Bodily ownership and self-location: components of bodily self-consciousness

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Abstract

Recent research on bodily self-consciousness has assumed that it consists of three distinct components: the experience of owning a body (body ownership); the experience of being a body with a given location within the environment (self-location); and the experience of taking a first-person, body-centered, perspective on that environment (perspective). Here we review recent neuroimaging studies suggesting that at least two of these components—body ownership and self-location—are implemented in rather distinct neural substrates, located, respectively, in the premotor cortex and in the temporo-parietal junction. We examine these results and consider them in relation to clinical evidence from patients with altered body perception and work on a variety of multisensory, body-related illusions, such as the rubber hand illusion, the full body illusion, the body swap illusion and the enfacement illusion. We conclude by providing a preliminary synthesis of the data on bodily self-consciousness and its neural correlates.

1. Introduction

Self-consciousness is not a simple phenomenon; a full explanation of self-consciousness must explain many things. But often progress can be made in understanding a complex phenomenon by understanding something rather simple at its heart, and progressing from there. Recent work on the psychology and neuroscience of self-consciousness can be seen as exemplifying this research strategy. Instead of focusing on 'higher' forms of self-consciousness involved in, for example, mastery of the 'I' concept (Bermúdez, 1998; Peacocke, 2008), mirror self-recognition (Gallup, 1975; Morin, 2006) and understanding of one's own identity over time (Gallagher, 2000; Morin, 2006), a number of researchers have instead focused on more basic, *bodily* forms of self-consciousness. In particular, they have explored the ways in which multisensory bodily illusions can modulate the experience of oneself as a bodily subject.

This research is characterised by a number of basic assumptions. The first is that the behavioural effects of manipulating proprioceptive, interoceptive and exteroceptive signals can serve as implicit measures of phenomena described in explicit reports of subjective experience. The second is that global aspects of bodily self-consciousness (pertaining to the experience of the body as a whole) can be studied by manipulating these sensory signals, despite the fact that their immediate processing is physiologically and computationally constrained to individual body parts (Ehrsson, 2007; Guterstam & Ehrsson, 2012; Lenggenhager, Tadi, Metzinger, & Blanke, 2007; see also Altschuler & Ramachandran, 2007; Mizumoto & Ishikawa, 2005; Petkova & Ehrsson, 2008; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2009).

Our aim in the following discussion is to provide some degree of validation for a third assumption driving this research, namely that bodily self-consciousness comprises at least three distinct components: the experience of owning a body (*body ownership*); the experience of being a body with a given location within our environment (*self-location*); and the experience of taking a first-person, body-centered, perspective on that environment (*perspective*) (Blanke & Metzinger, 2009; de Vignemont, 2011; Vogeley & Fink, 2003). Bodily self-consciousness might in principle include other components, for example sense of agency for bodily actions (see, Jeannerod, 2006), but these exceed the scope of the present analysis. In its strongest form, this assumption states that each of these three components is distinct from one another. Although we will not fully evaluate the stronger claim here, we think that there is good reason for thinking that

perspective is not wholly distinct from *self-location*, and thus that the strongest claim is false. Our discussion will focus on a weaker form of the assumption: that there are at least two components of bodily self-consciousness that are distinct from one another, namely *body ownership* and *self-location*.

Our evaluation of this assumption will initially focus on two studies: one by Ionta et al. (2011) and the other by Petkova et al. (2011). These studies exemplify the first two assumptions noted above: each of these studies had the explicit aim of combining multisensory stimulation, concurrently delivered to the participant's body and to a virtual body, with fMRI to study the neural mechanisms underlying global forms of bodily self-consciousness. And in both studies, the manipulation of these forms of bodily self-consciousness was thought to be demonstrated by both explicit reports and measurement of behavioural effects: a shift in the perceived self-location towards the location of the virtual body in Ionta et al.'s (2011) study, and by an increase in autonomic response to a threat towards the virtual body in Petkova et al.'s (2011) study. But more interesting for our purposes is the fact that whilst similar multisensory stimulation was used, the results of these two studies differed both with respect to the phenomenological effects inferred from participants' reports and behavioural measures, and the neural correlates of these effects. In particular, distinct changes in bodily self-consciousness were related to neural activity in either the temporo-parietal junction (TPJ) in Ionta et al. (2011), or in the ventral premotor cortex (vPMc) in Petkova et al. (2011).

Taken together, these two neuroimaging studies seem to provide a case for validating the assumption that there are at least two components of bodily self-consciousness, i.e., self- location and body ownership, that are distinct from one another. We outline this case by first comparing the experimental conditions used, the phenomenological effects of the visuo-tactile conflicts in both studies, and the different patterns of neural activation reported. It seems that, experimentally, it is possible to manipulate body ownership without altering self-location, but not the converse. We delineate the case for a double dissociation by drawing on clinical evidence also. We then move on to a more detailed comparison of the brain structures involved. In doing so, we provide a tentative synthesis, merging the functional and anatomical data from these two studies with previous models thought to account for ownership of isolated body parts (Ehrsson, 2012; Makin, Holmes, & Zohary, 2007; Tsakiris, 2010) and self-location (Blanke & Arzy, 2005; Blanke & Metzinger, 2009).

