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Neuropsychology and neurophysiology of self-consciousness
Multisensory and vestibular mechanisms

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Introduction

How do we become self-conscious or conscious of ourselves as the subject of experience? What are the brain structures involved in generating the experience of the conscious self? And are the underlying neurobiological processes different from those when we are conscious of other objects such as the oak tree standing in the garden? Despite recent neuroscientific efforts to study the neurobiological mechanisms of consciousness (such as the conscious perception of an oak tree; *i.e.* Laureys, 2005), self-consciousness has received much less attention and is deemed by many scientists as not yet approachable by empirical neuroscientific experimentation. Influential scholars such as William James (1890), Maurice Merleau-Ponty (1945), and James Gibson (1950) as well as recent philosophers (Bermudez *et al.*, 1995; Metzinger, 1993, 2003, 2005; Gallagher, 2000, 2005; Legrand, 2007) have proposed that the investigation of the psychological, physiological and neural mechanisms involved in bodily perception and bodily experience may be crucial for the understanding of self-consciousness. The present manuscript discusses several recent findings that seem to provide empirical evidence for the claim that crucial aspects of self-consciousness are linked to the bodily experiences of body ownership and self-location. *Body ownership* is defined by the immediate and continuous experience that our body and its parts belong to us, whereas *self-location* has been defined as the experience that the self is localized at the position of the body at a certain position in space. Psychologists and neuroscientists have started studying body ownership by examining self-attribution and self-location for isolated body parts of one's own body (Botvinick and Cohen, 1998; Ehrsson *et al.*, 2004) as well as one's own entire body (Arzy *et al.*, 2006a; Lenggenhager *et al.*, 2007).

Given the important concept of spatial reference frames in perception and experience we will start by introducing these aspects from cognitive neuroscience, physiology and neurology before discussing body ownership and self-location. Second, we will summarize research from our own laboratory showing that disturbances of bodily information with respect to specific spatial reference frames lead to deficits in body ownership and embodiment in neurological patients such as illusory own body perceptions of the entire body called autoscopic phenomena. Third, we will review experimental conditions of multisensory conflict that are prone to induce body illusions in healthy subjects including disturbed body ownership and embodiment. We argue that the elucidation of the neurobiological mechanisms of ownership and embodiment of one's entire body will be important for the development of neuroscientific models of self-consciousness and subjectivity and that these findings are likely to be relevant for philosophical theories on self and self-consciousness as proposed recently by the philosopher Thomas Metzinger (1993, 2003, 2005).

1. Spatial reference frames in body ownership and self-location

The problem of self-location/embodiment and self-attribution/body ownership is closely associated with how humans encode spatial information. The position of a given stimulus may be encoded with respect to the position of the body of the observer (*body-centered reference frame*), with respect to other extracorporeal objects (*object-centered reference frame*), or with respect to the invariant acceleration of the earth's gravitational field (*gravity-centered reference frame*) [see Fig. 1 and Paillard, 1971, 1991; Berthoz, 1991; Andersen *et al.*, 1993; Klatzky, 1998; Vogeley and Fink, 2003]. Under normal conditions, self-location and ownership are closely linked to the body-centered reference frame, but as we will see below, this association can break down leading to strikingly abnormal states of self-consciousness, spontaneously in neurological patients and experimentally in healthy subjects.

Body-centeredness

The representation of object location in space can be coded with respect to a body-centered reference frame that is with respect to the position of one's body[1]. Since the body is constituted of different segments, sub-reference frames can be distinguished and the spatial location of objects can be coded *e.g.* with respect to the head (head-centered reference frame), the hand or the trunk midline. Of particular importance for body-centered coding and self-consciousness are the proprioceptive senses – namely the kinesthetic sense (originating from the muscular proprioceptive receptors and other receptors from the musculoskeletal system) and the vestibular sense – allowing us to perceive bodily stimuli and to probably also experience our body as our property and as being localized in space. Afferent bodily sensory signals as well as efferent motor signals are involved in building up the dynamic, mostly unconscious, own body representation. Josef Gerstmann (1942) has described this representation as a

> *"model which one forms in one's mind of one's body or one's material self, in the course of life, and which one carries with one unwittingly, that is, outside of central consciousness. It is a kind of inner diagram representing one's body as a whole, as well as its single parts according to their location, shape, size, structural and functional differentiation and spatial interrelation, it also represents the cardinal directions of the body – right and left, anterior and posterior, up and down".*

Object-centeredness

The body-centered reference frame can be distinguished from the object-centered reference frame. In the latter, the spatial location of objects is coded with respect to other objects located in the extracorporeal space. Therefore, this coding is assumed to be independent of body-centered reference frames and the observer's body position[2]. Visual or auditory cues play a fundamental role in building up the object-centered reference frame by representing world-centred cues/landmarks. As the self is localized not only with respect to one's own bodily borders but also with respect to extrapersonal space and objects therein self-location may also be disturbed when the allocentric reference frame is disturbed.

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[1] The body-centered reference frame is often referred to as the *egocentric reference frame*. As we will here present examples showing that the self can be experienced as spatially distinct from one's body and as the term "ego" may be misleading or referring to diverse concepts in psychology, philosophy, and neurophysiology, we prefer to distinguish the more descriptive term body-centered reference frame from self-centered reference frame.

[2] This independence is only partly true as Gibson (1950) and Neisser (1988) have convincingly argued that body-centered signals also influence the object-centered reference frame.

