Multisensory Spatial Mechanisms of the Bodily Self and Social Cognition

A Commentary on Vittorio Gallese & Valentina Cuccio

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This commentary aims to find the right description of the pre-reflective brain mechanisms underlying our phenomenal experience of being a subject bound to a physical body (bodily self) and basic cognitive, perceptual, and subjective aspects related to interaction with other individuals (social cognition). I will focus on the proposal by Gallese and Cuccio that embodied simulation, in terms of motor resonance, is the primary brain mechanism underlying the pre-reflective aspects of social cognition and the bodily self. I will argue that this proposal is too narrow to serve a unified theory of the neurobiological mechanisms of both target phenomena. I support this criticism with theoretical considerations and empirical evidence suggesting that multisensory spatial processing, which is distinct from but a pre-requisite of motor resonance, substantially contributes to the bodily self and social cognition.

My commentary is structured in three sections. The first section addresses social cognition and compares embodied simulation to an alternative account, namely the attention schema theory. According to this theory we pre-reflectively empathize with others by predicting their current state of attention which involves predicting the spatial focus of attention. Thereby we derive a representational model of their state of mind. On this account, spatial coding of attention, rather than motor resonance, is the primary mechanism underlying social cognition. I take this as a theoretical alternative complementing motor resonance mechanisms.

The second section focuses on the bodily self. Comparison of the brain networks of the bodily self and social cognition reveals strong overlap, suggesting that both phenomena depend on shared multisensory and sensorimotor mechanisms. I will review recent empirical data about altered states of the bodily self in terms of self-location and the first-person perspective. These spatial aspects of the bodily self are encoded in brain regions distinct from the brain network of embodied simulation. I argue that while motor resonance might contribute to body ownership and agency, it does not account for spatial aspects of the bodily self. Thus, embodied simulation appears to be a necessary but insufficiently "primary" brain mechanism of the bodily self and social cognition.

The third section discusses the contributions of the vestibular system, i.e., the sensory system encoding head motion and gravity, to the bodily self and social cognition. Vestibular cortical processing seems relevant to both processes, because it directly encodes the world-centered direction of gravity and allows us to distinguish between motions of the own body and motions of other individuals and the external world. Furthermore, the vestibular cortical network largely overlaps with those neural networks relevant to the bodily self and social cognition. Thus, the vestibular system may play a crucial role in multisensory spatial coding relating the bodily self to other individuals in the external world.

Keywords

Attention schema | Bodily self | Embodied simulation | First-person perspective | Mirror neurons | Self-location | Social cognition | Vestibular system

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1 Introduction

The paper by Gallese and Cuccio provides an integrated theoretical framework explaining how the brain and body relate to social cognition, the human self, and language. The authors review empirical evidence from electrophysiological and neuroimaging studies supporting embodied simulation (ES) theory (Gallese & Cuccio this collection, p. 8). According to ES, the brain covertly simulates the bodily actions, perceptions, and emotions observed in other individuals by using parts of our neural architecture involved in acting, sensing, and feeling emotions. Thereby, we infer the goals, intentions, and states of mind of others in a pre-reflective and non-conceptual fashion. But the authors take this a step further and propose that ES is the key mechanism underlying, and hence unifying, both social cognition, the human self, and language. Throughout the paper, the authors emphasize the tight functional coupling between the body and the brain, which when taken into account bears the potential to significantly advance the scientific study of the hard problem of consciousness (Chalmers 1996).

This commentary on Gallese and Cuccio aims to find the right description of the brain mechanisms underlying pre-reflective aspects of both the bodily self and social cognition. Specifically, I will focus on Gallese and Cuccio's central claim that ES, based on motor resonance and neural processing in the motor system, is the primary brain mechanism underlying pre-reflective representations of the bodily self and social cognition (Gallese & Cuccio this collection, pp. 8–14). I ask the following questions: Could there be an alternative theory or empirical evidence countering the claim of a primacy of motor resonance underlying social cognition and the bodily self? Which brain mechanisms in addition to motor resonance might contribute to pre-reflective aspects of social cognition and the bodily self? I will defend the following three theses:

(1) Social cognition and the bodily self depend on multisensory spatial coding, which is distinct from motor resonance.