2. Experimental manipulation of whole-body ownership and self-location

Both studies by Ionta et al. (2011) and Petkova et al. (2011) elaborated on the paradigm used to induce illusory ownership of an artificial hand, known as the *rubber hand illusion* (RHI, Botvinick & Cohen, 1998). The RHI consists in feeling a tactile stimulus on one's own (unseen) hand and concurrently viewing a rubber hand being synchronously touched. Synchronous visuo-tactile stimulation induces an illusory perception that the rubber hand is one's own hand and evokes a shift in the perceived location of one's own hand towards the rubber hand. In addition, an apparent threat towards the rubber hand evokes an autonomic physiological response in the subject's body (as measured by an increase in skin conductance), providing evidence that the rubber hand is self-attributed and incorporated into the subject's mental body representation. Crucially, such effects are not induced if tactile and visual stimulations are de-synchronized, showing a strict dependence of the illusion upon the spatial-temporal congruency of visual and tactile signals (for reviews, see Makin, Holmes, & Ehrsson, 2008; Tsakiris, 2010). More recent studies applied tactile stimulation on the participants' back (Lenggenhager et al., 2007) or chest (Petkova & Ehrsson, 2008) whilst they observed a full body avatar being stroked congruently on its back from a third-person perspective (Lenggenhager et al., 2007), or they observed a mannequin being stroked congruently on its chest from a first-person perspective (Petkova & Ehrsson, 2008). This manipulation induced alterations in the experience of the whole body, similar to those described during the RHI. After synchronous visuo-tactile stimulation (as compared to asynchronous stimulation), participants gave higher scores to questionnaire items such as "I had the impression that the fake body was my own body". Moreover, they tended to mis-locate their own body towards the location where the virtual body was shown (Lenggenhager et al., 2007) and, physiologically, reacted more strongly to harmful stimuli approaching the fake body (Petkova & Ehrsson, 2008). The phenomena that these reports and measures have been used to track have been referred to as the "full body illusion" (FBI; Lenggenhager et al., 2007) or "the body swap illusion" (Petkova & Ehrsson, 2008). A related illusion is the "out-of-body illusion" (Ehrsson, 2007), in which bodily self consciousness is manipulated by administering tactile stimulation on the participants' chest, while they see a synchronous movement of a stimulator from a camera, placed 2 m behind them. Although in this

case the virtual body is not seen, in this setup participants feel having an "illusory body" at the location of the cameras (see also Guterstam & Ehrsson, 2012).

The studies by Ionta et al. (2011) and Petkova et al. (2011) are fMRI adaptations of the "full-body illusion" and the "body swap illusion" respectively. But, although they share a similar experimental approach—using multisensory stimulation to understand the neural bases of bodily self-consciousness—their results differ in terms of behavioural, phenomenological and neural outcomes. Here we review the differences in phenomenological and neural outcomes and propose that critical differences in the experimental paradigms can account for this divergence. This provides the basis for us to claim that the two studies manipulated distinct aspects of bodily self-consciousness, albeit by making use of a similar experimental paradigm.

In the study by Ionta et al. (2011), participants felt touch on their back while viewing videos of a human body (here referred to as the virtual body) being touched on its back. In the study by Petkova et al. (2011), participants felt touch on their chest while viewing a mannequin (here referred to as the virtual body), through a head-mounted display, being touched on its chest. Importantly, in Petkova's study the virtual body was viewed from the first-person perspective—i.e. from the location and perspective participants normally see their own chest—whereas in Ionta's study the virtual body was viewed from a third-person perspective—i.e. as if seen from behind, from a location and perspective other than that occupied by their own body. These differences in experimental design were associated with phenomenological differences between the two studies, as indicated by participants' explicit reports. Petkova's manipulation resulted in a sense of ownership for the virtual body, but did not modify the perceived location of the self in space. Participants in Ionta's study reported a feeling that their bodily self shifted from the space occupied by their physical body to a spatial position closer to where they saw the virtual body, and some participants also reported a sense of ownership for the virtual body. Additionally, there were idiosyncratic differences in the experienced self-location and visuo-spatial perspective on the virtual body: whilst some participants felt as though they were looking upward at the virtual body, others felt as though they were floating and looking down at the virtual body. In sum, while Petkova et al. manipulated the sense of body ownership, Ionta et al. primarily manipulated self-location with concomitant changes in visuo-spatial perspective (see Figure 1).

[INSERT FIGURE 1 HERE]

3. Neural bases of whole-body ownership and self-location

In the study in which participants self-identified with the mannequin stroked on the chest (Petkova et al., 2011), the posterior parietal cortex (PPc) and the ventral premotor cortex (vPMc) were more active when tactile information applied to the participant's body was spatially and temporally congruent with tactile stimulation seen on the virtual body (see Figure 2, red dots). Neural activity in the vPMc, but not in the PPc, was correlated with the strength of illusory ownership for the virtual body, which was assessed by post-scan questionnaires. Interestingly, a further experiment showed that the same areas were also activated during illusory ownership for a virtual hand (Petkova et al., 2011). Yet, these activations were stronger when the hand was visually perceived as part of the virtual body, as compared to when the hand was presented in isolation, as detached from the body. A subregion of the vPMc was constantly activated when illusory ownership for a virtual body part was evoked by synchronous visuo-tactile stimulation, independently of whether the hand or the abdomen of the virtual body was stimulated. According to the authors, this independence from the site of stimulation suggests that a given set of vPMc neurons integrates multisensory information across multiple body parts. Given the relationship between the activity in the vPMc and the subjective feeling of whole-body ownership, Petkova et al. claimed that a multisensory integration mechanism in the vPMc is responsible for the experience of a whole body as one's own.

