A neuroscientific account of how vestibular disorders impair bodily self-consciousness

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The consequences of vestibular disorders on balance, oculomotor control, and self-motion perception have been extensively described in humans and animals. More recently, vestibular disorders have been related to cognitive deficits in spatial navigation and memory tasks. Less frequently, abnormal bodily perceptions have been described in patients with vestibular disorders. Altered forms of bodily self-consciousness include distorted body image and body schema, disembodied self-location (out-of-body experience), altered sense of agency, as well as more complex experiences of dissociation and detachment from the self (depersonalization). In this article, I suggest that vestibular disorders create sensory conflict or mismatch in multisensory brain regions, producing perceptual incoherence and abnormal body and self perceptions. This hypothesis is based on recent functional mapping of the human vestibular cortex, showing vestibular projections to the primary and secondary somatosensory cortex and in several multisensory areas found to be crucial for bodily self-consciousness.

Keywords: vestibular system, body schema, body image, touch, caloric vestibular stimulation, bodily consciousness, multisensory integration

INTRODUCTION

The consequences of vestibular disorders are dramatic as they incorporate a wide range of symptoms including vertigo, loss of balance, and blurred vision. It is accepted that vertigo results from abnormalities of the inner ear or the vestibulocerebellum, while abnormal body and self perceptions have been described in patients with vestibular disorders. Altered forms of bodily self-consciousness include distorted body image and body schema, disembodied self-location (out-of-body experience), altered sense of agency, as well as more complex experiences of dissociation and detachment from the self (depersonalization). In this article, I suggest that vestibular disorders create sensory conflict or mismatch in multisensory brain regions, producing perceptual incoherence and abnormal body and self perceptions. This hypothesis is based on recent functional mapping of the human vestibular cortex, showing vestibular projections to the primary and secondary somatosensory cortex and in several multisensory areas found to be crucial for bodily self-consciousness.

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A NEUROSCIENTIFIC FRAMEWORK BASED ON THE MULTISENSORY NATURE OF THE VESTIBULO-THALAMO-CORTICAL PATHWAYS

The neuroscientific framework to understand bodily disorders in vestibular patients is based on the multisensory nature of the vestibulo-thalamo-cortical pathways, a finding that was unknown from Bonnier and Schilder when they described the consequences of vertigo on body perception. A vestibulo-visuo-somatosensory convergence has been found in all vestibular relays, including vestibular nuclei, thalamus, and cerebral cortex (see Figure 1 and Table 1 for details).

Normal sensorimotor development calibrates synergies between actions and their sensory consequences at both behavioral and neural levels (Held and Hein, 1963). For example, head rotations to the right are normally encoded with leftward optic flow and matching proprioceptive signals from the neck. Corresponding synergistic responses exist in all vestibulo-thalamo-cortical structures and recent studies showed that vestibular and visual responses combine “in a statistically optimal fashion,” in accordance with the predictions of Bayesian models (MacNeilage et al., 2007; Fetsch et al., 2012). Importantly, sensory conflicts may desynchronize calibrated synergies at the neural level (e.g., visuo-vestibular mismatch alters neural responses in vestibular nuclei; Waspe and Hein, 1978). Here, I propose similar mismatch is produced by various peripheral vestibular disorders (e.g., Menière’s disease, vestibular neuritis). I suggest that vestibular disorders provide the brain with erroneous vestibular signals about current self-motion and position, and create sensory conflicts (or mismatch) leading to a perceptual incoherence. That is, abnormal vestibular signals would induce misinterpretation of tactile, proprioceptive
Vestibular signals are processed in the brain, with a second level of vestibular processing taking place in the vestibular cortex. This region integrates vestibular information with visual and somatosensory signals. Vestibular signals are weighted higher when they contradict other sensory information, even when this information contradicts other sensory cues.

In the following sections, I describe a detailed neuroscientific account of how vestibular dysfunction can distort various aspects of the bodily self.

