily dependent upon vestibular gravitational cues to determine orientation, would experience themselves as looking upwards at Avatar 2. Whereas if the right *visual* gravitational cues were provided, some individuals may experience themselves as looking downwards at Avatar 2 (Ionta et al. 2011; Pfeiffer et al. 2013). This might allow the investigation of the relationship between *egocentric* perspectives and *egomotion* perspectives, by incorporating a second phase into a new experiment:

Experiment 2: Phase 1: experiment 1, described above. Phase 2: Participants continue to be stroked on their back and chest. Participants fixate upon Avatar 2 and observe it rotating about a horizontal axis, whilst being visibly stroked on its back and chest. Both reports of experienced orientation (upward vs. downward) and reports of experienced *egomotion* are gathered.

Participants may experience themselves as rotating around a horizontal axis in just the way they observe Avatar 2 rotating. Alternatively, they might experience themselves as revolving around Avatar 2. In particular, what would be of interest would be the way in which any resultant illusory experiences of *egomotion* might correlate with experienced *egocentric* orientation (upward vs. downward). Moreover, individual differences in experienced *egocentric* orientation might even predict the contents of experienced *egomotion*. This would be a major step in determining both the relative influence of vestibular processing on these forms of perspectival experience and the relationship between these forms of perspectival experience.

4 Perspectival variation in misalignment

In much recent philosophical and neuroscientific research on self-consciousness, the experienced *first-person perspective* is treated as a simple phenomenon identified with the experienced origin of an *egocentric* frame of reference centred upon an individual's own body (Blanke & Metz-

zinger 2009; Vogeley & Fink 2003). But *egocentric* perspective, despite being an *apparently* simple phenomenon, is in fact as potentially complex as the macroscopic structure of the body itself (Smith 2010). Human bodies are composed of a number of parts that are to some degree independently mobile, any of which may serve to centre a distinct *egocentric* frame of reference. As this observation is well known, we may presume that theorists who treat *egocentric* perspective as simple are assuming that locations in these various *egocentric* frames of reference are translated into a single, *ultimate* *egocentric* frame reference which itself determines *egocentric* perspectival phenomena.

However, neurophysiological and neuropsychological research on spatial representation suggests independent motivation for this ultimate frame being centred upon the head (e.g., Avillac et al. 2005) or the torso (e.g., Karnath et al. 1991). By rotating head and torso in opposite directions, an *egocentric* frame of reference centred upon the head can be misaligned with another frame centred upon the torso. In such a “misalignment” situation, a single object may be “to the right” with respect to the head and “to the left” with respect to the torso (Longo & Alsmith 2013). Following Christopher Peacocke's (1992) description of the phenomenology of experienced direction, one would hypothesise that differences in experienced posture would determine differences in *egocentric* perspectival experience.⁷ One could thus use mis-

7 Peacocke writes: “The use of a particular set of labeled axes in giving part of the content of an experience is not a purely notational or conventional matter. The appropriate set of labeled axes captures distinctions in the phenomenology of experience itself. Looking straight ahead at Buckingham Palace is one experience. It is another to look at the palace with one's face still toward it but with one's body turned toward a point on the right. In this second case the palace is experienced as being off to one side from the direction of straight ahead, even if the view remains exactly the same as in the first case” (1992, p. 62). Assuming that Peacocke's prediction is correct, then in this example changes in the *egocentric* perspectival structure of visual experience follow changes in the orientation of the torso. By misaligning the torso from the direction of the gaze, one discerns that (in the case as described) the appropriate set of labelled axes centre upon the torso. In the paradigm described in experiment 3, both head and torso may be misaligned with the individual's gaze. This makes it possible to determine the contribution of both head- and torso-centred frames of reference to the individual's *egocentric* perspectival experience of a given location. It would then be possible to discern whether, for the *egocentric* perspectival experience of a given location: (i) the appropriate set of axes centre on the torso; (ii) the axes centre on the head; (iii) both sets of axes make relative contributions to the structure of the experience.

alignment situations to determine the respective contributions of the head and the torso to the organisation of *egocentric* perspectival experience at a given point in time in the following experiment:

Experiment 3: Standing with their head and torso aligned or misaligned $\pm 15^\circ$, participants perform a task that involves either an *explicit* or only an *implicit egocentric* perspective (see below). The angular deviation of the stimulus in relation to the head and/or torso is recorded, such that one would be able to assess the respective contributions of each body-part's orientation to the participants' *egocentric* perspectival judgments. Participants would receive either galvanic vestibular stimulation (GVS) or tendon vibration stimulation to precisely assess the relative contribution of vestibular processes to *egocentric* perspective.

In more detail, the suggestions are these. For an explicit task, stimuli could be presented across the entire visual field in regular intervals, varying in distance and elevation, and participants would judge whether a stimulus presented looks “to their left or to their right”. A potential limitation of the explicit task is that in using overt left/right judgements, participants' responses may reflect a stipulated meaning of these terms that is independent of the *egocentric* perspectival structure of their experience. However, a recent study using a covert attentional cuing paradigm found that rotation of the torso primes participants to respond more quickly to visual stimuli appearing on the side of a computer screen congruent to the direction of rotation (Grubb & Reed 2002).⁸ One could adapt this paradigm to directly compare the respective influences of head and torso by rotating the head and/or the torso $\pm 15^\circ$ relative to the screen where stimuli would be presented. Target and cuing visual stimuli would appear on either congruent or incongruent sides of the screen and participants would make speed responses to indicate whether the target appears to the left or the right on each trial. Again, as

the angular deviation of the stimulus in relation to the head and/or torso would be known, one would be able to assess the respective contributions of each body-part's orientation to the participant's *egocentric* perspectival judgments.

Based on previous work, I would expect participants' judgements to implicate *both* their head *and* torso as determining their *egocentric* perspectival experience (Alsmith & Longo 2014). More specifically, I would expect that both head- and torso-centred reference frames would influence *explicit* and *implicit egocentric* perspectival phenomena (Longo & Alsmith 2013), though the exact weighting will be unequal at lateral extremes of each body part and will differ between individuals (Alsmith et al. in preparation). The further prediction would be that manipulating vestibular and proprioceptive processing will modulate felt postural misalignment and thereby systematically influence performance on *explicit* and *implicit egocentric* perspectival tasks.