Electrophysiological studies in monkeys have described neural populations in homologous premotor (and also posterior parietal) areas responding to tactile, visual and acoustic information administered on or close to the animal's body (Duhamel, Colby, & Goldberg, 1998; Graziano, Yap, & Gross, 1994; Rizzolatti, Scandolara, Gentilucci, & Camarda, 1981; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981), or even close to a reproduction of a part of the animal's body (Graziano, Reiss, & Gross, 1999; Graziano, Cooke, & Taylor, 2000). Most of these neurons respond selectively to stimuli directed to specific body parts (e.g. the arm, face, and torso), while other neurons have larger multisensory receptive fields, covering even a whole hemisoma. Petkova and colleagues suggest

that clusters of activation in the vPMc (and the PPc) reflect a homologous multisensory integration system in the human brain, in agreement with previous neuroimaging evidence (Bremmer et al., 2001; Brozzoli, Gentile, Petkova, & Ehrsson, 2011; Cardini et al., 2011; Gentile, Petkova, & Ehrsson, 2011; Makin et al., 2007; Serino, Canzoneri, & Avenanti, 2011). In addition, other studies from the same group suggested that multisensory integration in the vPMc is not only involved in the multisensory integration of body-related stimuli, but is also responsible for illusory ownership of body parts (Brozzoli, Gentile, & Ehrsson, 2012; Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004; Makin, Holmes, & Ehrsson, 2008). In an fMRI version of the RHI, Ehrsson showed that vPMc activity was stronger during synchronous than asynchronous visuo-tactile stimulation, was also stronger when subjects started experiencing the illusion, and was positively correlated with the strength of the illusion measured by questionnaires (Ehrsson et al., 2004; see also Ehrsson et al., 2005). In line with this view, a recent neuroimaging study revealed that vPMc neurons, which normally respond to visual stimuli presented close to the hand, also respond to visual stimuli presented close to a fake hand, but only after a sense of ownership for the fake hand has been induced through the RHI (Brozzoli et al., 2012). The claim that Petkova et al. (2011) make that similar multisensory integration mechanisms in the vPMc are responsible for the experience of a whole body as one's own, follows this research trend. However, ownership for the entire body would involve neurons with larger receptive fields allowing integration of multisensory information across multiple body parts, and, according to the authors, even across the entire body.

[INSERT FIGURE 2 HERE]

Apparently divergent results were reported by Ionta and colleagues (2011). They did not report any specific activation in the vPMc or the PPc, but showed that the right and left TPJ were critically involved in the FBI (see Figure 2; black dots). Neural activity in these areas was modulated when synchronous touch was applied on the participant's back and observed on the back of the virtual body. Analysis of post-scan subjective reports indicated that synchronous visuo-tactile stimulation could evoke two different visuo-spatial perspectives and, importantly, changes in self-location. Critically, the modulation of the TPJ activity varied as a function of

how participants felt themselves to be located and orientated with respect to the virtual body. For participants who felt themselves to be looking upwards at the virtual body (up-group), the estimated self-location was higher and TPJ activity was lower during synchronous compared with asynchronous visuo-tactile stimulation. For participants who felt themselves at a lower location and to be looking downwards, the estimated self-location was lower and TPJ activity was higher during synchronous compared with asynchronous stimulation. Thus, TPJ activity reflected individual differences in experienced self-location and visuo-spatial perspective. Accordingly, Ionta et al. (2011) claimed that multisensory integration at the TPJ underlies the subjective feeling of being located within a body, occupying a given location in space, and experiencing the world from that location.

The TPJ is an important multisensory area, integrating inputs from the tactile, proprioceptive and visual systems, and, critically, from the vestibular system (Blanke & Arzy, 2005; Lopez & Blanke, 2011; Lopez, Halje, & Blanke, 2008). A vestibular contribution to self-location seems of relevance here because the sensations of elevation and floating reported by the participants of Ionta et al.'s study are close to vestibular illusions reported by patients with damage to the otolithic vestibular system and the central vestibular structures (Schilder, 1935). Several regions of the TPJ located around the posterior end of the Sylvian fissure, such as the angular, supramarginal and superior temporal gyrus, and the regions located in the depth of the Sylvian fissure, such as the parietal operculum, insula and the retroinsular cortex, are strongly involved in vestibular processing (Chen, DeAngelis, & Angelaki, 2010; Grüsser, Pause, & Schreiter, 1990; Lopez, Blanke, & Mast, 2012). Lesions or seizures in the TPJ may alter the experience of self-location, such as during what are often called out-of-body experiences. Out-of-body experiences refer to the sensations of being located outside the physical body (i.e. disembodied self-location) and of seeing and perceiving the world and sometimes oneself from a location outside one's own physical body, as if taking a third-person perspective on one's body (Blanke, Landis, Spinelli, & Seeck, 2004; Blanke & Mohr, 2005; Blanke, Ortigue, Landis, & Seeck, 2002). The TPJ has been related to perspective taking in tasks requiring shifts from the first- to the third-person perspective to solve spatial and sensory-motor tasks (Blanke et al., 2005; Farrer & Frith, 2002; Ruby & Decety, 2001). Thus, clinical, neurophysiological and neuroimaging data about the TPJ strongly support the involvement of this area in self-location and perception of the world from a perspective originating from one's position in space.