### DISTORTED BODY SCHEMA AND BODY IMAGE

#### CLINICAL DESCRIPTION

Vestibular disorders may impair two fundamental aspects of mental body representations known as body schema and body image. They refer to different types of representations of body configuration and metric properties, including the size and shape of body parts, and body position in space (e.g., Gallagher, 2005; Berlucchi and Aglioti, 2010; de Vignemont, 2010; Longo et al., 2010; Serino and Haggard, 2010). Although body schema and body image have been proposed to be of mostly proprioceptive and visual origin, a vestibular contribution was postulated over a century ago. Bonnier (1893, 1905) described striking examples of distorted perceptions of the body shape and size in vestibular patients. For example, one of his patients “felt his head became enormous, immense, losing itself in the air; his body disappeared and his whole being was reduced to only his face.” Interestingly, Bonnier coined the term “aschématie” (indicating a “loss” of the schema) to describe distorted representations of the volume, shape, and position of the body and body segments (Vallar and Papagno, 2003; Vallar and Rode, 2009).

Several decades later, Schilder (1935) described distorted body schema and image in vestibular patients who reported that the “neck swells during dizziness,” “extremities had become larger,” or “feet seem to elongate” (p. 117). Altogether, these sensations are comparable to neurological symptoms of asomatognosia (e.g., Dieguez et al., 2007), even if evoked solely by peripheral vestibular disorders.

#### EXPERIMENTAL EVIDENCE

Several lines of evidence from neurology and experimental psychology support the idea that abnormal body image and schema might change due to misinterpretation of bodily signals created by vestibular disorders. All of them are based on studies showing the influence of caloric (CVS) and galvanic (GVS) vestibular stimulation on the perceived shape and size of the body. Rode et al. (2012) described a patient with Wallenberg’s syndrome who reported a macrosomatognosia restricted to his left hemiface. In this patient, CVS temporarily alleviated distorted face perception. CVS also changed the perceived shape and position of phantom limbs in paraplegics (Le Chapelin et al., 2001). Similarly, CVS evoked the perception of a phantom limb in amputees who did not experience phantoms before, or altered the phantom perception in those who experienced phantoms already (André et al., 2010). This indicates that CVS can influence mental representations of a no-longer existing body segment and suggests that vestibular signals project to multisensory brain regions representing the body’s metric properties. Yet, these observations were based on self-movement perception showing that even in the case of large visual-vestibular conflicts, vestibular information is not disregarded and both signals are “mandatorily fused” (Prsa et al., 2012).

Other studies suggest that during multisensory conflicts, vestibular cues are weighted higher (Butler et al., 2010; Fetsch et al., 2012). These data indicate that participants strongly rely on vestibular signals, even when this information contradicts other sensory cues.
Table 1 | Evidence of multisensory integration in three vestibulo-thalamo-cortical structures.

| Anatomical structure | Evidence of multisensory integration |
|----------------------|--------------------------------------|
| Vestibular nuclei     | Vestibular nuclei neurons respond to vestibular, visual (optokinetic stimulation: Waespe and Hein, 1978), tactile, proprioceptive (Roy and Cullen, 2004) and eye movements signals (Trimmer and Robinson, 1960). These neurons integrate signals from otoths and semicircular canals afferents to discriminate between head translations and head tilts, as well as to distinguish between active (or voluntary) and passive (or involuntary) head movements (review in Angelaki and Cullen, 2008). |
| Thalamus              | Vestibular thalamic neurons are characterized by very similar responses that have been described for vestibular nuclei neurons, i.e., they respond to visual, tactile, and proprioceptive stimuli (review in Lopez and Blanke, 2011). For example, about half of the vestibular neurons in the cat LGN respond to optokinetic stimulation (Mayer and Putkonen, 1979) and most of them are also driven by saccadic eye movements. Vestibular neurons in the VPL, VPM, and VR respond to proprioceptive signals from joints and muscles (Deecke et al., 1977; Blum and Gilman, 1979) and code for passive movements of the neck, shoulders, legs, and vertebral column. Thalamic vestibular neurons also respond to tactile stimulation applied to the animal's paws (Eisen et al., 1970). |
| Cerebral cortex       | Vestibulo-visuo-somatosensory convergence has been reported in the PVC, at the junction of the insula with the retinotopic and somatosensory cortex (Grüsser et al., 1990a,b, 1994; Guldin and Grüsser, 1998). Visual–vestibular convergence has also been reported in the extrastriate visual area MST, a major region for self-motion perception based on optic flows (Bremmer et al., 1999; Gu et al., 2009). Vestibulo-somatosensory convergence has been reported in the intraparietal sulcus and primary somatosensory cortex in monkeys (areas 2v and 3v in the hand/arm and neck/trunk representations) and in the secondary somatosensory cortex in humans (Schwartz and Fredrickson, 1971; Brotini et al., 1995, 2001, 2005; Guldin and Grüsser, 1998; Bremmer et al., 2002; Fassol et al., 2009). |

only on patients' reports. Lopez et al. (2012b) demonstrated similar influence of CVS by using psychophysical measures in healthy participants. The influence of CVS on the perceived shape and size of the body was measured using a tactile distance comparison task and a proprioceptive judgment task. The results showed that CVS known to stimulate the right cerebral hemisphere modified the perceived size of the left hand, thus appeared to be enlarged. This finding was later corroborated by the application of GVS (Ferrè et al., 2013).