5 Perspectival variation in sensorimotor control

Arguably, one of the core structural features of the experience of intentionally-directed bodily movement is the presentation of the agent as the “perspectival source” of the motion experienced (Horgan et al. 2003; Marcel 2006). However, a strikingly robust experimental finding is that individuals will correct for a deviation introduced into a movement they perform via a bias in visual input, thereby ensuring the action they intend achieves its goal, whilst nevertheless *not* reporting such corrections in their movement (Fournier & Jeannerod 1998; Knoblich & Kircher 2004; Slachevsky et al. 2001). Recent developments of this paradigm have adapted it to test *explicit egomotion* perspectival experience in walking movements, by using a motion-tracked avatar, observed from the rear. Kannape and colleagues found that by introducing a slight bias into the subject's visual experience of the trajectory of the avatar, they could induce subjects to perform appropriate corrective movements in walking to a target, whilst not noting the discrepancy between their actual movements and the avatar (Kannape

⁸ It is perhaps worth noting that by “congruent” I intend the more general sense of the term, as often used in describing the design of behavioural studies, the meaning of which is equivalent to “in agreement”. I do not intend the more specific geometrical sense of the term, which expresses identity of a certain kind, typically of form.

et al. 2010). Again, the corrections went largely unnoticed within a certain range of angular deviation between observed and actual movements.⁹ Thus, a natural explanation of the pattern of data is that the mechanisms enabling the experience of agency present bodily movements in a manner that is far more coarse-grained than the level of detail required to make corrective changes in movement trajectory. In short, *egomotion* perspectives structure experiences of intentionally-directed bodily movement. They do so by specifying what we might call coarse-grained phenomenal grooves, within which a movement must unfold if it is to seem like the movement that the subject intended or is trying to perform.

Strangely, as yet the potential contributions of the vestibular system to the structuring of agentive experience by *egomotion perspective* have not been manipulated. Moreover, as noted, the work that has been done in this area has been restricted to *explicit egomotion* perspectival phenomena. A natural further step would be to investigate the nature of vestibular processing in implicit *egomotion* perspective, by controlling a participant's optic flow in a manner corresponding to the control of the avatar's motion in Kannape and colleagues' original study.

Experiment 4: Study 1: Participants view a textured environment via HMD in which optical flow fields are regulated by their motion-tracked movements. Study 2: Participants control a motion-tracked, real-time avatar seen from behind. In both studies, participants are tasked with walking directly towards a virtual target. All the while, they either receive GVS or sham stimulation and visual feedback (optic flow or avatar position) that is either faithful to motion-tracking or systematically deviated left/right of the participant's mid-line, as a function of distance from a point of displacement onset.

Participant trajectory could thus be compared to the dynamics of the flow field or avatar trajectory and participants could be

asked to rate the degree to which their movements in the virtual environment or the movements of the avatar corresponded to their actual movements, as respective measures of *implicit* and explicit *egomotion* perspectival experience. The question would be whether, in trials in which GVS is applied, the range of angular deviation in which participants would judge that movements in the virtual environment correspond to their own would be equal to or larger than trials in which participants receive only biased visual feedback. If the latter occurs, then in the evocative terms used above, it would suggest that vestibular processes are one of the determinants of the coarseness of the phenomenal groove specified by an *egomotion* perspective.

6 Conclusion

I began by contrasting a taxonomic approach to the vestibular system with the structural approach I have taken in the bulk of this commentary. I then provided an analysis of perspectival structure. Employing that analysis and following the structural approach, I proposed three lines of empirical investigation that would selectively manipulate and measure vestibular processing and perspectival structure.

Day & Fitzpatrick (2005) quip that vestibular processes provide a "silent sense" (see also §2.2.1 of the target article). I suggested at the outset that (following the taxonomic approach) it might be surprisingly difficult to say with any precision why vestibular processing provides a sense of its very own. But even if it is true, that is, if the experiments described yield the expected results, they would show that vestibular processing is hardly silent. Indeed, each of the proposed lines of investigation would be a step towards a better understanding of how vestibular processes affect myriad forms of perspectival structure, all of which would further demonstrate the centrality of vestibular processing to our experiential life. In any case, my hope is that these remarks display the extent to which I have found Lenggenhager and Lopez's work to be not only inspirational, but also a rich and fruitful avenue for interdisciplinary research into the structural features of conscious experience.

⁹ The authors write that "deviations of 5°, 10°, and 15° lead to many erroneous self-attributions", found to be "decreasing in magnitude with increasing angular deviation" (Kannape et al. 2010, p. 1631). As broached above, one explanation of this pattern would be that deviations below 15° all fall (to a greater or lesser degree) within the phenomenal groove of the action specified by the task.