In conclusion, the participants in Petkova et al.'s study experienced ownership for a body that was not their own. Induction of a sense of ownership for the virtual body through synchronous visuo-tactile stimulation was associated with changes in neural activity mainly in the vPMc (and partially in the PPc). By contrast, the study by Ionta et al. (2011) primarily modified experienced self-location. The change in the experience of self-location was related to activity in the TPJ. Despite the fact that the two studies applied similar visuo-tactile conflicts, there were phenomenological and neural differences between them. Taken together, they provide evidence that visuo-tactile integration in the vPMc appears critical for the experience of owning a body, whereas the integration of visual, tactile and vestibular signals at the TPJ reflects self-location and visuo-spatial perspective.

4. Are self-location and body ownership distinct components of self-consciousness?

Except during some rare and short-lived illusions occurring in healthy and neurological populations, we usually experience ourselves as being located within the body that we experience as our own (an experience referred to as embodied self-location). In the words of William James, we normally experience "the feeling of the same old body always there" (James, 1890, p. 242), suggesting that body ownership and self-location are normally strongly associated. Yet, the two neuroimaging studies discussed above suggest that both experiences are implemented in partially dissociable neural structures. To what extent is it possible to dissociate these two components of bodily self-consciousness at the level of subjective experience? In order to provide such evidence one should demonstrate, under appropriate experimental conditions, a change in body ownership with no change in self-location, and conversely, a change in self-location without any change in body ownership. That is one should demonstrate a double dissociation between the two components.

In the body swap illusion (Petkova et al., 2011), body ownership is manipulated, whilst self-location is unaffected. Subjects experienced ownership for a body that was not their own, yet their own visuo-spatial perspective was maintained and their experienced self-location remained unchanged and centered on the physical body. The FBI (Ionta et al., 2011) does not induce the

converse pattern. Although the main aim of Ionta et al.'s study was to investigate the experience of self-location, they also induced some changes in body ownership, as shown by questionnaires and subjective reports (see e.g., Participant 4, who after synchronous visuo-tactile stroking reported "I was looking at my own body from above"). Thus, in the FBI, changes in self-location were accompanied by changes in body ownership and self-identification with the virtual body. In the out-of-body illusion (Ehrsson, 2007), participants have the illusory experience of being located at the position of the camera. Interestingly, Guterstam and Ehrsson (2012) recently showed that such a shift in self-location towards an extracorporeal location was associated with a feeling of disownership for one's own physical body. After synchronous visuo-tactile stimulation inducing the out-of-body illusion, skin conductance response to a threat approaching the physical body was reduced as compared to that measured after asynchronous visuo-tactile stroking. Thus, also in this case, a shift in self-location was associated to an alteration of body ownership.

Therefore, while it is possible to alter the experience of owning a body without any shift in experienced self-location (Petkova et al., 2011), it has not been shown experimentally that one can experience a change in self-location without a change in body ownership. Taking solely the experimental evidence into account, there is a case for a single dissociation only. Yet, clinical evidence and new research conducted on the RHI supports the stronger claim of a double dissociation.

Extensive examination of neurologically normal subjects who have experienced an out-of-body experience is congruent with results from experimentally-induced illusory alterations to bodily self-consciousness. During out-of-body experiences most people report a loss of connection between the self and their physical body, suggesting concomitant changes of self-location and body ownership (e.g. "I felt no connection [...] between me, up against the ceiling and the body in the bed", (Green, 1968), p. 100). However, in some instances (about one third of the population), the disembodied self-location was associated with strong self-identification and some experience of ownership of the physical body (e.g. "I was always conscious of being connected to *my* own physical body and felt it drawing me back after a while like a powerful magnet" (Green, 1968, p. 102, our italics). Similar observations were made by Blackmore (1984) who found that 24% of subjects reporting OBEs claimed there was a connection between their disembodied self and the seen body. These observations are also supported by reports in neurological patients. Devinsky et al. (Devinsky, Feldmann, Burrowes, & Bromfield, 1989) have

reported several cases in which self-identification and connections with the physical body seem to be preserved during experience of disembodiment (e.g. case 6: "I could see *my body* in the bed"; case 5: "she then looked down and saw *her body*"; case 8: "drifting outside *my body*"). Another striking clinical example of dissociation between self-location and ownership is heautoscopy, during which patients experience seeing a double of themselves in the extrapersonal space (Blanke et al., 2004; Blanke & Mohr, 2005; Brugger, Blanke, Regard, Bradford, & Landis, 2006; Brugger, Regard, & Landis, 1997). Most patients report a strong self-identification and affinity with the seen body while their sense of self-location is strongly disturbed (Heydrich & Blanke, 2013). Indeed, although ownership is usually experienced for the autoscopic (double) body, self-location is ambiguous and often alternates between the physical body and the autoscopic body. In some instances, patients experienced bi-location (Furlanetto, Bertone, & Becchio, 2013; Heydrich & Blanke, 2013). Thus, it seems reasonable to propose that self-location and body ownership can doubly dissociate. It follows that, in some instances, body ownership and self-location can be behaviorally distinguished, which strengthens the view that they rely on rather distinct neural mechanisms.