**NEUROPHYSIOLOGICAL HYPOTHESIS**

Neuroimaging studies have revealed the implication of the posterior parietal cortex in body shape and size perception. In particular, the perception of the current position of body segments is thought to rely on the superior parietal lobule and intraparietal region (Wulffert et al., 1998; Felician et al., 2004; Corradi-Dell’Acqua et al., 2008, 2009). The inferior parietal lobule is also particularly relevant since electrical stimulation of the angular gyrus distorts the body schema in epileptic patients (Bottini et al., 2002) and because transcranial direct current stimulation applied over the right angular gyrus modified body representations (Spitoni et al., 2013). Neuroimaging studies further revealed the implication of the parietal operculum and posterior insula as they contain somatotopic representations of the body (Eickhoff et al., 2007; Corradi-Dell’Acqua et al., 2009; Hashimoto and Inaka, 2013). Importantly, these parietal and insular regions process vestibular signals and the parietal operculum has even been proposed as the core vestibular cortex (Guldin and Grüsser, 1998; Eickhoff et al., 2004; Lopez et al., 2012a; zu Eulenburg et al., 2012). It is interesting to note that animal data revealed vestibulo-somatosensory convergence in parietal cortex, intraparietal sulcus, and operculo-insular cortex (Grüsser et al., 1990a,b; Bremmer et al., 2002). Bottini and colleagues showed that the parieto-insular cortex is a region where CVS interferes with tactile perception (Bottini et al., 1995, 2001, 2005; Ferrè et al., 2012). Accordingly, abnormal vestibular signals arriving in these regions during vertigo attacks may interfere with somatosensory processing. The misinterpretation of postural somesthetic signals from the neck may explain the patients’ reports that their neck or head is enlarged. In support of this view is the fact that CVS and GVS produce similar effects in healthy volunteers (Lopez et al., 2012b; Ferrè et al., 2013).

**EMBODIMENT OR THE SENSE OF UNITY BETWEEN THE SELF AND THE BODY**

**CLINICAL DESCRIPTION**

Vestibular patients may lose connection with their body and may be subject to an out-of-body experience (OBE). During an OBE, subjects localize their self outside their body, at a location that is often elevated (i.e., floating in the room), and experience seeing the environment from this disembodied location. Subjects may also experience seeing their own body (i.e., autoscopy), a double with which they strongly self-identify (Brugger, 1997; Blanke et al., 2004; Blanke and Mohr, 2005; Lopez et al., 2008; Blanke, 2012). Yet, clear cases of full-blown OBES due to vestibular disorders seem very rare. Bonnier (1995) described the case of a loss of self-body unity: “it seemed to [the patient] that he was divided into two persons, one who had not changed posture, and another new person on his right, looking somewhat outwardly. Then the two somatic individuals approached each other, merged, and the vertigo disappeared.” Illusory perceptions of doubles in vestibular pathology were also reported by Skworzoff (1931): one patient...
saw herself (i.e. autoscopy) for a moment in day light (Case 5, p. 764). Another patient saw and felt every day his own double (Case 6, p. 764). The same patient also reported in some instances sensations of flying, which could be evocative of an onolithic dysfunction.

**EXPERIMENTAL EVIDENCE**

Vestibular stimulation in healthy participants can strongly modify experienced self-location. GVS creates illusory motion of the entire body, i.e., dissociation between the perceived self-location (that appears tilted toward the cathode) and physical body location (Fitzpatrick and Day, 2004; Lenggenhager et al., 2008). Lopez et al. (2008) have proposed that such dissociation between self and body location reflects a type of partial disembodiment that is reminiscent of OBES of neurological origin. Another indirect evidence of a vestibular contribution to embodied self-location comes from the observation that OBES are more frequent in patients lying than sitting or standing upright (Blanke and Mohr, 2005). According to Green (1968), about 73% of OBES occur spontaneously when healthy subjects are lying down, and less often in sitting or standing subjects, suggesting a strong contribution of gravitational vestibular signals to self-location and embodiment.