Gravity-centeredness

We would like to distinguish a third reference frame, the gravity-centered or geocentric reference frame, and emphasize its importance (see Paillard, 1991). The gravity-centered reference frame is mainly linked to gravitational acceleration whose direction is constant, constituting an invariant spatial reference. Indeed, we have a constant knowledge of the vertical orientation and of which way is up (Snyder, 1999), and there are many empirical data showing that such knowledge improves spatial judgments. Sensory signals encoding the gravity-centered reference frame primarily stem from the otolithic vestibular receptors that are sensitive to linear acceleration coding the position of the head with respect to the gravitational acceleration (Mittelstaedt, 1991, 1992; Bronstein, 1999; Lopez *et al.*, 2007b). This is complemented by somatosensory signals relating pressure cues from any part of the body that might be in contact with any gravity-resisting surface (Mittelstaedt, 1992). Self-location and ownership may also be impaired in cases of disturbed vestibular or somatosensory information leading to an altered gravity-centered reference frame as shown by data from orbital and parabolic flights (Lackner, 1992; Kornilova, 1997).

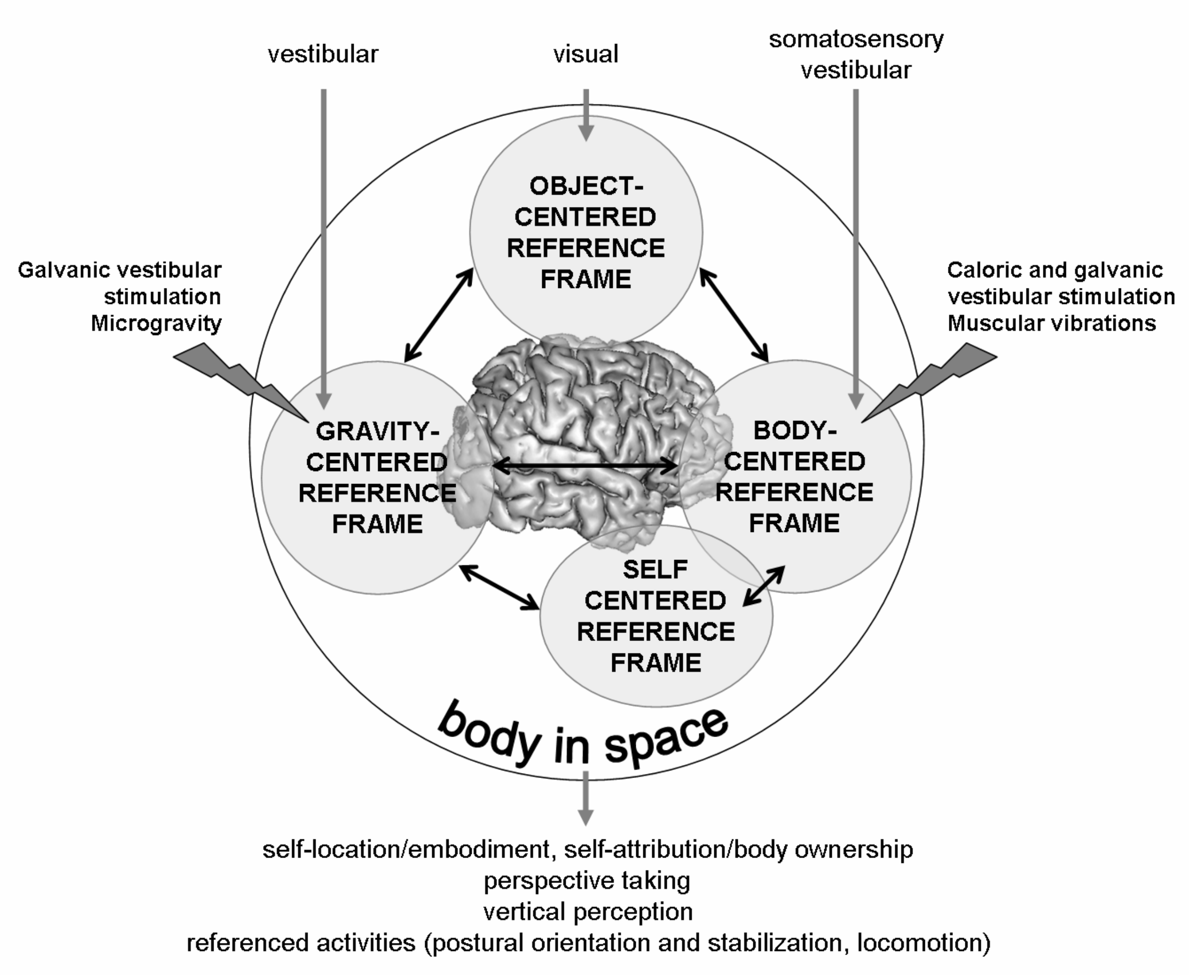


Fig. 1: Integration of the spatial reference frames. Representation of objects and body location in space can be defined with respect to an object-centered reference, a gravity-centered reference, a body-centered and a self-centered reference. Experimental manipulations of the proprioceptive cues (*e.g.* stimulation of the muscular proprioceptive receptors through mechanical tendon vibrations; caloric and galvanic stimulations of the peripheral vestibular receptors) disturb body-centered and gravity-centered spatial coding and impair central representation of "body in space". Consequently, physical body orientation in space is altered. Neurological disturbances such as epileptic seizure or focal brain damage impairing central integration of the different spatial frameworks disturb feeling of embodiment and body ownership.

Bodily signals that are relevant for self-location and ownership are likely to be encoded with respect to all three reference frames, but as we will argue below, multisensory information processing within body-centered and gravity-centered reference frames seems to be of key importance in the present context. In the next two sections, we further support this proposition by reviewing evidence of abnormal embodiment and body ownership in the case of multisensory disintegration in neurological patients with autoscopic phenomena and during experimentally induced multisensory conflicts in healthy subjects. Based on these observations we also suggest to define a fourth spatial reference frame. The importance of this *self-centered reference frame* is suggested by "egocentric" descriptions that have been reported as originating from a location and visuo-spatial perspective that does not coincide with one's physical body location (Brugger, 2002; Blanke *et al.*, 2004). Hence, we propose that the self-centered reference should be introduced to unambiguously describe these mental states (see below).