Convergent evidence suggesting a distinction between body ownership and self-location comes from recent work on the RHI. In order to demonstrate induction of the RHI, most studies collected subjective ratings of questionnaires and measured the extent to which the perceived location of one's own hand shifts towards the rubber hand (i.e. "proprioceptive drift"; see Tsakiris, 2010 for a review). Rohde et al. (Rohde, Di Luca, & Ernst, 2011) recently demonstrated a dissociation of the proprioceptive drift and subjective ratings of ownership for the rubber hand (see also Carruthers, 2013 for a review). We believe that this dissociation is possible because the two measures actually tap into different components of bodily self- consciousness manipulated through the RHI, i.e. self-location (as measured by proprioceptive drift) and body ownership (as measured by subjective ratings). Accordingly, Longo et al. (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008) performed a principal component analysis of an extensive set of questionnaire responses about the RHI in order to identify the main components of the process of embodying a rubber hand (see Tajadura-Jimenez, Longo, Coleman, & Tsakiris, 2012 for the same approach to the "enfacement" illusion). Longo et al. (Longo et al., 2008) clearly found that *ownership* and *location*, although strongly linked, were independent components in their analyses, suggesting that they independently contribute to the RHI.

In conclusion, there is accumulating evidence suggesting that body ownership and self-location are distinct aspects of bodily self-consciousness, whose neural correlates can be experimentally dissociated and identified, respectively, in the vPMc/PPc and in the TPJ. This cumulative evidence supports the (weaker) assumption that has driven research into bodily self-consciousness—that body ownership and self-location are distinct components of the experience of oneself as a bodily subject. Although a change in self-location without any change in ownership has not yet been produced experimentally, clinical evidence and recent work on the RHI suggest that the two are distinct components of bodily self-consciousness with distinct neural correlates. One question, then, is whether it is possible to produce a change in experienced self-location without altering the sense of ownership for one's physical body in order to provide experimental evidence of a double dissociation of body ownership and self-location. We will not address this here, but leave it as an open question. A second open question is how these two components interact to contribute to the experience of the bodily self. In the last section of this article, we offer a more detailed survey of the brain structures associated with body ownership and self-location, thereby establishing a framework in which this issue might be addressed.

5. Synthesising research on bodily self-consciousness

We have argued that bodily self-consciousness is made up of, but is not limited to, two distinguishable components: body ownership and self-location. In this section we provide a more thorough comparison of the brain structures involved in each kind of experience. In so doing we provide a preliminary synthesis of the neural data on bodily self-consciousness. We will start by describing neural mechanisms devoted to representing the body, initially looking at the processing of unimodal body-related information and then moving on to the integration of body-related information from multiple senses. We will show how different levels of multisensory integration might support different components of bodily self-consciousness, and, in particular, body ownership and self-location. We will synthesize these processes in a distributed model of neural body representations in the human brain.

5.1   *Unisensory body representations*

At a first sight, the body is represented in the brain in a number of unisensory areas. Touch applied on a part of the body activates a specific part of the map of the body surface represented in the primary somatosensory cortex in the post-central gyrus (Marshall, Woolsey, & Bard, 1937; Penfield & Boldrey, 1937). Vision of different body parts selectively activates portions of the extrastriate body area (EBA; Downing, Jiang, Shuman, & Kanwisher, 2001) and occipito-temporal cortex (Orlov, Makin, & Zohary, 2010). Hearing sounds produced by body parts (e.g. two hands clapping) activates in a somatotopic manner portions of the inferior frontal gyrus (IFG) and inferior parietal lobe (IPL; see Aglioti & Pazzaglia, 2011), two regions of the fronto-parietal action-observation network. Smelling body odours activates a set of cortical regions including the posterior cingulate cortex, occipital gyrus, angular gyrus, and the anterior cingulate cortex (Aglioti & Pazzaglia, 2011; Lundstrom, Boyle, Zatorre, & Jones-Gotman, 2008). Two lines of evidence suggest that unimodal body representations might not be sufficient to give rise to the experience of the body. First of all, usually lesions to unisensory cortices induce sensory specific deficits, but do not induce disturbances in bodily experience. For instance, a lesion to the somatosensory cortex results in hemianesthesia, i.e. a lack of tactile sensation from the controlesional side of the body, but it does not induce disturbances in bodily experience *per se* (Ronchi & Vallar, 2010). Second, manipulation of unisensory signals rarely induces alteration in body perception (but see Longo, Pernigo, & Haggard, 2011). Rather, as the cases of multisensory illusions reviewed here suggest, experience of the body might result from multisensory integration mechanisms (see Blanke, 2012; Serino & Haggard, 2010).

5.2   *Multisensory body representations*

Unisensory processing of body-related information is thought to serve as input to the multisensory processes taking place in the PPc and the vPMc (see Macaluso & Driver, 2005 and Graziano & Cooke, 2006 for reviews on human and monkey data, respectively). These regions are largely interconnected (Koch et al., 2010; Matelli & Luppino, 2001), but may still have partially dissociable functions.