References

- Alsmith, A. (2012). What *reason*, consciousness in interaction: The role of the natural and social environment in shaping consciousness. In F. Paglieri (Ed.) (pp. 3-17) Amsterdam, NL: John Benjamins Press.
- Alsmith, A., Ferre, F., Haggard, P. & Longo, M. (unpublished). Isolating the origin(s) of perceptual perspective: The misalignment paradigm.
- Alsmith, A. & Longo, M. (2014). Where exactly am I? Self-location judgements distribute between head and torso. *Consciousness and Cognition*, 24, 70-74. [10.1016/j.concog.2013.12.005](https://doi.org/10.1016/j.concog.2013.12.005)
- Avillac, M., Denève, S., Olivier, E., Pouget, A. & Duhamel, J.-R. (2005). Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience*, 8, 941-949. [10.1038/nn1480](https://doi.org/10.1038/nn1480)
- Blanke, O. & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences*, 13 (1), 7-13. [10.1016/j.tics.2008.10.003](https://doi.org/10.1016/j.tics.2008.10.003)
- Boroditsky, L. (2000). Metaphoric structuring: Understanding time through spatial metaphors. *Cognition*, 75 (1), 1-28. [10.1016/S0010-0277\(99\)00073-6](https://doi.org/10.1016/S0010-0277(99)00073-6)
- Campbell, J. (1994). *Past, space, and self*. Cambridge, MA: MIT Press.
- Casasanto, D. & Boroditsky, L. (2008). Time in the mind: Using space to think about time. *Cognition*, 106 (2), 579-593. [10.1016/j.cognition.2007.03.004](https://doi.org/10.1016/j.cognition.2007.03.004)
- Day, B. L. & Fitzpatrick, R. C. (2005). The vestibular system. *Current Biology*, 15 (15), R583-R586. [10.1016/j.cub.2005.07.053](https://doi.org/10.1016/j.cub.2005.07.053)
- Ehrsson, H. (2007). The experimental induction of out-of-body experiences. *Science*, 317 (5841), 1048-1048. [10.1126/science.1142175](https://doi.org/10.1126/science.1142175)
- Fourneret, P. & Jeannerod, M. (1998). Limited conscious monitoring of motor performance in normal subjects. *Neuropsychologia*, 36 (11), 1133-1140. [10.1016/S0028-3932\(98\)00006-2](https://doi.org/10.1016/S0028-3932(98)00006-2)
- Gibson, J. J. (1950). *The perception of the visual world*. Boston, MA: Houghton Mifflin.
- Grubb, J. D. & Reed, C. L. (2002). Trunk orientation induces neglect-like lateral biases in covert attention. *Psychological Science*, 13 (6), 553-556. [10.1111/1467-9280.00497](https://doi.org/10.1111/1467-9280.00497)
- Horgan, T. E., Tienson, J. L. & Graham, G. (2003). The phenomenology of first-person agency. *Physicalism and mental causation* (pp. 323-340). Exeter, UK: Imprint Academic.
- Howard, I. P. (2012). *Perceiving in depth, volume 1: Basic mechanisms*. Oxford, UK: Oxford University Press.
- Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D. & Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron*, 70 (2), 363-374. [10.1016/j.neuron.2011.03.009](https://doi.org/10.1016/j.neuron.2011.03.009)
- Kannape, O. A., Schwabe, L., Tadi, T. & Blanke, O. (2010). The limits of agency in walking humans. *Neuropsychologia*, 48 (6), 1628-1636. [10.1016/j.neuropsychologia.2010.02.005](https://doi.org/10.1016/j.neuropsychologia.2010.02.005)
- Karnath, H. O., Schenkel, P. & Fischer, B. (1991). Trunk orientation as the determining factor of the 'contralateral' deficit in the neglect syndrome and as the physical anchor of the internal representation of body orientation in space. *Brain*, 114, 1997-2014. [10.1093/brain/114.4.1997](https://doi.org/10.1093/brain/114.4.1997)
- Knoblich, G. & Kircher, T. T. J. (2004). Deceiving oneself about being in control: Conscious detection of changes in visuomotor coupling. *Journal of Experimental Psychology: Human Perception and Performance*, 30 (4), 657-666. [10.1037/0096-1523.30.4.657](https://doi.org/10.1037/0096-1523.30.4.657)
- Lenggenhager, B., Tadi, T., Metzinger, T. & Blanke, O. (2007). Video ergo sum: Manipulating bodily self-consciousness. *Science*, 317 (5841), 1096-1099. [10.1126/science.1143439](https://doi.org/10.1126/science.1143439)
- Longo, M. & Alsmith, A. (2013). Where is the ego in egocentric representation? *Perception ECVF Abstract Supplement*, 42, 53-53.
- Mach, E. (1896/1959). *The analysis of sensation and the relation of the psychical to the physical* (C. M. Williams, Trans.). New York: Dover Publications.
- Macpherson, F. (2011a). *The senses: Classical and contemporary readings*. Oxford, UK: Oxford University Press.
- (2011b). Taxonomising the senses. *Philosophical Studies*, 153 (1), 123-142. [10.1007/s11098-010-9643-8](https://doi.org/10.1007/s11098-010-9643-8)
- Marcel, A. J. (2006). The sense of agency: Awareness and ownership of action. In J. Roessel & M. Eilan (Eds.) *Agency and self-awareness: Issues in philosophy and psychology* (pp. 48-93). Oxford, UK: Oxford University Press.
- Merleau-Ponty, M. (Ed.) (2002). *Phenomenology of perception*. London, UK: Routledge.
- Metzinger, T. (2003). *Being no one: The self-model theory of subjectivity*. Cambridge, MA: MIT Press.
- (2009). Self models. *Scholarpedia*, 2, 4174-4174.
- Mittelstaedt, H. (1992). Somatic versus vestibular gravity reception in man. *Annals of the New York Academy of Sciences*, 656 (1), 124-139. [10.1111/j.1749-6632.1992.tb25204.x](https://doi.org/10.1111/j.1749-6632.1992.tb25204.x)
- (1996). Somatic graviception. *Biological Psychology*, 42 (1-2), 53-74. [10.1016/0301-0511\(95\)05146-5](https://doi.org/10.1016/0301-0511(95)05146-5)

- Moll, H. & Meltzoff, A. N. (2011). Perspective taking and its foundation in joint attention. *Perception, causation and objectivity* (pp. 286-304). Oxford, UK: Oxford University Press.
- Peacocke, C. (1992). *A study of concepts*. Cambridge, MA: MIT Press.
- (1999). *Being known*. New York, NY: Oxford University Press.
- Perry, J. (1993). *The problem of the essential indexical and other essays*. Oxford, UK: Oxford University Press.
- Petkova, V. I. & Ehrsson, H. H. (2008). If I were you: Perceptual illusion of body swapping. *PLoS ONE*, 3 (12), e3832. [10.1371/journal.pone.0003832](https://doi.org/10.1371/journal.pone.0003832)
- Petkova, V. I., Khoshnevis, M. & Ehrsson, H. H. (2011a). The perspective matters! Multisensory integration in ego-centric reference frames determines full body ownership. *Frontiers in Psychology*, 2 (35), 1-7. [10.3389/fpsyg.2011.00035](https://doi.org/10.3389/fpsyg.2011.00035)
- Petkova, V. I., Björnsdotter, M., Gentile, G., Jonsson, T., Li, T.-Q. & Ehrsson, H. H. (2011b). From part-to whole-body ownership in the multisensory brain. *Current Biology*, 21 (13), 1118-1122. [10.1016/j.cub.2011.05.022](https://doi.org/10.1016/j.cub.2011.05.022)
- Pfeiffer, C., Lopez, C., Schmutz, V., Duenas, J. A., Martuzzi, R. & Blanke, O. (2013). Multisensory origin of the subjective first-person perspective: Visual, tactile, and vestibular mechanisms. *PLoS ONE*, 8 (4), e61751. [10.1371/journal.pone.0061751](https://doi.org/10.1371/journal.pone.0061751)
- Pfeiffer, C., Serino, A. & Blanke, O. (2014). The vestibular system: A spatial reference for bodily self-consciousness. *Frontiers in Integrative Neuroscience*, 8, 1-13. [10.3389/fnint.2014.00031](https://doi.org/10.3389/fnint.2014.00031)
- Serino, A., Alsmith, A., Costantini, M., Mandrigin, A., Tajadura-Jimenez, A. & Lopez, C. (2013). Bodily ownership and self-location: Components of bodily self-consciousness. *Consciousness and Cognition*, 22 (4), 1239-1252. [10.1016/j.concog.2013.08.013](https://doi.org/10.1016/j.concog.2013.08.013)
- Slachevsky, A., Pillon, B., Fournieret, P., Pradat-diehl, P., Jeannerod, M. & Dubois, B. (2001). Preserved adjustment but impaired awareness in a sensory-motor conflict following prefrontal lesions. *Journal of Cognitive Neuroscience*, 13 (3), 332-340. [10.1162/08989290151137386](https://doi.org/10.1162/08989290151137386)
- Smith, A. J. T. (2010). Comment: Minimal conditions on the simplest form of self-consciousness. In T. Fuchs, H. Sattel & P. Henningsen (Eds.) *The embodied self: Dimensions, coherence, disorders* (pp. 35-41). Stuttgart, GER: Schattauer.
- Vaitl, D., Mittelstaedt, H., Saborowski, R., Stark, R. & Baisch, F. (2002). Shifts in blood volume alter the perception of posture: further evidence for somatic graviception. *International Journal of Psychophysiology*, 44 (1), 1-11. [10.1016/S0167-8760\(01\)00184-2](https://doi.org/10.1016/S0167-8760(01)00184-2)
- Vogeley, K. & Fink, G. R. (2003). Neural correlates of the first-person-perspective. *Trends in Cognitive Sciences*, 7 (1), 38-42. [10.1016/S1364-6613\(02\)00003-7](https://doi.org/10.1016/S1364-6613(02)00003-7)
- Zahavi, D. (2005). *Subjectivity and selfhood: Investigating the first-person perspective*. Cambridge, MA: MIT Press.