Thus, motor resonance may be a necessary but insufficiently "primary" brain mechanism of social cognition and the bodily self (cf. section 1, 2).

(2) The brain networks underlying social cognition and the bodily self largely overlap. Specific functional associations exist (a) between motor resonance and body ownership/agency and (b) between multisensory spatial coding and self-location/the first-person perspective (cf. section 2).

(3) The vestibular system, i.e., the sensory system encoding head motion and gravity, might provide unique information used for multisensory spatial coding that relates the bodily self to other individuals and the external world. This is further suggested by the large overlap existing between the human vestibular cortex and the brain networks underlying the bodily self and social cognition (cf. section 3).

My commentary is structured in three sections. In the first section I shall compare ES to an alternative theory of social cognition that assigns priority to spatial coding of attention, rather than to motor resonance. I shall show that both theories bear the potential that their proposed brain mechanisms cooperatively work together in order to support social cognition. The second section addresses the bodily self. I shall review data from neurological patients and full-body illusion experiments, which highlight the importance of two spatial aspects of the bodily self not mentioned by Gallese and Cuccio, i.e., self-location and the first-person perspective. These spatial aspects of the bodily self depend primarily on multisensory integration and on cortical processing outside regions involved in ES. Furthermore, comparisons between the brain networks encoding the bodily self and social cognition show large overlaps, suggesting shared functional mechanisms. In the third section I propose that because multisensory spatial processing appears to be critical for

the bodily self and social cognition, important contributions may come from the vestibular system (Lenggenhager & Lopez this collection). I shall show that the vestibular cortical network largely overlaps with the brain networks underlying the bodily self and social cognition. I shall discuss potential contributions of vestibular cortical processing to these target phenomena and suggest directions for future research.

2 Is social cognition based on motor resonance or attention tracking?

Social cognition refers to cognitive processes, perceptions, and subjective experiences related to interaction with conspecifics. This section asks: Which are the brain mechanisms underlying pre-reflective aspects of social cognition? Could there be alternative theories and empirical evidence countering the primary role of motor resonance?

Gallese and Cuccio propose that social cognition mainly depends on ES based on motor resonance and processing of mirror neurons (see citations in Gallese & Cuccio this collection). Mirror neurons were initially discovered in fronto-parietal networks of the macaque monkey brain. They are a specific type of canonical neuron involved in planning and executing hand actions and were found to be activated both when the monkey executed a specific grasping or reaching action and when the monkey passively observed somebody performing similar actions (Gallese et al. 1996; Rizzolatti et al. 1996). Neuroimaging studies in humans also showed mirror neuron-like activation patterns at the level of populations of neurons in distinct brain regions—mainly the ventral premotor cortex (vPM), the intraparietal sulcus (IPS), but also the insula cortex and the secondary somatosensory cortex (Rizzolatti & Sinigaglia 2010; see also figure 1a gray dots). ES proposes that based on mirror neurons the brain maps observed actions into an action space, into motor potentialities, within our hierarchically-organized motor system, and thereby infers and predicts the action goals of the individual. In this way it penetrates the state of mind of the other, and thus links self and other in a pre-reflective

empathical fashion (Gallese & Cuccio this collection, p. 7).