2. Multisensory disintegration in body-centered and gravity-centered reference frames leads to abnormal self-location and ownership

Autoscopic phenomena are illusory reduplications of one's own body that are sometimes associated with striking abnormalities in embodiment and body ownership. Several types of autoscopic phenomena have been described (see Hécaen and Ajuriaguerra, 1952; Devinsky *et al.*, 1989; Brugger, 2002; Blanke *et al.*, 2004, 2007; Bünning and Blanke, 2005). The main autoscopic phenomena are called "autoscopic hallucination", "heautoscopy", and "out-of-body experience". They occur after damage to temporo-parietal cortex or temporo-occipital cortex and are due to distinct patterns of multisensory disintegration of information from bodily and surrounding space leading to characteristic phenomenological differences (Brugger *et al.*, 1997; Blanke *et al.*, 2002, 2004, 2007) including self-attribution and the location of the self or subject (see Brugger, 2002).

2.1. Phenomenology

The phenomenological experiences associated with the different autoscopic phenomena are summarized in Fig. 2. In autoscopic hallucinations, heautoscopy and out-of-body experience patients see an illusory own body in extrapersonal space but they differ systematically with respect to self-location and self-attribution of the illusory body.

First, patients with autoscopic hallucinations suffer from pure visual own body illusions of which an example is described by Bhaskaran *et al.* (1990):

> *"The image [of his own face] first appeared at a distance of about 30 cm in front of him, more towards the left, and persisted for three to four minutes. He could identify the face and upper part of the body including the color of the shirt and the expression of the face".*

These patients do not self-attribute the illusory body (*i.e.* they do not misattribute this body as their own) and do not localize the self at the position of the illusory body (*i.e.* there is no abnormal embodiment), so that self-location is habitual and at the physical body position. With respect to the abovementioned spatial reference frames, the "autoscopic self" is accordingly encoded normally with respect to the body-, object- and gravity-centered reference frames.

Second, contrasting with autoscopic hallucinations, heautoscopy patients may experience the self to be localized at their habitual position or at the position of the illusory body (abnormal embodiment). These patients always self-attribute the illusory body, at least partly and temporarily (see Brugger *et al.*, 1994, 1997, 2006; Blanke *et al.*, 2004 [patient 2 and 4]). Self-location and the visuo-spatial perspective are either reported as if seeing the world from the physical body (normal body-centered reference frame) or from the position of the illusory body (abnormal or altered body-centered reference frame)[3]. The "heautoscopic self" is encoded normally (in most instances) with respect to the gravity-centered reference frame. Patients generally do not report disembodiment (even if localizing themselves at the position of the illusory body), but rather a sensation of doubling of the self or co-existence of two selves (Blanke and Mohr, 2005). We propose that in these cases one may also speak of an abnormality of the self-centered reference frame. Heautoscopy is often associated with somatosensory and vestibular sensations (Brugger *et al.*, 1997). The abnormal body- and self-centered reference frame in heautoscopy is highlighted by this example from Blanke *et al.* (2004; patient 5):

> *The patient "was sitting at a table in a room of the hospital while a nurse was re-adjusting a venous catheter on his right arm. [He experienced] slow backward rotation into a horizontal position. There, he suddenly saw himself standing behind the nurse. He stated that: "He looked like myself, but ten years younger and was dressed differently than I was at that moment". [He] saw only the upper part of himself, including the trunk, head, shoulders, arms and hands. [The patient] had the impression of seeing the scene either from his rotated position ("look[ing] at the ceiling") or from the initial sitting position in the chair prior to the seizure. The different perspectives changed a few times during the episode".*

Finally, localization and attribution of the self with an illusory body at an extracorporeal position is complete in out-of-body experiences. In this third form of autoscopic phenomena patients always localise the self outside their body and experience to see their body from this disembodied location. The encoding of self-location with respect to body-centered and gravity-centered reference frames is thus abnormal as the self is disembodied, not localized in one's body borders (abnormal body-centered reference frame) as well as localized at an elevated extracorporeal location (abnormal gravity-centered reference frame). The self-centered and object-centered reference frames are preserved. As in the case of heautoscopy, out-of-body experiences are associated with somatosensory and vestibular illusions such as "elevation, flying, lightness vertigo, sinking" (Blanke *et al.*, 2004). The following example from Blanke *et al.* (2004; patient 2) illustrates how patients report disturbed embodiment and self-attribution during an out-of-body experience:

> *"The patient was lying in bed and awakened from sleep, and the first thing she remembered was "the feeling of being at the ceiling of the room". She "had the impression that I was dreaming that I would float above [under the ceiling] of the room". The patient also saw herself in bed (in front view) and gave the description that "the bed was seen from above"… The scene was in colour, and was visually clear and realistic".*

To reiterate, abnormal body ownership and embodiment in these three autoscopic phenomena range from absent (autoscopic hallucination), to partial (heautoscopy), to fully abnormal (out-of-body experience) ownership and embodiment with another body in another location in the extrapersonal space (Blanke *et al.*, 2007). Moreover, based on a phenomenological analysis and the analysis of the other associated symptoms we propose that the different subtypes arise from systematic differences in abnormalities in the way self-location and ownership are encoded with respect to the body-centered and gravity-centered reference frames (Fig. 2). The object-centered reference frame remains unaffected whereas the self-centered reference frame is only disturbed in heautoscopy (Blanke and Mohr, 2005).

[3] Peter Brugger (2002) has referred to this non-body-centered perspective as an alter-ego-centered perspective.