Vestibular Sense and Perspectival Experience

A Reply to Adrian Alsmith

Bigna Lenggenhager & Christophe Lopez

To answer Alsmith's questions about the existence of a vestibular sense, we outline in the first part of our reply why we believe the vestibular sense is a true "sixth sense". We argue that vestibular information constitutes distinct sensory events and that absolute coding of body orientation and motion in the gravity-centered space is the important unique feature of the vestibular system. In the last part of our reply, we extend Alsmith's experimental suggestions to investigate the vestibular contribution to various perspectival experiences.

Keywords

Absolute coding | Gravity | Otoliths | Perspective | Self-motion | Vestibular sense | Vestibular thresholds | Vestibular-evoked potentials

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1 Is there a vestibular sense?

The first section of Alsmith's commentary ("Structural vs. taxonomic approaches to vestibular processes") raises an important question: *is there a vestibular sense?* The enduring lack of a clear answer to this seemingly simple question might stem from the old assumption that there are five and only five senses, all of

which giving rise to a distinct conscious sensation. The relatively late identification of the anatomical structures that code self-motion ([Wade 2003](#); [Lopez & Blanke 2014](#)) has probably further contributed to the neglect of the "vestibular sense" in philosophy and science. We comment below on two questions raised by

Alsmith concerning this debate: (1) *Are vestibular events sensory events?* and (2) *Are vestibular events of a specific kind, i.e., distinct from other sensations?*

(1) Are vestibular events sensory events? Several criteria have been proposed to determine whether an event is sensory or not (Macpherson 2011).¹ Following this type of approach, vestibular events can be described as sensory events because a sensory organ is dedicated to coding gravito-inertial forces and because there is a phenomenal experience associated with vestibular stimulation. Indeed, there are many situations during which passive own-body motions are characterized by distinct self-motion sensations. Imagine, for example, a situation in which we are sitting with eyes closed in the train and feel the departure, or when we are standing with eyes opened in a lift and experience vertical movement of the body. In such situations visual and somatosensory signals do not (or only weakly) contribute, but changes in vestibular signaling result in the conscious perception of self-motion, i.e., of “being translated forward” or “being elevated”.

Self-motion perception due to vestibular stimulation is also testable in the laboratory using motorized motion platforms (rotating chairs or translational platforms, see Palla & Lenggenhager 2014): participants are usually tested sitting on a chair, while non-vestibular sensory signals are largely excluded by having the participant’s body strapped to the chair and stabilized with cushions, by testing participants with eyes closed, by reducing auditory cues via white noise presented in headphones, and by testing participants with gloves and long sleeves (e.g., Grabherr et al. 2008; Hartmann et al. 2013; Lopez et al. 2013; Macaudo et al. 2014; Valko et al. 2012). Participants are able to accurately detect and report self-motion and its direction, which forms the basis for the measurement of *vestibular thresholds*, which are comparable to auditory or tactile thresholds. When accelerations are

applied above the threshold of the mechanoreceptors in the inner ear (e.g., above $0.6^\circ/\text{s}^2$ for rotations around the vertical axis), a motion sensation emerges in healthy participants, which in our opinion is the sensory event corresponding to the vestibular sensation “I was moved”. Such sensory events therefore constitute the basis of what has often been referred to as the “sixth sense” (Goldberg et al. 2012; Wade 2003; Berthoz 2000). Further compelling support comes from patients with dysfunctions of the peripheral vestibular apparatus like benign paroxysmal positional vertigo, vestibular neuritis, or Menière’s disease, who experience strong vestibular sensations in the form of vertigo (Brandt 1999).

We acknowledge, however, that in situations where we actively move the head with eyes opened in space, vestibular signals from self-motion do not give rise to such distinct “vestibular” sensation of self-motion. As explained in our target article, in conditions of active, self-generated head movements, vestibular signals are cancelled or strongly attenuated in the vestibular nuclei (Cullen 2011; Roy & Cullen 2004). This is probably why the vestibular sense has been termed a “silent sense” by some authors (Day & Fitzpatrick 2005).

(2) Are vestibular sensory events of a specific kind, i.e., distinct from other sensations? Vestibular sensations are sensations of own-body rotations, translations, and orientation (sensation of whole-body orientation with respect to the vertical) in space. Such sensations may in principle also emerge from the stimulation of other sensory systems, such as the visual, somatosensory and auditory systems. Impressively, illusory self-motion might be evoked by large optic flows, tactile stimulation under the feet, or displacement of auditory stimuli (Berthoz et al. 1975; Dichgans et al. 1972; Lackner & DiZio 2001, 2005; Våljamäe 2009). These findings resulted in Alsmith’s claim that “one may begin to seriously consider the possibility that vestibular processing does not constitute a form of sensory processing of its own kind” (this collection, p. 2). Yet if vestibular processing does

¹ For example, according to Macpherson, four main approaches to describe the senses can be distinguished: “the representational criterion,” “the phenomenal character criterion,” “the proximal stimulus criterion,” and “the sense-organ criterion” (2011).



Figure 1: A) *Crise de désinvolture* (2003) an artwork by Philippe Ramette. Copyrights: © 2015, ProLitteris, Zurich. All rights are reserved. Reproduction and any other use without permission - except for the individual and private use - is prohibited. B) Drawing of the “haunting sway”, a “gravity-defying” device that was originally developed in the US in the 1890s for amusement parks. The visitors had the impression that they were turning with the sway, while actually the room was turning around them.

not constitute a distinct form of sensory perception, to which type of sensory processing does it belong? Some authors have proposed that vestibular processing might relate to *proprioception* (since the vestibular system detects own body motions) or to *exteroception* (since it detects gravitational acceleration), but these propositions link vestibular processing to a function rather than a sensory modality. As recently pointed out by Macpherson (2011), “it is not even clear which sensory modality equilibration should be assimilated to, if indeed it should be assimilated to any” (p. 18).