5.3   Multisensory integration in the PPc: reference frame transformations

One fundamental function of multisensory integration in the PPc is the transformation of tactile, visual, proprioceptive, auditory and vestibular signals originally related to single, mobile body parts (e.g. hand, arm, head and trunk) into stable spatial representations projected onto a torso-centred reference frame. Neurophysiological data in monkeys shows that the PPc contains several distinct, but functionally connected, neural populations coding multisensory stimuli relative to a variety of body-part-centered reference frames (see Andersen & Buneo, 2002; Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005; Colby, 1998; Grefkes & Fink, 2005). Computational models have contributed to an explanation of how different reference frames interact and combine in the PPc (see e.g. Pouget, Deneve, & Duhamel, 2002). In addition, the consequences of PPc lesions strongly suggest that the PPc is a crucial brain structure for combining several reference frames (see Berlucchi & Aglioti, 2010 for a review). Patients with PPc lesions are strongly impaired when performing tasks requiring on-line coding of body posture (Schwoebel & Coslett, 2005), when attending to body parts on the left in the case of a right lesion (i.e. personal neglect; Committeri et al., 2007) and when describing the spatial relations between body parts in the case of a left lesion (i.e. autotopagnosia; Ogden, 1985). Virtual lesions induced by transcranial magnetic stimulation applied over the PPc affect the capacity for coding and remapping of multisensory information across different body parts (Azanon, Longo, Soto-Faraco, & Haggard, 2010; Bolognini & Maravita, 2007; see also Corradi-Dell'Acqua, Tomasino, & Fink, 2009; Lloyd, Morrison, & Roberts, 2006 for fMRI evidence). Taken together, these findings suggest that activity in the PPc is necessary to encode multisensory spatial representations of body parts centered on different reference frames. We suggest that such recoding is a precondition for a coherent experience of the self as located within a whole body.

5.4   Multisensory integration in the vPMc: triggering body ownership

As noted above, activation of the vPMc has been related to the induction of the RHI (Ehrsson et al., 2005; Ehrsson et al., 2004) and the body swap illusion (Petkova et al., 2011): vPMc activity increases during synchronous visuo-tactile stimulation (in particular at the

beginning of the illusion) and is correlated with questionnaire responses. Accordingly, Ehrsson proposed that multisensory integration at the vPMc might be sufficient for yielding the sense of body ownership, in a bottom-up fashion (Ehrsson, 2012; Makin et al., 2007). This proposal fits with the evidence that vPMc lesions induce disorders of bodily awareness, such as anosognosia for hemiplegia (i.e. lack of awareness of motor deficits in the contralesional limbs; Berti et al., 2005) and asomatognosia (i.e. lack of awareness of parts on one's own body; Arzy, Overney, Landis, & Blanke, 2006). Nevertheless, although multisensory integration at the vPMc might be necessary for the induction of an illusion of body ownership, the experience of ownership might result from activation elsewhere (see below). Cardini et al. (2011) have recently shown that the vPMc is active when subjects received tactile stimulation on their own face and viewed another face being touched. In addition, the vPMc was activated more when the seen face belonged to another person, rather than to themselves (see also Serino, Pizzoferrato, & Ladavas, 2008). Together with the evidence of higher vPMc activation at the beginning of the RHI/body swap illusion in conditions of synchronous visuo-tactile stimulation, Cardini et al.'s findings suggest that increased activity at the vPMc might reflect the strength of the integration of multisensory cues from one's own body and another bodily object, which could be either another person's body or a reproduction of a human body. This mechanism might *trigger* an experience of ownership for the "other" body, without vPMc activation actually underpinning the experience of ownership (see below, and see also Tsakiris, 2010; Tsakiris, Prabhu, & Haggard, 2006 for comments).

5.5 *Over and above multisensory integration*

Bottom-up multisensory integration at the vPMc might not be sufficient to enable body ownership for at least one fundamental reason. If this were the case, signals from any external object could potentially be integrated with bodily-related signals inducing a sense of ownership for that object. However, this does not normally occur, since the RHI is not induced (or it is much weaker) when visuo-tactile stimulation is applied to a non-corporeal object (Armel & Ramachandran, 2003; Haans, Ijsselsteijn, & de Kort, 2008; Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris & Haggard, 2005) or when the rubber hand is placed in a position that is anatomically incompatible with the subject's posture (Costantini & Haggard, 2007; Lloyd, 2007; Pavani, Spence, & Driver, 2000). Tsakiris (2010) argued that the sense of body ownership

also depends on top-down processes, which act over and above multisensory integration mechanisms and help distinguish between objects that can and cannot be attributed to one's body as a function of their visual appearance and anatomical coherence with the physical body. According to Tsakiris, these test-for-fit processes would be computed in the right TPJ, a region that could harbour a structural model of the body. Indeed, TMS applied over the TPJ facilitates the experience of ownership for non-corporeal objects, suggesting that interfering with sensory processing at the TPJ can disrupt the test-for-fit processes and increases the likelihood of self-attributing non-corporeal objects into one's body schema (Tsakiris, Costantini, & Haggard, 2008).

5.6 *Body ownership from the inside*

Despite the fact that most previously cited literature clearly refers to processing of external bodily related signals, processing and integration of interoceptive signals from *inside* the body is a critical aspect of bodily self-consciousness. Interoception, the sense of the physiological condition of the body, is a ubiquitous information channel used to represent one's body from within. A renewed interest in this topic in the neuroscientific community has led to the identification of the insular cortex as a key area for sensory self-monitoring. The posterior insula has primarily been involved in interoceptive representations of the body (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004), and the anterior insula has primarily been involved in integrating bodily signals with environmental, emotional and motivational representations (Berlucchi & Aglioti, 2010; Craig, 2009). A PET study by Tsakiris and colleagues (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007) suggests that the insula also underpins bodily self-consciousness during the RHI because activation of the right insula was positively correlated with the strength of the RHI. Interestingly, a recent study has shown that interoceptive awareness, measured by a heartbeat detection task, is negatively correlated with the intensity of the RHI. Subjects with higher interoceptive awareness were less prone to experience the illusion (Tsakiris, Tajadura-Jiménez, & Costantini, 2011; see Tajadura-Jimenez et al., 2012 for similar results for the "enfacement" illusion). This result suggests that subjects with high interoceptive awareness (linked to insula function) are less ready to experience ownership for other stimuli, probably because they have a stronger sense of ownership for their own body. Finally, insular lesions, especially those on the right hemisphere, are associated with somatoparaphrenia, that is,

the delusional belief that one part of one's own body, usually the contralesional upper limb, belongs to someone else (Baier & Karnath, 2008; see also Vallar & Ronchi, 2009 for a review).