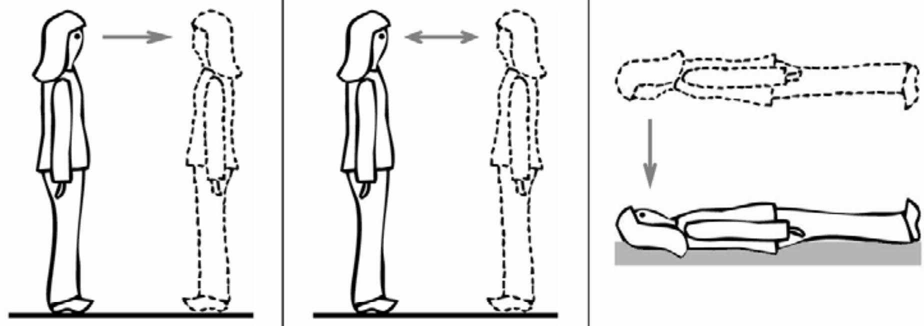
	autoscopic hallucination	heautoscopy	out-of-body experience
Phenomenology			
Multisensory disintegration	visual	somatosensory and vestibular (canals)	somatosensory and vestibular (otolith)
Body-centered	+	++	++
Gravity-centered	-	-	+
Disturbed embodiment	-	+	+++
Disturbed body ownership	-	+++	+++

Fig. 2. Phenomenology and physiopathology of autoscopic phenomena. For each own body illusion, the physical position of the patient's body is schematically represented by solid lines and that of the illusory body by dashed lines. The direction of the visuo-spatial perspective is indicated by an arrow pointing away from the location the patient has the impression she/he is located at (self-location). The patient has the impression to see the environment from the physical body in the case of autoscopic hallucination, from the illusory body in the case of out-of-body experience, and alternatively or simultaneously from the physical and the illusory body in the case of heautoscopy. Autoscopic phenomena are characterized by distinct abnormalities in body-centered and gravity-centered reference frames (see text; drawings by Lovisa Halje after Blanke *et al.*, 2004).

2.2. Multisensory disintegration leads to a breakdown of body- and gravity-centered reference frames and autoscopic phenomena

The analyses by Blanke *et al.* (2004) and Blanke and Mohr (2005) suggest that autoscopic phenomena result from a failure to integrate multisensory bodily information. These authors proposed that autoscopic phenomena result from a disintegration in bodily space (due to conflicting somatosensory and visual information) and a second disintegration between corporal and extracorporeal space (due to conflicting visual and vestibular information). Here we extend this model by proposing that spatial coding in body- and gravity-centered reference frames is disturbed in patients with autoscopic phenomena and that the lack of coherent central integration between these different frameworks leads to abnormal embodiment and body ownership (see Fig. 2, lower part).

While the body-centered reference frame is disturbed in all three forms of autoscopic phenomena, differences are mainly due to differences in strength and type of the vestibular dysfunction and the resulting disturbance of the gravity-centered reference frame and its integration with the body-centered reference frame. Out-of-body experiences are associated with a strong vestibular disturbance, probably of otolithic origin (see Blanke *et al.*, 2004), leading to abnormal gravity-centered coding and disintegration between body-centered and object-centered reference frames and strongly abnormal self-location and body ownership. Heautoscopy is associated with a moderate and more variable vestibular disturbance, presumably originating from the semicircular canals, leading to abnormal body-centered coding but relatively normal gravity-centered coding. The strong disturbance of body-centered processing in heautoscopy is assumed to lead to alternating or simultaneous self-location at the physical and illusory body and strongly altered body ownership. Finally, autoscopic hallucinations are not associated with abnormal gravity-centered coding and minimally abnormal body-centered coding. The high frequency of visual hallucinations and hemianopia in patients with autoscopic hallucinations further suggests that deficient visual processing of bodily information is the main causing factor for abnormal body-centered coding in autoscopic hallucinations. In this last form of autoscopic phenomena, the habitual body-centered self-location and visuo-spatial perspective is therefore preserved and embodiment as well as body ownership remains unaffected.

To summarize, these neurological data suggest that vestibular otolithic processing seems to be of particular importance in coding self-location/embodiment, whereas self-attribution/body ownership seems to be related to somatosensory as well as vestibular otolithic and/or semicircular canal information. As both mechanisms are less impaired in autoscopic hallucinations, abnormal processing of visual bodily information seems less important for body ownership and embodiment. Moreover, these different types of autoscopic phenomena have been linked to distinct brain regions. Early studies implicated posterior brain regions including the temporal, parietal, or occipital lobe (Devinsky *et al.*, 1989; Brugger *et al.*, 1997). More recently, Blanke and colleagues (Blanke *et al.*, 2002, 2004; Bünning and Blanke, 2005; Blanke and Arzy, 2005) showed that out-of-body experiences and heautoscopy are primarily associated with damage or electrical stimulation at the temporo-parietal junction (TPJ; see Fig. 3) whereas autoscopic hallucinations are associated with damage in temporo-occipital cortex (Blanke and Castillo, 2007). This has been confirmed by Maillard *et al.* (2004) and Brandt *et al.* (2005) and in a recent study of 37 neurological cases with out-of-body experiences, heautoscopy, or autoscopic hallucinations due to focal brain damage that have been reported in the medical literature since 1923 (Blanke and Mohr, 2005).