Although vestibular, visual, and somesthetic signals may all support self-motion perception, this does not mean that the phenomenal experience of self-motion based on vestibular signals is similar to the experience based on visual signals. Actually, they may strongly differ in their content since, for example, the vestibular system is specialized in coding

high-frequency movements whereas the visual system is tuned to low-frequency movements (see also next paragraph).² And even at the neurophysiological level, vestibular signals interact very early with visual and somatosensory signals; yet this does not mean that these signals provide the exact same sensation of body motion and orientation. An analogy might be when we observe a person speaking: both auditory and visual signals from the speaker’s lip movements contribute to the experience of listening to a voice; nevertheless both signals provide clearly distinct sensations and experiences. We believe the same holds for vestibular processing. Vestibular sensations might be clearly distinct sensations, but in daily life they are often integrated with other senses, confounding a pure conscious sensation (Angelaki & Cullen 2008; Angelaki et al.

² We add that while visual, auditory, and somatosensory signals about self-motion can be suppressed, vestibular signals about body accelerations are *necessarily present*.

2009). Vestibular-only neurons are found in the vestibular nuclei, which are not influenced by visual signals or eye movements, suggesting that vestibular signals are not entirely fused with other sensory signals (Goldberg et al. 2012). Similarly, intracranial stimulations in epileptic patients have showed that pure vestibular sensations could be evoked during electrical stimulations of the superior temporal cortex and insula (Penfield 1957; Kahane et al. 2003; Mazzola et al. 2014).

2 A unique feature of the vestibular system: The representation of absolute self-motion and orientation

As mentioned by Alsmith, the vestibular system, unlike other sensory systems, does not code unique properties of sensory inputs such as loudness or hue. Yet, as already argued in the target article, the coding of *absolute* self-motion in space and self-orientation within gravity-related space is unique to the vestibular system. While relative (self-) motion and orientation can be detected by other sensory systems (e.g., vision and proprioception), gravity itself is not directly visible to these senses.³ Because vestibular organs contain gravito-inertial sensors, they provide a coding of body translations and rotations that is independent from external references (unlike visual, auditory, and somatosensory coding of whole-body motions). For this reason, vestibular organs code self-motion even when the eyes are closed, while we are jumping on a trampoline, or swimming in the sea.

With these properties the vestibular system, especially otolith signaling, also gives us the sensation of an “up” and a “down” by encoding gravitational acceleration. This process might be less accessible to consciousness in normal circumstances, as gravitational pull is constantly acting on vestibular mechanoreceptors. However, there is a large body of data showing that an “internal model of gravity” (predicting how objects move in the physical world according to Newton’s laws; McIntyre et al. 2001) which is strongly

based on otolith processing, shapes at a pre-conscious level several aspects of the visual perception of objects, body movements, and structure (e.g., Indovina et al. 2005; Lacquaniti et al. 2013; Lopez et al. 2009; Maffei et al. 2015; Yamamoto & Yamamoto 2006). A further illustration of the importance of the coding of body orientation in a gravity-centered space can be provided by the “tilted room illusion,” in which the furniture is aligned in a way that is incongruent with gravitational vertical (see figure 1A for an example by the French artist Philippe Ramette⁴), which has been used in a moving version as well in theme parks (the haunting swing, a “gravity-defying” ride, see figure 1B). Experiments conducted in this type of tilted environment have shown that the participant’s perception and posture are biased by tilted visual references, but not totally (Jenkin et al. 2003; Oman 2003). Merleau-Ponty has nicely noted the ambiguity of space-coding regarding the experience of *up* and *down*: “A direction can only exist for a subject who traces it out, and although a constituting mind eminently has the power to trace out all directions in space, in the present moment this mind has no direction and, consequently, it has no space, for it is lacking an actual starting point or an absolute here that could gradually give a direction to all determinations of space” (2012). It is interesting to note Merleau-Ponty’s claim that what is missing for the experience of up and down is an “absolute”. Merleau-Ponty also explains that “[w]e cannot, then, understand the experience of space through the consideration of the contents, nor through that of a pure activity of connecting, and we are confronted by that ‘*third spatiality*’ that we foreshadowed above, which is neither the spatiality of things in space, nor that of spatializing space [...] We need an ‘*absolute within the relative*’, a space that does not skate over appearances, that is anchored in them and depends upon them” (2012, p. 296–297; our italics). Although Merleau-Ponty did not mention the vestibular system when he described the necessity of a “third spatiality,” we now know that the otolithic sys-

³ Of course we can infer about (the direction of) gravity by the relative motion and specific properties of certain objects; however this process is much slower, less intuitive, and not always applicable.

⁴ To be precise, Ramette does not glue the furniture to the roof or wall, but rather “glues” himself to the wall. His position is thus tilted compared to gravity, not the furniture.

tem provides the “absolute within the relative” he mentions and allows the coding of absolute self-orientation in space (see also [Berthoz 2011](#) for a detailed account).

3 Vestibular system and perspectival experience—Experimental suggestions

In this last part we elaborate on the experimental suggestions provided by by Alsmith, proposed in order to investigate more fine-grained forms of perspectival perceptions and their interaction with vestibular processes. In the target article we used the term first-person perspective (mainly in the context of mental perspective taking and out-of-body experiences) to refer to an egocentric visuo-spatial perspective. Alsmith proposes a subdivision of this perspective into three forms of perspectival structures: “origin,” “egocentric frame of reference,” and “focal point of sensory flow (egomotion),” which might be differentially influenced by vestibular signals. While we do not necessarily agree on the importance and justification of these (and *exactly these*) components, we appreciate the experimental suggestions, on which we will briefly comment below.

3.1 Experiments I and II: Changing vestibular processes through change in perspective

A common approach to testing the influence of the vestibular system on high-level cognition is to alter vestibular information during a specific task—for example a perspective-taking task. This can be done either by applying galvanic ([Lenggenhager et al. 2008](#)) or caloric ([Falconer & Mast 2012](#)) vestibular stimulation, by natural vestibular stimulation ([Van Elk & Blanke 2014](#)), by exposing participants to microgravity ([Grabherr et al. 2007](#)), by changing the body orientation relative to gravity ([Arzy et al. 2006](#)), or by testing patients with vestibular dysfunction ([Grabherr et al. 2011](#)). What Alsmith describes⁵ in the first two experiments

mentioned in the commentary is the opposite approach, namely assessing vestibular processing during specific tasks, or bodily states, respectively.⁶ We believe that this is a potentially powerful way to better understand vestibular implication in fine-grained aspects of the bodily self and their interrelation—both in experimental work and research in patients with bodily-self disturbances (see e.g., [Brugger & Lenggenhager 2014](#) for a recent review). We would like, however, to point out a few important issues that should be considered.