5.7   *The body in the world: self-location*

We not only experience our bodies as our own, we also experience ourselves as occupying a given location in the world with a given perspective. In order for this to occur bodily-related inputs, computed in the different brain areas reviewed above, need to be integrated with environmental information signaling the position and the orientation of the body with respect to external space. Two sources of information seem critical for this: vestibular signals that code the orientation and movement of the body with respect to gravity, and visual signals related to external objects, which code the orientation and movement of the body with respect to the environment. Although most studies have described the contribution of visual signals in coding self-location, others have highlighted the role of vestibular signals in unifying bodily experience by merging signals from bodily, retinal and geocentric space in multimodal areas (Lopez & Blanke, 2007; Paillard, 1991). As documented above, TPJ activity is necessary for computing self-location and visuo-spatial perspective, because it receives converging visual, tactile, proprioceptive and vestibular signals about body orientation with respect to the environment (Blanke & Arzy, 2005; Bottini et al., 2001; Lopez et al., 2008). The idea that we experience the world from a single visuo-spatial perspective, despite the fact that multiple reference frames are used to code external events, has recently been pointed out by philosophical (Bermúdez, 1998; Husserl, 1973/1997), neurophysiological (see e.g., Colby, 1998; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997), and neuropsychological research (see e.g., dissociation between neglect for personal, peripersonal and extrapersonal space; Bisiach, Perani, Vallar, & Berti, 1986; Cowey, Small, & Ellis, 1994; Halligan & Marshall, 1991). Multisensory integration at the TPJ seems necessary for stable self-location and coherent perspectival experience of this form. In this sense, the experience of self-location seems a minimally necessary condition for self-consciousness (Blanke & Metzinger, 2009), and also for awareness of external events.

Interestingly, a large body of evidence suggests that the TPJ is also involved in more abstract cognitive abilities, such as mind reading (Saxe & Wexler, 2005), theory of mind (Vogeley & Fink, 2003) and empathy (Decety & Lamm, 2007). All these functions imply a shift

of perspective, from one's own cognitive or emotional point of view to that of another. More moderately, the TPJ might underlie the ability to represent and manipulate one's own physical or cognitive/emotional perspective on the world and on others.

5.8   *Synthesis*

In summary, bodily self-consciousness comprises the concurrent experience of (a) a body as one's own, and (b) this body as located in space. These two components of bodily self-consciousness depend on a series of neural processes distributed along a network of different brain areas, which are illustrated in Figure 3. First, body related signals are initially processed in unisensory brain regions, mainly in the parietal (SI) and occipital (EBA) cortices. Unisensory body related inputs then converge and are integrated in multisensory areas in the parietal, premotor and insular cortices. In particular, the vPMc contains neural populations which integrate multisensory cues (visual, tactile, auditory) among different body parts and are responsive when participants experience a part of their body or their whole body as their own. On the other hand, body self-consciousness ought to include a mechanism that continuously maps *on-line* where the different body parts are in space and in relationship to each other. Such a process is probably implemented in the PPc because this area contains neural populations which respond to multisensory information as referenced to single body parts, and also transforms these body-part-centered signals in common reference frames. In addition, body ownership seems to be modulated by *off-line* body representations (Carruthers, 2008), specifying which sensory cues can or cannot be attributed to the body, depending on perceptual (coded in right inferior parietal cortex) and structural (coded in the left parietal cortex) constraints. Internal body states, which are mainly processed in the insular cortices, also contribute to bodily self-consciousness, underlying the experience of the body from the inside. Finally, the body is experienced as occupying a given location in the world and as being the locus of one's perceptual perspective. The convergence of vestibular and visual signals in the TPJ is critical for one's being able to locate one's own body in a world-centered reference frame (Blanke & Metzinger, 2009; Ionta et al., 2011).

[INSERT FIGURE 3 HERE]

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Taken together the processes listed above constitute a multi-componential model underlying the experience of the bodily self, in which the different components are processed by distinguishable, interacting, neural systems. The notion of a distributed representation of the body might resemble the concept of the "neuromatrix" by Melzack (1990), who proposed that bodily experience results from the interaction of several nodes of interconnected brain areas. At variance with Melzack, however, we can now benefit from the wealth of knowledge about the location and function of these areas.

5.9   Limits of the model

We are aware that the present model is not exhaustive, as it neglects at least two fundamental aspects of bodily experience.