**NEUROPHYSIOLOGICAL HYPOTHESIS**

A neurophysiological model by Blank and colleagues posits that during GVS a **triple sensory misintegration**, with conflicting vestibular, visual, and somatosensory signals, may occur in multisensory brain regions such as the temporo-parietal junction (Blanke et al., 2002, 2004; Blanke and Mohr, 2005; Lopez et al., 2008; Blanke, 2012). This model is supported by the fact that vestibular sensations (e.g., floating, lightness, elevation) occur often during OBES of neurological origin (Denvinsky et al., 1989; Blanke et al., 2002, 2004; Lopez et al., 2010; Heydrich et al., 2011). In addition, brain areas that are the most commonly damaged in OBES overlap with the vestibular cortex at the temporo-parietal junction (Blanke et al., 2004; Ionta et al., 2011). Altogether, these data suggest a close relation between the phenomenological experience of a disembodied self and vestibular misintegration (Lopez and Blanke, 2007; Lopez et al., 2008; Blanke, 2012). Accordingly, the loss of self-body unity in vestibular patients may be due to sensory mismatch created by vertigo attacks at the temporo-parietal junction and posterior insula, two regions the metabolism of which is strongly disorganized by vestibular disorders (Bense et al., 2004; Alessandrini et al., 2013). Interfering with the temporo-parietal junction by electrical stimulation has also been showed to induce both OBES and vestibular sensations (Pennfield, 1955; Blanke et al., 2002; Dr Riddler et al., 2007). Vertigo attacks may produce a similar type of interference as those intracranial stimulations, but to a weaker extent, since full-blown OBES were rarely reported in vestibular pathology.

**AGENCY**

**CLINICAL DESCRIPTION**

The loss of self-body connection described above is also evident in the motor control domain. A minimal sense of selfhood has been related to the sense of agency, the experience of being the agent of one’s own actions (Franck et al., 2001; Jeannerod, 2006, 2009).

Interestingly, vestibular patients report more often than healthy participants the experience of “not being in control of their self” (Sang et al., 2006; Jourgué-Renaud, 2008b). For example, a patient with a bilateral Ménière’s disease reported during vertigo attacks “watching something happen and not being a part of it. It’s just a feeling of not being there, participating in what’s going on” (Case 2, p. 532 in Grigsby and Johnston, 1989). Vertigo patients often report that their actions do not seem to match their intentions. Even when tested at a compensated stage of a vestibular loss, patients perceive instability and dizziness during walking and standing despite no evident sign of postural imbalance.

**EXPERIMENTAL EVIDENCE**

To date, the role of vestibular signals in the sense of agency has not been measured experimentally. However, it has been showed that GVS evoked in healthy participants significantly stronger feeling of “not being in control of the self” than control stimulation (Lopez et al., 2012b). In addition, GVS altered the ability to perform and predict hand movements (Bresciani et al., 2002; Guillaud et al., 2011), but agency was not measured directly in these experiments.

**NEUROPHYSIOLOGICAL HYPOTHESIS**

Vestibular patients may report altered sense of agency because vestibular organs do not correctly encode the consequences of their actions. Patients tend to underestimate their body displacements and misinterpret the direction of body movements (Cohen, 2000; Borel et al., 2004), revealing the crucial role of vestibular signals in spatial updating during active and passive whole-body motions (e.g., Frissen et al., 2011; Campos et al., 2012). Errors in sensory coding can introduce a mismatch between vestibular, visual, and somatosensory feedback about self-initiated movements, as well as a discrepancy with the efferent signals from the motor command. Behavioral studies showed that agency is based on congruent sensory feedback from one’s own action, introducing a mismatch (amplitude or direction of motion) between the visual and proprioceptive consequences of an action impairing agency (Fourneret and Jeannerod, 1998; Farrer et al., 2003b, 2003a; Kannape et al., 2010). I speculate that an additional factor may be responsible for distorted sense of agency in vestibular patients: a **temporal mismatch** between an action and the sensory feedback from this action. Interestingly, perception of time is altered in vestibular patients (Israel et al., 2004) and introducing a delay between the executed and seen movement disturb agency (Franck et al., 2001). Neuroimaging studies have revealed that the insula and the temporo-parietal junction are involved in agency (Spinici et al., 1997; Farrer and Frith, 2002; Farrer et al., 2003a, 2003b, 2004, 2008b). This reiterates the contribution of two main vestibular regions to a crucial bodily experience of self-consciousness. In light of these points, vestibular dysfunctions are therefore likely to create a spatiotemporal mismatch between efferent motor commands and feedback from an action, resulting in a disturbed sense of agency.