I would like to point out that motor resonance, i.e., the mapping of observed actions into motor potentialities, necessarily depends on multisensory spatial coding. I argue that this is the case because of five points: First, the brain has access to the physical world only through the different sensory receptors of the body that bombard it with exteroceptive (e.g., vision, audition), proprioceptive (somatosensory, vestibular), and interoceptive (somatosensory, visceral) signals. Second, these multisensory signals must be integrated according to their spatial and temporal parameters (Stein & Stanford 2008) to inform neural representations of the states of the body and of the world around us—including the agents whose actions are subject to motor resonance. Third, the observed movements of these agents are coded in coordinates distinct from the egocentric spatial frame of reference upon which our motor system operates. Fourth, the brain must necessarily perform spatial transformations of the observed movements by the other agent into the egocentric frame of reference, upon which motor resonance can operate. In sum, multisensory spatial coding is a pre-requisite of motor resonance.

According to Gallese and Cuccio, the outcomes of such multisensory spatial coding are readily available to the brain network of ES through anatomical connections to the vPM that are "anatomically connected to visual and somatosensory areas in the posterior parietal cortex and to frontal motor areas" (Gallese & Cuccio this collection, p. 10). However, it seems that the multisensory spatial coding required for a precise description of complex motor acts might be computationally costly. Might there be a computationally more effective alternative by which multisensory spatial coding is used to decode the intentions of observed agents?

The attention schema (AS) theory of awareness (Graziano 2013; Graziano & Kastner 2011) proposes that brain mechanisms related to attention and spatial coding, which are distinct from neural processing relevant to ES, primarily underlie pre-reflective aspects of social cognition. Graziano and Kastner define *atten-*

tion as an information-handling mechanism of the brain that serves to give priority to some information (e.g., representational features) out of several equally probable alternatives that are in constant competition for awareness. Furthermore, *awareness* is defined as the process of consciously experiencing something, it is the process of relating the subject (i.e., a phenomenal self, see also Metzinger 2003) to the object/content of experience. Graziano and Kastner summarize AS as follows:

> [Awareness is information and] depends on some system in the brain that must have computed [it] [...]; otherwise, the information would be unavailable for report. [...] People routinely compute the state of awareness of other people [and] the awareness we attribute to another person is our reconstruction of that person's attention. [...] The same machinery that computes socially relevant information [...] also computes [...] information about our own awareness. [...] Awareness is [...] a perceptual model [...] a rich informational model that includes, among other computed properties, a spatial structure. [...] Through the use of the social perceptual machinery, we assign the property of awareness to a location within ourselves. (Graziano & Kastner 2011, pp. 98–99)

Related to social cognition, AS proposes that by using a schematic representation of the state of attention of other individuals—including a prediction of the spatial location of their focus of attention—we predict the current state of awareness of the individual, which is informative about their intentions and potential future actions. In short: Awareness of others is an attention schema. As compared to ES, AS is a relatively recent theory that requires extensive empirical studies. Yet the evidence so far shows that indeed the brain has a neural circuitry for monitoring the spatial configuration of one's own attention independent of the sensory modality (Downar et al. 2000), including the direction of gaze (Beck & Kastner 2009; Desimone &

Duncan 1995). These structures are the proposed neural expert system upon which AS is based and consist of the right-hemispheric temporo-parietal junction (TPJ) and superior temporal sulcus (STS) (see figure 1a in black). Notably, this expert system relevant to AS shows little anatomical overlap with the neural structures relevant to ES (figure 1a compare black with gray).

Because the AS relies on coding of the spatial relationship between the location of the observed individual and the likely spatial location of this individual's attention (i.e., independent of a particular sensory modality), the required spatial computations seem simple and straightforward. They require two points, i.e., the individual as a reference point and the potential spatial location of the attention of that individual. According to AS, using such spatial labeling the brain is able to simultaneously track the aware and attending minds of several individuals simultaneously. Thus, spatial coding in the context of AS appears to be less complex and less computationally demanding than spatial transformations underlying ES (see above).