First, we experience our body in movement, interacting with the world and others (Merleau-Ponty, 1962). That is, besides the sense of ownership, we also experience intentional movements as realisations of our agency (Bayne, 2008; Pacherie, 2008). It is through our body that we move and act, feed ourselves and satisfy our needs, and more abstractly, satisfy our drives and motivation. In this vein, Gallese and Sinigaglia (Gallese & Sinigaglia, 2010) have proposed that bodily self-consciousness is constituted by the anticipation and control of action, such that our bodily self-consciousness is essentially a form of agentive experience. More moderately, it is clear that body representations interface with the motor system and with the executive system, representing actions and goals (Andersen & Buneo, 2002; Dorris & Glimcher, 2004). A long tradition in neuroscience supports the view that body representations as well as space representations are not simply sensory *or* motor, but rather *both* sensory *and* motor (Rizzolatti et al., 1997; Rizzolatti, Fogassi, & Gallese, 2002).

Secondly, for the sake of producing a synthesis, we presented bodily experience in isolation, whereas our body constantly interacts with objects, obstacles and artifacts in the environment and these interactions affect body representation. An extensive literature has shown that body-related signals are integrated with information pertaining to external stimuli occurring in the space near the body to constitute a multisensory representation of peripersonal space (Graziano & Cooke, 2006; Ladavas, 2002; Rizzolatti et al., 1997). A prominent line of research

has shown that using tools to interact with objects in the environment both shapes peripersonal space representation (see Ladavas & Serino, 2008; Maravita & Iriki, 2004 for reviews) and alters the perception of the body itself (Canzoneri et al., 2013; Cardinali et al., 2009; Longo & Serino, 2012 for comments). We did not include this topic in the current presentation of our model as it would take us beyond the scope of the present paper.

Finally, recent advances in the field of social neuroscience have highlighted the social nature of human beings and the most relevant stimuli we interact with are our conspecifics. On this view it has even been proposed that it might be misleading to study cognition in isolated human subjects. Thus, a full understanding of human cognition ought to take into account how cognition shapes and is shaped by social interaction. The body is our interface with others (see e.g., Adolphs, 2009; Decety & Lamm, 2007; Gallese, Keysers, & Rizzolatti, 2004; Saxe, 2006), and therefore it is possible that social interactions shape the experience we have of our body (Ambrosini, Blomberg, Mandrigin, & Costantini, 2013; Cardellicchio, Sinigaglia, & Costantini, 2012; Cardini, Tajadura-Jimenez, Serino, & Tsakiris, 2012; Costantini, Ambrosini, Sinigaglia, & Gallese, 2011; Costantini, Committeri, & Sinigaglia, 2011; Costantini et al., 2013; Serino, Giovagnoli, & Ladavas, 2009; Teneggi, Canzoneri, di Pellegrino, & Serino, 2013).

Thus, the different levels of body representations we reviewed here need to be integrated with other systems in order to support the motor and social functions of human cognitive systems. However, these important topics are beyond the scope of this review.

6. Conclusions

We have taken the opportunity offered by two recent neuroimaging studies (Ionta et al., 2011; Petkova et al., 2011) to discuss how neuroscientific investigation can inform and contribute to theories about key aspects of our experience as human beings such as bodily self-consciousness. Traditionally bodily self-consciousness has almost exclusively been addressed by more theoretical investigations in the fields of psychology and philosophy. Moreover, work on bodily self-consciousness has typically relied on several assumptions. Taking Ionta et al.'s and Petkova et al.'s results as our starting point, we have made a case in support of one of these assumptions: that body ownership and self-location are distinct components of bodily self-consciousness. Offering a detailed comparison of the processing and neural structures necessary

for these components, we then provided a synthesis of this functional and anatomical data with previous models of the ownership of individual body parts and of self-location. This review serves as a demonstration of the importance of integrating different approaches in the study of mind: the sum of single experimental findings, however powerful, will not allow us to understand the core of an issue under investigation. Rather, we need wider, theoretically ambitious models that integrate different bodies of evidence in a multidisciplinary fashion. In this short review we have sought to provide an example of this approach, applied to the field of body representations that support bodily self-consciousness.

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8. References

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Figures captions

Figure 1. Multisensory illusions manipulating bodily self-consciousness. In the full body illusion (A) participants receive a tactile stimulation on their back, while viewing a virtual body placed several centimeters in of front of them receiving a concurrent homologous stimulation. In the body swap illusion (B), participants receive a tactile stimulation on their chest while viewing a mannequin, occupying the same position as their own body, receiving a concurrent homologous stimulation.

Figure 2. Brain areas associated with different manipulations of bodily self-consciousness. Areas where activation significantly changes during synchronous visuo-tactile stimulation as compared to asynchronous stimulation during the full body illusion (A) and the body swap illusion (B).

Figure 3. A distributed model of bodily self-consciousness. Unisensory, body-related information is computed in specialized regions of the parietal cortex (S1: primary somatosensory cortex) and occipito-temporal cortex (EBA: extrastriate body area), and then integrated in the posterior parietal cortex (PPc) and ventral premotor cortex (vPMc). Such multisensory integration mechanisms concur with experience of the body as a whole and experience of the body as one's own. Concurrently, interoceptive and emotional signals are processed in the insular, constituting another fundamental component of self-awareness. The bodily self is also experienced as being located in space and with a first-person perspective by virtue of the integration of multisensory body-related and vestibular signals at the temporo-parietal junction (TPJ). In sum, bodily self-consciousness results from the computation of a distributed network of neural processing, each with a fairly specific function, but which together result in phenomenally integrated bodily experiences.