Alsmith suggests that we measure time-locked vestibular-evoked potentials without stating more precisely what vestibular stimulation to use. However, this is crucial, since there are various ways to test vestibular processing, mostly by stimulating a specific part of the vestibular system (see e.g., [Palla & Lenggenhager 2014](#) for a recent review). One possibility (in the suggested experiment) could be to use sound-induced vestibular-evoked potentials. The advantage of these is that they can be recorded in a static condition, unlike other forms of vestibular stimulation (e.g., rotatory evoked cortical potentials; [Keck 1990](#)), which is important for the suggested full-body illusion paradigms. When designing experiments along these lines, it is indispensable to know what part of the vestibular system is stimulated by the used technique. Sound-induced cortical vestibular potentials, for example, represent cortical processing of otolith signals, mainly from the saccule, thus coding preferentially linear movements in the vertical plane (i.e., up and down movements in a standing position). If we rather expect a difference in coding the front-back movement, as proposed in Experiments 1 and 2, a vestibular stimulation of the utricle might be more appropriate (e.g., [Todd et al. 2014](#), using evoked-potentials by impulsive accelerations). Since testing all different aspects in all the proposed conditions is technically impossible, the specific vestibular stimulation should be carefully chosen based on the hypothesis. Alternatively,

⁵ This idea of measuring vestibular processes during situations of altered sense bodily self evolved in the framework of a grant entitled “Finding Perspective” awarded to Adrian Alsmith, Christophe Lopez and colleagues by the Volkswagen Foundation.

⁶ A similar approach has been used for other sensory processes such as the measure of body temperature during the rubber hand illusion ([Lenggenhager et al. 2014](#); [Moseley et al. 2008](#)) or the full-body illusion ([Macauda et al. 2014](#); [Salomon et al. 2013](#)).

more indirect measures could be used to test a vestibular implication, such as changes in posture or stability during various experimentally-induced alterations in the bodily self, e.g., via dynamic posturography using a moving platform, as it is commonly used in clinical settings (e.g., Ghulyan et al. 2005).

3.2 Experiment III: Egocentric perspective

In the third proposed experiment, Alsmith considers which (bodily) reference (e.g., eye, head or body centered) is taken as the egocentric reference frame. The fact that there are multiple bodily frames of reference has been nicely shown in a classical task where ambiguous letters (e.g., d/p) are written on the skin. They are typically perceived differently depending on the bodily location on which they are written (Sekiyama 1991); and interestingly the perspective can be modified by vestibular stimulation (Ferrè et al. 2014). Alsmith here suggests that there is a need to investigate the egocentric perspective both with implicit and explicit measures in a situation where body and head⁷ are misaligned, as previously done to test spatial cognition (Schindler 1997) and heading direction during passive motion (Ni et al. 2013). This is a very interesting suggestion; however from the experimental description it is not entirely clear how Alsmith thinks that the vestibular contribution should be investigated. Furthermore, his hypothesis only concerns the respective contribution of head and torso position, but not its vestibular contribution. He suggests that participants might receive galvanic vestibular stimulation or tendon vibration stimulation to investigate “the relative contribution of vestibular processes to egocentric perspective.” One way to test this could be to align the participant’s head and torso, but use tendon vibration or galvanic vestibular stimulation in order to induce an illusory tilt or turn the participant’s head, thus inducing an illusory misalignment of the head and body. By doing the suggested task in such a condition, vestibular or proprioceptive contribution could be isolated.

While this is theoretically very interesting, there might be practical difficulties: vestibular and proprioceptive illusions are usually susceptible to huge individual differences, and inducing illusory shift of $\pm 15\%$ could be difficult. Furthermore, in the proposed experiment that misaligns body and head around the yaw axis, gravitational cues do not differ between the position of the torso and the head in the misaligned condition. Adapting the experiment to a lying-down position,⁸ where body and head would be at different angles with respect to gravity, could help investigating the otolithic influence on perspective.

4 Conclusion

In response to Alsmith’s inspiring theoretical suggestions, we have argued that there is a true vestibular sense, with distinct and important properties. We believe and agree with Alsmith that better understanding its contribution to various aspects of experiential life is crucial and that this might also facilitate taxonomic and structural approaches. Alsmith’s response exemplifies, in our view, the mutual benefit of an interdisciplinary dialogue, as his thorough analysis of current experimental data, paired with new theoretical considerations, leads to concrete experimental suggestions, which might reshape theoretical considerations depending on the potential results. In our reply we have pointed out some possible methodological difficulties, some possible ways to overcome these, and some new directions such experimental work could take. In particular, we are optimistic that analyzing vestibular processing in the brain using electrophysiological approaches will provide in the near future important new data about the vestibular contribution to the sense of self. We hope that our reply will help foster interdisciplinary collaborations that further investigate the role of the vestibular system in shaping our mind.

⁷ Additionally, eye-position could be manipulated.

⁸ Or generally test various body orientations (e.g., as in Lopez et al. 2009).