Which of these seemingly distinct brain mechanisms proposed by AS and ES more plausibly underlies social cognition: the neural expert system decoding the state of attention according to AS or the mirror mechanism system decoding observed motor plans according to ES? It has been proposed that AS and ES may in principle work together. Graziano and Kastner propose that the expert system of AS may take a leading role by formulating a hypothesis about the state of awareness of an individual that is likely to drive further behavior and therefore provide a set of predictions based upon which motor resonance could more efficiently perform simulations (Graziano & Kastner 2011). Motor resonance would thus add richer detail to the state-of-attention hypothesis made by the expert system.

This combined mechanism is compatible with the predictive processing principle (Clark this collection; Hohwy 2013, this collection), which has been proposed relevant to the bodily self (Apps & Tsakiris 2013; Limanowski &
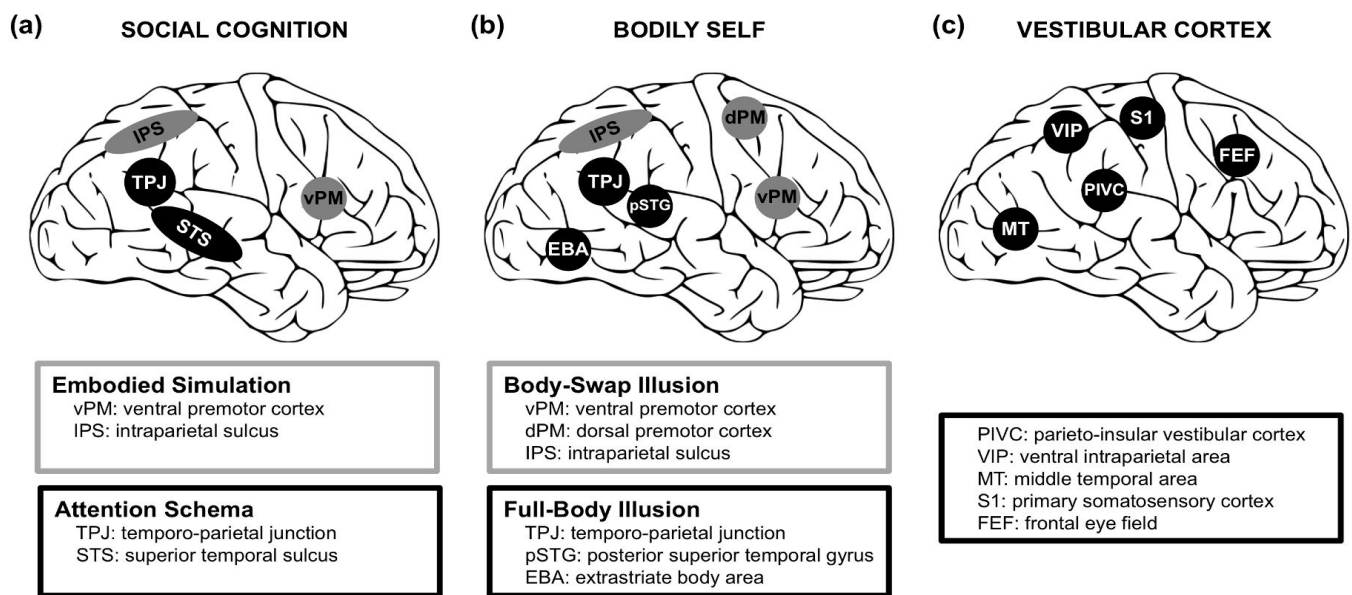
Figure 1: Summary of cortical brain regions involved in social cognition, the bodily self, and vestibular processing. (a) Whereas for social cognition there is little overlap between the brain regions proposed relevant for the attention schema (*in black*) and embodied simulation (*in gray*), both sets of brain regions overlap with (b) the brain network of the bodily self as identified by full-body illusion experiments manipulating self-location and first-person perspective (*in black*) and the body-swap illusion manipulating mainly body ownership (*in gray*). (c) The human vestibular cortical regions (*in black*) are widely distributed and overlap with several regions relevant to both the bodily self and social cognition. (The images are derived from images by NASA, licensed under creative commons.)