**DEPERSONALIZATION AND DEREALIZATION**

**CLINICAL DESCRIPTION**

Most of the bodily disturbances described in the previous sections are part of depersonalization, a dissociative disorder characterized...
by the loss of familiarity of the self and surrounding and by a detachment from the self, that may be experienced as unreal (Simmel and Abougel, 2006). Early in the last century, Schilder (1914, 1935) already proposed a vestibular contribution to depersonalization and derealization (DD). More recently, Griggs and Johnston (1989) collected experiences of DD in Menière’s disease patients and described DD as “a sense of unreality” and claimed “I feel like I’m outside of myself. I feel like I’m not in myself” (p. 531). Another patient reported “I am not actually being there or having anything to do with my body” (p. 532). More recently, the use of the Cox and Swinson (2002) questionnaire revealed that vestibular patients have more frequent and more severe DD symptoms than controls (Sang et al., 2006; Jauregui-Renaud et al., 2008b). Symptoms included sensations of “déjà vu,” “body feels strange” and the experience of feeling “spacey” or “spaced out.”

**EXPERIMENTAL EVIDENCE**

Yen Pik Sang et al. (2006) applied CVS in healthy volunteers and showed that it increased the frequency of DD symptoms such as “surroundings seem strange and unreal,” “time seems to pass very slowly” and “body feels strange/different in some way.” This finding was confirmed during bilateral CVS (Lopez et al., 2012b). It is not known, however, how these effects persist.

**NEUROPHYSIOLOGICAL HYPOTHESIS**

Discrepancy between vestibular and other body-related signals may deteriorate the experience of the body and surroundings, leading to DD. In line with this view is the observation that various sensory dysfunctions increase the frequency of DD symptoms. (vestibular, visual, auditory: Jauregui-Renaud et al., 2008b; somatosensory: Lenggenhager et al., 2012). The superior temporal and inferior parietal cortices are the best candidates to explain the vestibular influence on DD. During stimulation of the superior temporal cortex, Penfield (1947, 1955) evoked sensations of “déjà vu” and altered self-body relations (“I feel queer, as though I were not here,” “Penfield, 1947, p. 342). Interestingly, the sites of these stimulations overlapped those where vestibular sensations were evoked. In a PET study, Simeon et al. (2001) showed that DD were related to changes in brain metabolisms in regions that were also activated by CVS and GVS (superior temporal gyrus and temporo-parietal junction). Of particular interest here is the study by Bense et al. (2004) showing that very similar regions have been activated during the evocative induction of DD with CVS. This anatomical overlap strongly suggests that vestibular dysfunction disorganizes brain metabolism, multisensory integration, and eventually structures and connections in the multisensory temporo-parietal cortex, and this may be the underlying mechanism of DD in vestibular patients.

**CONCLUSION**

A better understanding of cortical vestibular processing, as well as of how CVS and GVS influence body and self perceptions, has provided the basis for a neuroscientific account of a so far under-recognized type of vestibular symptom – alterations in bodily self-consciousness. I have summarized evidence showing that abnormal forms of bodily self-consciousness in vestibular disorders may result from sensory conflict or mismatch in multisensory brain regions. This hypothesis should now be put under scientific scrutiny by correlating changes in bodily self-consciousness (e.g., subjective reports using DD questionnaires and objective measures of altered sense of agency and self-location; Kannape et al., 2010) with changes in metabolism and structure in the vestibular cortex (e.g., Bense et al., 2004; voxel-based morphometry: zu Eulenburg et al., 2010). In addition, I have drawn parallels between experimental evidence and clinical observations in vestibular patients to clarify the neural and sensory mechanisms of bodily self-consciousness. Future research in the field should endeavor to make the same comparisons to further our understanding of the underlying multisensory mechanisms of bodily self-consciousness (see Blanke, 2012). In particular, several bodily experiences should now be systematically quantified in vestibular patients to obtain a full description of the consequences of vestibular dysfunctions, including changes in the patient’s self, mood, and personality. I am optimistic that these data will also impact on the multisensory models of self-consciousness currently developed by neuroscientists and philosophers and in which the contribution of the vestibular system is often neglected.

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