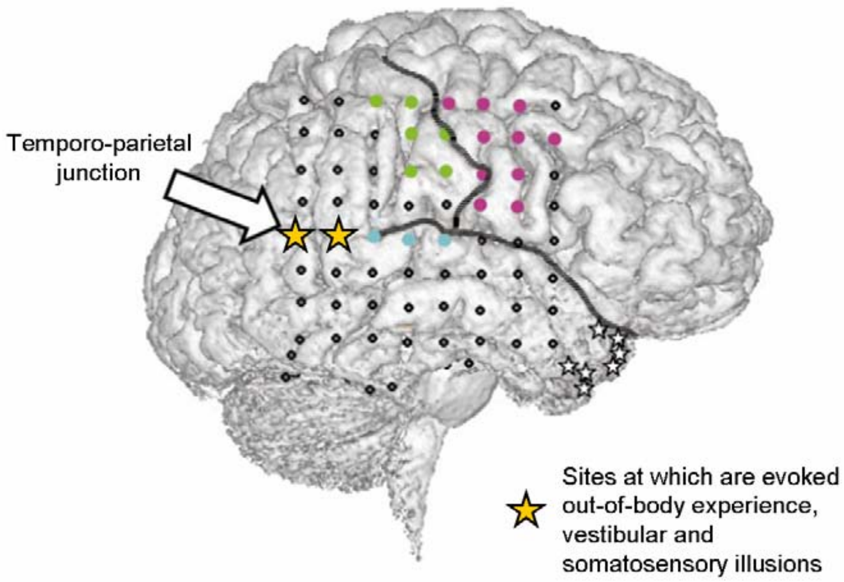


Fig. 3. Neural basis of out-of-body experiences. The contribution of vestibular processing to embodiment is suggested by the observation that cortical electrical stimulations at the same site in temporo-parietal junction evoke vestibular illusion and out-of-body experience. Modified after Blanke *et al.*, 2002.

3. Manipulating the experience of one's own body through multisensory conflicts

The abovementioned examples in neurological patients suggest important links between disturbed vestibular and somatosensory cortical processing – in other words between disintegration of body-centered and gravity-centered reference frames – and abnormal body ownership and embodiment. We therefore believe that altering information processing with respect to both spatial reference frames through multisensory conflict might be an efficient way to study and disturb the experience of one's own body, eventually inducing situations of disembodiment and abnormal body ownership.

Apart from the abovementioned neurological data, there is increasing evidence that vestibular signals are important for experience, perception, and cognition of one's own body. Because vestibular signals encode three-dimensional head movements in space, the vestibular system is a fundamental basis for the body-centered reference frame. In addition, since the vestibular system is sensitive to linear accelerations, it encodes gravitational acceleration generating an invariant frame of reference (the gravity-centered reference frame) [see Paillard, 1971, 1991]. There are several reasons to believe that stimulation of the vestibular system alters own body experience, because it also interferes with own body perception and cognition. Thus, patients with vestibular loss have impaired spatial cognition (see Smith *et al.*, 2005 for a review) and neurophysiological observations have shown that peripheral vestibular stimulations modify awareness of corporeal deficits in brain damaged patients (Vallar *et al.*, 1993; Karnath and Dieterich, 2006). Moreover, neuroimaging studies in healthy subjects revealed that vestibular afferents, although projecting to many brain regions, have dense connections with the TPJ, a region that has been shown to be involved in own-body cognition, multisensory integration as well as heautoscopy and out-of-body experiences. In the next sections we will review the effects of natural vestibular stimulation (such as modifying the subject's own body position with respect to the gravity) and artificial stimulations of the peripheral vestibular apparatus (caloric and galvanic vestibular stimulations) on own body perception and cognition as well as body ownership and embodiment.

3.1. Position of the observer's body

The fact that out-of-body experiences are more frequent in the supine than the upright position suggests that there is a gravitational influence on embodiment and body ownership in addition to a contribution of somatosensory cues. On the basis of an analysis in 176 healthy subjects, Green (1968) reported that ~73% of out-of-body experience occurred when subjects were lying down (see Fig. 4A):

> *"I had gone to bed at about 11.30 p.m. and was unable to sleep. I was lying on my back when I realized that I was hovering over the bed, looking down on myself".*
>
> *"While lying on my back in bed with my eyes closed, preparing to go to sleep I find myself moving upwards in a horizontal position … Sometimes I go up so high I must be ¼ to ½ mile from my bed". (Green, 1968; p. 51)*

Similarly, more than 80% of neurological patients with out-of-body experiences were in supine position (see Fig. 4B; Blanke and Mohr, 2005). A recent neuroimaging study in healthy subjects also showed that neural mechanisms of embodiment in TPJ and occipito-temporal cortex are affected by the subject's body position with respect to gravity (Arzy *et al.*, 2006b), especially when the imagined self-location was congruent with the subject's physical body position. In addition, the authors described increased activity in the lateral occipito-temporal cortex that was stronger in the sitting than supine position (this area probably corresponds to the extrastriate body area [Downing *et al.*, 2001] and the lesion location in patients with autoscopic phenomena [Blanke and Mohr, 2005]). These data suggest interactions between embodiment, vestibular processing, and autoscopic phenomena at the TPJ and in the occipito-temporal cortex.