References

- Alsmith, A. (2015). Perspectival Structure and Vestibular Processing. In T. Metzinger & J. M. Windt (Eds.) *Open MIND*. Frankfurt a. M., GER: MIND Group.
- Angelaki, D. E. & Cullen, K. E. (2008). Vestibular system: The many facets of a multimodal sense. *Annual Review of Neuroscience*, 31, 125-150. [10.1146/annurev.neuro.31.060407.125555](https://doi.org/10.1146/annurev.neuro.31.060407.125555)
- Angelaki, D. E., Klier, E. M. & Snyder, L. H. (2009). A vestibular sensation: Probabilistic approaches to spatial perception. *Neuron*, 64, 448-461. [10.1016/j.neuron.2009.11.010](https://doi.org/10.1016/j.neuron.2009.11.010)
- Arzy, S., Thut, G., Mohr, C., Michel, C. M. & Blanke, O. (2006). Neural basis of embodiment: Distinct contributions of temporoparietal junction and extrastriate body area. *Journal of Neuroscience*, 26 (31), 8074-8081. [10.1523/JNEUROSCI.0745-06.2006](https://doi.org/10.1523/JNEUROSCI.0745-06.2006)
- Berthoz, A. (2000). *The brain's sense of movement*. Cambridge, MA: Harvard University Press.
- (2011). La conscience du corps. In A. Berthoz & B. Andrieu (Eds.) *Le corps en acte: Centenaire Maurice Merleau Ponty* (pp. 9-22). Nancy, F: Presses Universitaires de Nancy.
- Berthoz, A., Pavard, B. & Young, L. R. (1975). Perception of linear horizontal self-motion induced by peripheral vision (linearvection) basic characteristics and visual-vestibular interactions. *Experimental Brain Research*, 23 (5), 471-489. [10.1007/BF00234916](https://doi.org/10.1007/BF00234916)
- Brandt, T. (1999). *Vertigo. Its multisensory syndromes*. London, UK: Springer.
- Brugger, P. & Lenggenhager, B. (2014). The bodily self and its disorders: Neurological, psychological and social aspects. *Current Opinion in Neurology*, 27 (6), 644-652. [10.1097/WCO.0000000000000151](https://doi.org/10.1097/WCO.0000000000000151)
- Cullen, K. E. (2011). The neural encoding of self-motion. *Current Opinion in Neurobiology*, 21 (4), 587-595. [10.1016/j.conb.2011.05.022](https://doi.org/10.1016/j.conb.2011.05.022)
- Day, B. L. & Fitzpatrick, R. C. (2005). The vestibular system. *Current Biology*, 15 (15), R583-R586. [10.1016/j.cub.2005.07.053](https://doi.org/10.1016/j.cub.2005.07.053)
- Dichgans, J., Held, R., Young, L. R. & Brandt, T. (1972). Moving visual scenes influence the apparent direction of gravity. *Science*, 178, 1217-1219.
- Falconer, C. J. & Mast, F. W. (2012). Balancing the mind: Vestibular induced facilitation of egocentric mental transformations. *Experimental Psychology*, 59 (6), 332-339. [10.1027/1618-3169/a000161](https://doi.org/10.1027/1618-3169/a000161)
- Ferrè, E. R., Lopez, C. & Haggard, P. (2014). Anchoring the self to the body: Vestibular contribution to the sense of self. *Psychological Science*, 25 (11), 2106-2108. [10.1177/0956797614547917](https://doi.org/10.1177/0956797614547917)
- Ghulyan, V., Paolino, M., Lopez, C., Dumitrescu, M. & Lacour, M. (2005). A new translational platform for evaluating aging or pathology-related postural disorders. *Acta Oto-Laryngologica*, 125 (6), 607-617. [10.1080/00016480510026908](https://doi.org/10.1080/00016480510026908)
- Goldberg, J. M., Wilson, V. J., Cullen, K. E., Angelaki, D. E., Broussard, D. M., Büttner-Ennever, J. A. & Minor, L. B. (2012). *The vestibular system. A sixth sense*. New York, NY: Oxford University Press.
- Grabherr, L., Karmali, F., Bach, S., Indermaur, K., Metzler, S. & Mast, F. W. (2007). Mental own-body and body-part transformations in microgravity. *Journal of Vestibular Research*, 17 (5-6), 279-287.
- Grabherr, L., Nicoucar, K., Mast, F. W. & Merfeld, D. M. (2008). Vestibular thresholds for yaw rotation about an earth-vertical axis as a function of frequency. *Experimental Brain Research*, 186 (4), 677-681. [10.1007/s00221-008-1350-8](https://doi.org/10.1007/s00221-008-1350-8)
- Grabherr, L., Cuffel, C., Guyot, J.-P. & Mast, F. W. (2011). Mental transformation abilities in patients with unilateral and bilateral vestibular loss. *Experimental Brain Research*, 209 (2), 205-214. [10.1007/s00221-011-2535-0](https://doi.org/10.1007/s00221-011-2535-0)
- Hartmann, M., Furrer, S., Herzog, M. H., Merfeld, D. M. & Mast, F. W. (2013). Self-motion perception training: Thresholds improve in the light but not in the dark. *Experimental Brain Research*, 226 (2), 231-240. [10.1007/s00221-013-3428-1](https://doi.org/10.1007/s00221-013-3428-1)
- Indovina, I., Maffei, V., Bosco, G., Zago, M., Macaluso, E. & Lacquaniti, F. (2005). Representation of visual gravitational motion in the human vestibular cortex. *Science*, 308 (5720), 416-419. [10.1126/science.1107961](https://doi.org/10.1126/science.1107961)
- Jenkin, H. L., Dyde, R. T., Jenkin, M. R., Howard, I. P. & Harris, L. R. (2003). Relative role of visual and non-visual cues in determining the direction of “up”: Experiments in the York tilted room facility. *Journal of Vestibular Research*, 13 (4-6), 287-293. [10.1016/j.actaastro.2005.01.030](https://doi.org/10.1016/j.actaastro.2005.01.030)
- Kahane, P., Hoffmann, D., Minotti, L. & Berthoz, A. (2003). Reappraisal of the human vestibular cortex by cortical electrical stimulation study. *Annals of Neurology*, 54 (5), 615-624.
- Keck, W. (1990). Rotatory evoked cortical potentials in normal subjects and patients with unilateral and bilateral vestibular loss. *European Archives of Oto-Rhino-Laryngology*, 247 (4), 222-225. [10.1007/BF00178989](https://doi.org/10.1007/BF00178989)
- Lackner, J. R. & DiZio, P. (2001). Somatosensory and proprioceptive contributions to body orientation, sensory localization, and self-calibration. In R. J. Nelson (Ed.) *The somatosensory system: Deciphering the brain's own body image* (pp. 121-140). Boca Raton, FL: CRC Press.