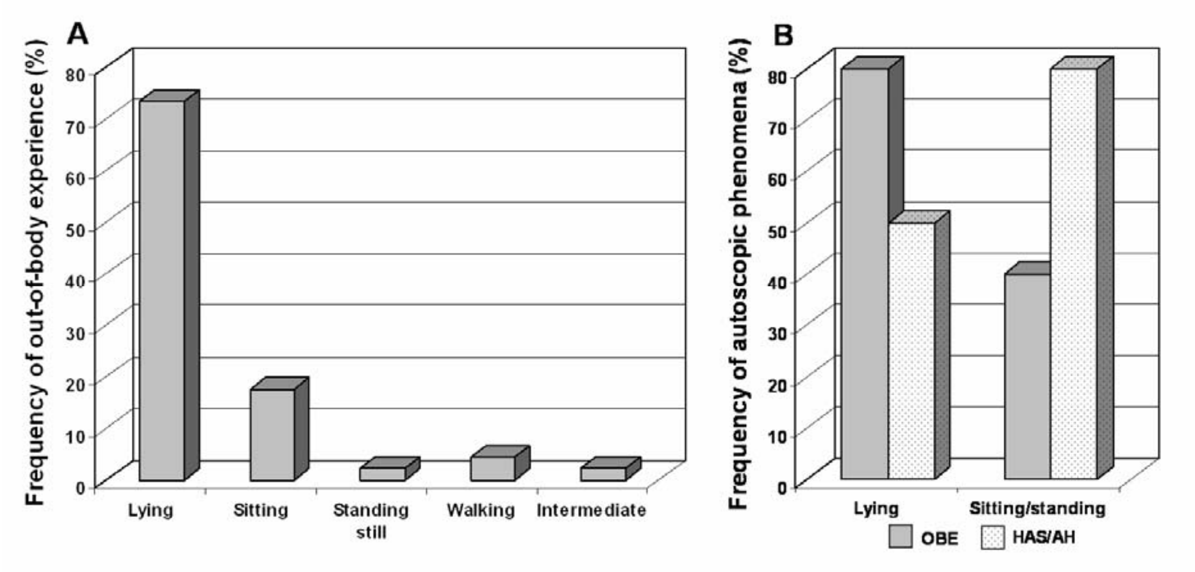


Fig. 4. Physical body position and autoscopic phenomena. (A) Frequency of out-of-body experiences associated with different physical body positions in healthy subjects. The position "intermediate" refers to non-relaxed sitting such as "riding a motor-cycle at speed". Drawn after the data from Green, 1968. **(B)** Frequency of out-of-body experience (OBE) and heautoscopy (HAS) / autoscopic hallucination (AH) associated with different physical body position in neurological patients. Drawn after the data from Blanke and Mohr, 2005.

3.2. Effects of artificial vestibular stimulations

Artificial stimulations of the peripheral vestibular organ have been carried out using caloric vestibular stimulation and galvanic vestibular stimulation either for clinical evaluation in patients or for scientific purposes in healthy subjects[4]. These two kinds of vestibular stimulation techniques differ in many respects such as the physiological mechanisms by which they stimulate the peripheral vestibular apparatus and the associated illusions (see Fig. 5). Nevertheless, caloric and galvanic vestibular stimulation are two methods that stimulate the vestibulo-cortical pathways and activate the vestibular cortex and key areas of self-consciousness[5].

[4] Artificial stimulations of the vestibular apparatus have also been carried out using vibrations applied to the level of the mastoid bones, and using auditory stimulations (*e.g.* using auditory clicks at 102 dB) known to stimulate the saccular otolithic receptors.

[5] Numerous vestibular cortical projections have been evidenced in the human cortex. Neuroimaging studies during caloric and galvanic stimulation of the peripheral vestibular apparatus showed that the vestibular cortex is centered on the temporo-parietal cortex, superior temporal gyrus and the posterior insula (parieto-insular vestibular cortex). Vestibular projections have also been evidenced in the primary somatosensory cortex (precentral gyrus: areas 2v and 3av), premotor cortex (area 6v), anterior insula, frontal eye fields, cingulate gyrus, precuneus and hippocampus. For a detailed description of the vestibular-receiving areas, please refer to the reviews from Berthoz (1996), Fukushima (1997), Guldin and Grüsser (1998), Brandt and Dieterich (1999) and Lopez *et al.* (2005, 2007a).