- (2005). Vestibular, proprioceptive, and haptic contributions to spatial orientation. *Annual Review of Psychology*, 56, 115-147. [10.1146/annurev.psych.55.090902.142023](https://doi.org/10.1146/annurev.psych.55.090902.142023)
- Lacquaniti, F., Bosco, G., Indovina, I., La Scaleia, B., Maffei, V., Moscatelli, A. & Zago, M. (2013). Visual gravitational motion and the vestibular system in humans. *Frontiers in Integrative Neuroscience*, 7 (101). [10.3389/fnint.2013.00101](https://doi.org/10.3389/fnint.2013.00101)
- Lenggenhager, B., Lopez, C. & Blanke, O. (2008). Influence of galvanic vestibular stimulation on egocentric and object-based mental transformations. *Experimental Brain Research*, 184 (2), 211-221. [10.1007/s00221-007-1095-9](https://doi.org/10.1007/s00221-007-1095-9)
- Lenggenhager, B., Hilti, L., Palla, A., Macaudo, G. & Brugger, P. (2014). Vestibular stimulation does not diminish the desire for amputation. *Cortex*, 54, 210-212. [10.1016/j.cortex.2014.02.004](https://doi.org/10.1016/j.cortex.2014.02.004)
- Lopez, C. & Blanke, O. (2014). Nobel Prize centenary: Robert Bárány and the vestibular system. *Current Biology*, 24 (21), R1026-R1028. [10.1016/j.cub.2014.09.067](https://doi.org/10.1016/j.cub.2014.09.067)
- Lopez, C., Bachofner, C., Mercier, M. & Blanke, O. (2009). Gravity and observer - body orientation influence the visual perception of human body postures. *Journal of Vision*, 9 (5), 1-14. [10.1167/9.5.1](https://doi.org/10.1167/9.5.1)
- Lopez, C., Falconer, C. J. & Mast, F. W. (2013). Being moved by the self and others: influence of empathy on self-motion perception. *PloS One*, 8 (1), e48293-e48293. [10.1371/journal.pone.0048293](https://doi.org/10.1371/journal.pone.0048293)
- Macaudo, G., Bertolini, G., Palla, A., Straumann, D., Brugger, P. & Lenggenhager, B. (2014). Binding body and self in visuo-vestibular conflicts. *European Journal of Neuroscience*, 13, 556-571. [10.1038/nrn3292](https://doi.org/10.1038/nrn3292)
- Macpherson, F. (2011). Individuating the senses. In F. Macpherson (Ed.) *The senses: Classic and contemporary philosophical perspectives* (pp. 3-43). Oxford, UK: Oxford University Press.
- Maffei, V., Indovina, I., Macaluso, E., Ivanenko, Y. P., A. Orban, G. & Lacquaniti, F. (2015). Visual gravity cues in the interpretation of biological movements: Neural correlates in humans. *NeuroImage*, 104, 221-230. [10.1016/j.neuroimage.2014.10.006](https://doi.org/10.1016/j.neuroimage.2014.10.006)
- Mazzola, L., Lopez, C., Faillenot, I., Chouchou, F., Mauguière, F. & Isnard, J. (2014). Vestibular responses to direct stimulation of the human insular cortex. *Annals of Neurology*, 76 (4), 609-619. [10.1002/ana.24252](https://doi.org/10.1002/ana.24252)
- McIntyre, J., Zago, M., Berthoz, A. & Lacquaniti, F. (2001). Does the brain model Newton's laws? *Nature Neuroscience*, 4 (7), 693-694. [10.1038/89477](https://doi.org/10.1038/89477)
- Merleau-Ponty, M. (2012). *Phenomenology of perception*. London, UK: Routledge.
- Moseley, G. L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A. & Spence, C. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proceedings of the National Academy of Sciences, USA*, 105, 13169-13173. [10.1073/pnas.0803768105](https://doi.org/10.1073/pnas.0803768105)
- Ni, J., Tatalovic, M., Straumann, D. & Olasagasti, I. (2013). Gaze direction affects linear self-motion heading discrimination in humans. *European Journal of Neuroscience*, 38 (8), 3248-3260. [10.1111/ejn.12324](https://doi.org/10.1111/ejn.12324)
- Oman, C. M. (2003). Human visual orientation in weightlessness. *Levels of Perception* (pp. 375-398). New York, NY: Springer.
- Palla, A. & Lenggenhager, B. (2014). Ways to investigate vestibular contributions to cognitive processes. *Frontiers in Integrative Neuroscience*, 8 (40). [10.3389/fnint.2014.00040](https://doi.org/10.3389/fnint.2014.00040)
- Penfield, W. (1957). Vestibular sensation and the cerebral cortex. *Annals of Otology, Rhinology & Laryngology*, 66, 691-698.
- Roy, J. E. & Cullen, K. E. (2004). Dissociating self-generated from passively applied head motion: Neural mechanisms in the vestibular nuclei. *Journal of Neuroscience*, 24, 2102-2111. [10.1523/JNEUROSCI.3988-03.2004](https://doi.org/10.1523/JNEUROSCI.3988-03.2004) 24/9/2102
- Salomon, R., Lim, M., Pfeiffer, C., Gassert, R. & Blanke, O. (2013). Full body illusion is associated with widespread skin temperature reduction. *Frontiers in Behavioral Neuroscience*, 7 (65). [10.3389/fnbeh.2013.00065](https://doi.org/10.3389/fnbeh.2013.00065)
- Schindler, G. K. (1997). Head and trunk orientation modulate visual neglect. *Neuroreport*, 8 (12), 2681-2685. [10.1097/00001756-199708180-00009](https://doi.org/10.1097/00001756-199708180-00009)
- Sekiyama, K. (1991). Importance of head axes in perception of cutaneous patterns drawn on vertical body surfaces. *Perception and Psychophysics*, 49 (5), 481-492. [10.3758/BF03212182](https://doi.org/10.3758/BF03212182)
- Todd, N. P. M., McLean, A., Paillard, A., Kluk, K. & Colebatch, J. G. (2014). Vestibular evoked potentials (VsEPs) of cortical origin produced by impulsive acceleration applied at the nasion. *Experimental Brain Research*, 232 (12), 3771-3784. [10.1007/s00221-014-4067-x](https://doi.org/10.1007/s00221-014-4067-x)
- Valko, Y., Lewis, R. F., Priesol, A. J. & Merfeld, D. M. (2012). Vestibular labyrinth contributions to human whole-body motion discrimination. *Journal of Neuroscience*, 32 (39), 13537-13542. [10.1523/JNEUROSCI.2157-12.2012](https://doi.org/10.1523/JNEUROSCI.2157-12.2012)
- Van Elk, M. & Blanke, O. (2014). Imagined own-body transformations during passive self-motion. *Psychological Research*, 78 (1), 18-27. [10.1007/s00426-013-0486-8](https://doi.org/10.1007/s00426-013-0486-8)

- Väljamäe, A. (2009). Auditorily-induced illusory self-motion: A review. *Brain Research Reviews*, 61 (2), 240-255. [10.1016/j.brainresrev.2009.07.001](https://doi.org/10.1016/j.brainresrev.2009.07.001)
- Wade, N. J. (2003). The search for a sixth sense: The cases for vestibular, muscle, and temperature senses. *Journal of the History of the Neurosciences*, 12 (2), 175-202. [10.1076/jhin.12.2.175.15539](https://doi.org/10.1076/jhin.12.2.175.15539)
- Yamamoto, S. & Yamamoto, M. (2006). Effects of the gravitational vertical on the visual perception of reversible figures. *Neuroscience Research*, 55 (2), 218-221. [10.1016/j.neures.2006.02.014](https://doi.org/10.1016/j.neures.2006.02.014)