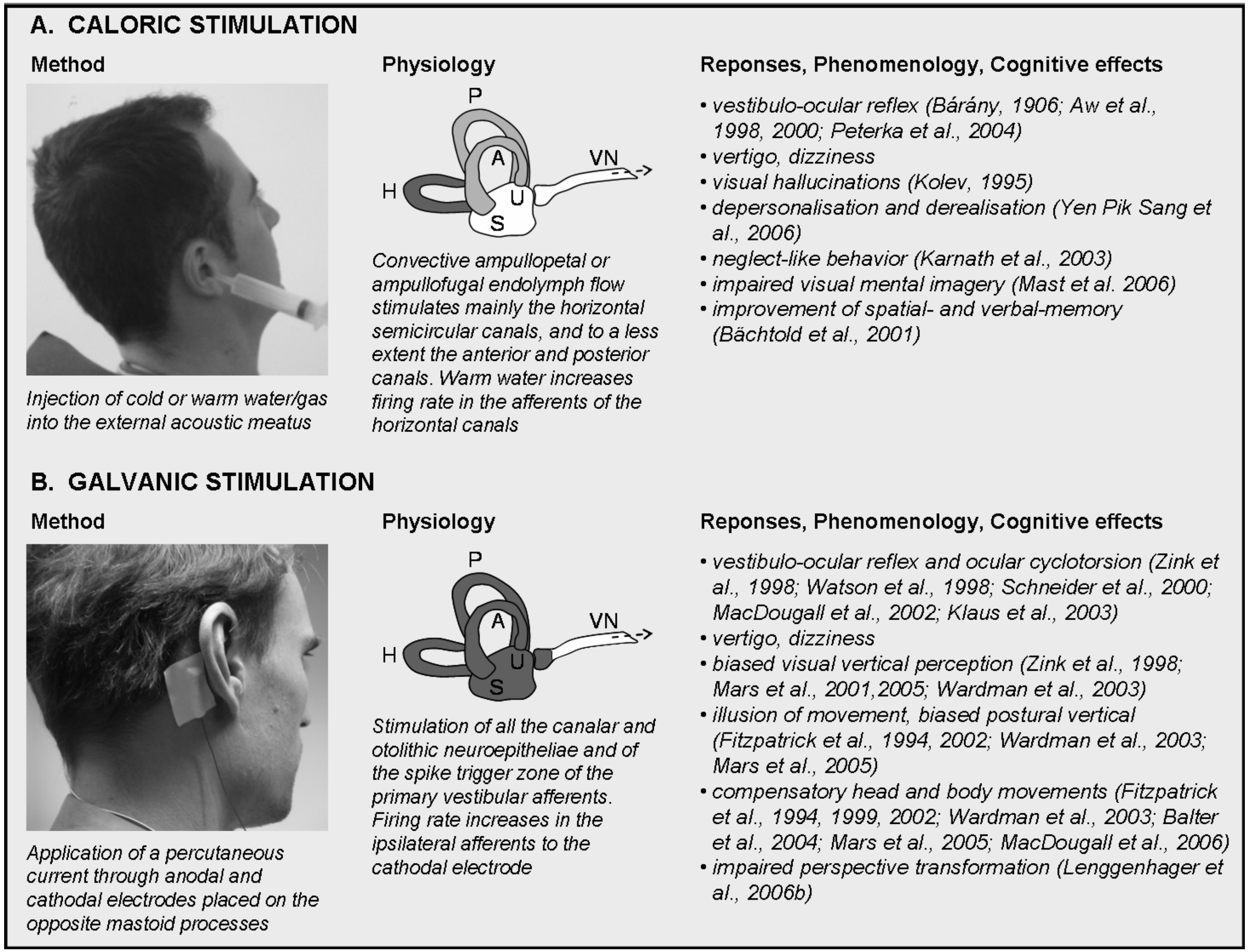


Fig. 5. Methods for artificial stimulations of the peripheral vestibular apparatus. Caloric vestibular stimulation **(A)** consists of irrigating the external acoustic meatus with water or gas at lower or higher temperature than the body temperature while galvanic vestibular stimulations **(B)** consist of applying percutaneous current on the mastoid processes. For each method, the sites of the activation are represented by dark grey (structure strongly stimulated) and light grey (structure weakly stimulated) areas on a schematic representation of the vestibular end organ. A: anterior semi-circular canal, H: horizontal semi-circular canal, P: posterior semi-circular canal, S: saccule, U: utricle, VN: vestibular nerve.

Caloric vestibular stimulations

Caloric vestibular stimulation was initially developed by Robert Bárány, who received the Nobel Prize in 1914 for his work on the vestibular apparatus. Caloric stimulations consist of irrigating the external acoustic meatus with warm or cold water or gas creating convective ampullopetal or ampullofugal endolymph flow (Fig. 5A). This stimulation creates neural signals similar to those that are triggered when the head is physically rotating. It is assumed that the horizontal semicircular canals are mostly stimulated during caloric irrigation, but a weak stimulation of the vertical semicircular canals also seems to occur. Typically, caloric vestibular stimulation evokes a caloric nystagmus (rapid reflexive eye movements), a strong conscious feeling of body rotation (often leading to vertigo and a sensation of dizziness), as well as interference with own-body perception and cognition (Karnath *et al.*, 2003; Mast *et al.*, 2006).

Probable influence of caloric vestibular stimulation on self-consciousness and embodiment is supported by the observation that caloric stimulations may induce in healthy subjects transient depersonalization and derealisation symptoms, like detachment from the body and experience of unreality (Yen Pik Sang *et al.*, 2006). These have been described as similar to those reported by patients with out-of-body experiences and disembodiment (see Simeon *et al.*, 1997, 2000). These findings suggest that caloric vestibular stimulation interferes with self-processing and embodiment, inducing in healthy subjects depersonalization/derealisation symptoms that have also been observed in vestibular-defective patients (Grigsby and Johnston, 1989; Yen Pik Sang *et al.*, 2006) and neurological patients with autoscopic phenomena (Blanke and Mohr, 2005)[6]. However, caloric vestibular stimulation has not been reported to evoke full-blown out-of-body experiences or states of full disembodiment, probably because an additional disintegration of somatosensory signals encoded within body-centered reference frames is necessary.

The effects of caloric vestibular stimulation have also been shown on neural mechanisms of self-attribution of body parts. Bisiach and colleagues (1991) reported the case of a patient suffering from left-sided spatial hemineglect and somatoparaphrenia (due to right parietal damage) who misattributed her left hand as her mother's left hand. Interestingly, this deficit in hand self-attribution briefly disappeared after her left contralesional ear was irrigated with cold water (caloric vestibular stimulation). Although interference of whole body ownership has not been studied using caloric vestibular stimulations in healthy subjects, this clinical case study suggests an interfering effect of vestibular stimulations with the mechanisms of ownership, an effect further supported by the modification of the illusory perceptions of body parts in amputated and paraplegic patients (phantom limb perception; André *et al.*, 2001; Le Chapelain *et al.*, 2001). These authors were able to evoke phantom limb illusions below the injury level by caloric vestibular stimulation in patients who did not previously report such illusions. In the patients who have previously experienced phantom illusions, they were able to evoke deformed phantom limbs. Collectively, these results speak in favor of an influence of vestibular processing on the experience of ownership for body parts. This is further corroborated by several observations in neglect patients showing that caloric stimulation may affect somatosensory processing and awareness for bodily symptoms (Cappa *et al.*, 1987; Vallar *et al.*, 1993; Rode *et al.*, 1992; Bottini *et al.*, 1995, 2005; see

[6] Depersonalization has been reported in vestibular-defective patients with or without vertigo. Grigsby and Johnston (1989), reported depersonalization in two patients suffering from Menière's disease. A first patient, a 32 year old woman, reported having *"like a sense of unreality. I feel like I'm outside of myself. I feel like I'm not in myself […] Sometimes, I feel like I'm sitting up on my head or something"*. A second patient, a 34 year old woman with a bilateral Menière's disease, reported depersonalization as *"I'm not actually being there or having anything to do with my body"* in conjunction with an alteration of the perception of time.

Vallar *et al.*, 1997 for an overview). Finally, interference of caloric vestibular stimulations with spatial neglect, and disturbed own body experience is supported by the finding that the brain regions most often damaged in neglect patients like the superior temporal cortex, inferior parietal lobule and insula (Karnath *et al.*, 2004; see Vallar, 1998 for a review) overlap with the vestibular cortex.

Galvanic vestibular stimulations

The second kind of artificial vestibular stimulation we would like to describe is galvanic vestibular stimulation (GVS) that consists of the application of a small percutaneous current at ~1 mA through electrodes placed on the mastoid processes (Fig. 5B). As a general rule GVS is binaural with the anode fixed on one mastoid process and the cathode fixed on the contralateral one, but other configurations have also been used (for an overview see Fitzpatrick and Day, 2004). During GVS the mechanoelectrical transduction of the hair cells is bypassed and the applied current directly modulates the level of hyperpolarization of the vestibular neuroepithelia and stimulates the spike trigger zone on the primary vestibular afferents. The cathodal electrode is the stimulating electrode, resulting in an increased firing rate in the ipsilateral primary vestibular afferents and a decreased firing rate in the contralateral vestibular afferents (on the anodal side). Many studies showed that GVS produces a signal that evokes nystagmic eye movements and ocular cyclotorsion (Zink *et al.*, 1998; Schneider *et al.*, 2000; MacDougall *et al.*, 2002), and deviation of the perceived visual vertical towards the anode (Zink *et al.*, 1998; Mars *et al.*, 2001, 2005). Since all vestibular afferents are simultaneously stimulated by the GVS, there is no physiological equivalent to this unnatural vestibular stimulation. According to Fitpatrick and Day (2004), GVS would be centrally interpreted as a head rotation towards the cathode, mostly in the roll plane, weakly in the yaw plane, and as a small horizontal acceleration towards the cathode.

Does GVS disturb mechanisms of embodiment and body ownership? Several studies have so far investigated the effects of GVS on self-location (Fitzpatrick *et al.*, 1994, 2002; Wardman *et al.*, 2003; Balter *et al.*, 2004; Mars *et al.*, 2005). As phenomenologically experienced by the subjects, GVS elicites an illusion of self-tilt towards the cathode with respect to the gravitational vertical (Mars *et al.*, 2005). This postural illusion was observed while the subject's head was fixed so that there is a clear dissociation between the perceived body position (or self-location) and the physical body position that remained vertically oriented[7]. We suggest that this tilt in self-location with respect to the physical body position is related to the experience of disembodiment or abnormal self-location observed in patients with autoscopic phenomena in whom vestibular illusions are frequent (Blanke *et al.*, 2002, 2004; for more details see Lenggenhager *et al.*, 2006a). Furthermore, we have recently shown that GVS interferes with own body cognition (mental own-body imagery), especially when subjects use a body-centered mental transformation strategy *i.e.* imagining themselves as rotating their body in space towards a position in extracorporeal space (Lenggenhager *et al.*, 2006b). To the best of our knowledge, there is no study dealing with the effects of GVS on self-attribution.

Neuroimaging studies showed that regions centered on the TPJ respond to GVS associated with illusory own body tilt and/or motion (Bucher *et al.*, 1998; Lobel *et al.*, 1998; Bense *et al.*, 2001; Fink *et al.*, 2003; Stephan *et al.*, 2005; Eickhoff *et al.*, 2006). Interestingly in the scope of the present reflections, regions activated by GVS overlap with the key structures for embodiment and mental own-body imagery such as the parietal and temporo-occipital cortices (Zacks *et al.*, 1999; Creem *et al.*, 2001; Blanke *et al.*, 2005; Kosslyn *et al.*,

[7] This self-tilt can be described as a misalignment between self-centered and body-centered reference frames by vestibular stimulation.

1998; Vingerhoets *et al.*, 2001). Regions activated by GVS might also be linked to the cortical mechanism of self-attribution since the TPJ has been involved in the self-attribution of seen movements and agency (Farrer *et al.*, 2003, 2004) as well as first-person-perspective taking (Vogeley and Fink, 2003). In an fMRI study, Tsakiris and colleagues (2006) recently showed that coding ownership for one's hands is associated with activity in the posterior insula, the region considered as the core of the vestibular cortex (Brandt and Dieterich, 1999). Based on these data, we speculate that GVS might allow to experimentally manipulate and investigate the neural mechanism of self and self-consciousness, especially self-location and ownership.

Conclusion

In conclusion, a coherent central integration of sensory and motor information with respect to body-centered and gravity-centered references is necessary for accurate processing of one's own body, self, and self-consciousness. Embodiment and body ownership are disturbed in patients with out-of-body experiences and heautoscopy suggesting deficient multisensory integration with respect to body- and gravity-centered reference frames in these patients. We have also emphasized the possibility of disturbing the mechanisms of embodiment and body ownership through experimental manipulation of these reference frames by using artificial vestibular stimulations. Whereas the contribution of signals in body-centered references for neurobiological mechanisms underlying embodiment and body ownership is well documented, the contribution of gravity-centered signals to these mechanisms has not received similar attention, but seems especially relevant for self-location. We believe that vestibular signals, by providing concurrent information about gravity and one's body position and movement in space, that is by providing signals in gravity- and body-centered reference frames, play a key role in unifying bodily and extracorporeal signals necessary for coding self-location and ownership as embodied (in the body) and embedded (in the spatial world). This is in line with Jacques Paillard's proposition (1991) claiming that body-centered and object-centered reference frames "are basically derived from the [gravity-centered frame] (within which all terrestrial living systems have been moulded) and that they can not be studied independently". Based on this proposition and on our own observations, we suggest that the gravity-centered reference frame and vestibular cues in a more general manner are fundamental for the experience of one's own body and eventually self-consciousness. Accordingly, in out-of-body experiences, disturbed self-location and ownership is tightly associated with vestibular sensations and damage to the core region of vestibular cortex. We believe that performing caloric and galvanic vestibular stimulations in healthy subjects should allow to disturb the integration of multisensory bodily information and investigate the neural basis of ownership and self-location. We are optimistic that such an approach will contribute to the development of neuroscientific data-driven theories of self, self-consciousness, and subjectivity. Importantly, these findings extend and corroborate philosophical and psychological theories introduced by Merleau-Ponty and Gibson and might foster further fruitful encounters between neuroscience and philosophy of mind (Bermudez *et al.*, 1995; Metzinger, 1993; Gallagher, 2005).

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