Blankenburg 2013; Seth this collection). According to *predictive processing* the brain constantly predicts the potential causes of sensory input by minimizing prediction errors via update of the predicted causes or by action that changes sensory input (Friston 2005). Applying the predictive processing principle to Graziano and Kastner's proposal that AS is a hypothesis-generating tool to which ES adds further detail, one could conceive of both mechanisms as different predictive processing modules aimed at anticipating the state of awareness and of intentional actions observed in others. Although no empirical study so far has addressed this specific hypothesis, a recent functional magnetic resonance imaging study found that predictive processing principles accounted for the blood oxygen-level dependent activity related to the perception of faces, which is an important perceptual function for social cognition in the human species (Apps & Tsakiris 2013).

These common and distinct predictions based on ES, AS, and predictive processing call for empirical research aimed at providing evidence to further refine, integrate, or reject them.

3 Multisensory and motor mechanisms of the multifaceted bodily self

The *bodily self* refers to the phenomenal experience of being an experiencing subject (i.e., a phenomenal self) bound to a physical body, which gives rise to the dual nature of the body (Husserl 1950; Gallese & Cuccio this collection, p. 2). The unified experience of being a bodily self can be decomposed into different aspects, including the experience that we identify with a particular body (self-identification or *body ownership*), the experience that the self is situated in a specific spatial location (*self-location*), that we take a specific experiential perspective at the world (*first-person perspective*), and that we are the authors of our actions, including having control of attentional focus (*agency*; (Blanke 2012; Ehrsson 2012; Jeannerod 2003; Metzinger 2003).

In their paper, Gallese & Cuccio highlight the relevance of mirror mechanisms, in particular related to processing in the cortical motor system, to the sense of body ownership and the sense of agency, in particular in the context of action and action observation:

> This minimal notion of the self, namely the bodily self as power-for-action […], tacitly presupposes ownership of an action-capable agentive entity; hence, it primarily rests upon the functionality of the motor system. (this collection, p. 10)

However, recent philosophy of mind and cognitive neuroscience research reveals the crucial role of *spatial aspects of the bodily self*, consisting of a first-person perspective and self-location. In this section I shall compare the brain network contributing to spatial aspects of the bodily self with the brain network underlying body ownership and ask: Do these neuroimaging results support the proposal that motor resonance is a primary mechanism underlying all aspects of the bodily self? What is the relationship between the neural networks of the bodily self and social cognition? Which functional associations can be derived from this?

3.1 Brain mechanisms of spatial aspects of the bodily self

The phenomenal experience of being a subject is associated with a spatial location, which typically is the space of the physical body (see also Alsmith & Longo 2014; Limanowski & Hecht 2011). However, there are exceptions to these prototypical states of the bodily self in neurological disorders and experimental illusions pointing to a specific set of brain regions involved in spatially linking the phenomenal self to the physical body.

Which brain mechanisms link the phenomenal self to the physical body to give rise to the dual nature of the body as lived body and as physical object? Research in neurological patients who have had out-of-body experiences (OBE) shows that damage or interference with the right TPJ can lead to dissociations between the bodily self and physical body (Blanke et al. 2004; Blanke et al. 2002; De Ridder et al. 2007; Ionta et al. 2011). During an OBE, patients typically experience a disembodied self-location in elevation above their physical body, and an altered first-person perspective that originates from an elevated location in the room and is directed downwards at the physical body (Blanke et al. 2004; Metzinger 2009). These patients do not identify with their physical body but with an illusory double outside of the borders of the physical body. At the phenomenological level, self-location and the first-person perspective are often experienced as having their spatial origin in the same position. However, during OBE there are instances where self-location can be dissociated from the first-person perspective in different sensory modalities (De Ridder et al. 2007). Further evidence from asomatic OBEs and bodiless dreams suggests that a phenomenal first-person perspective may be reducible to a single point in space (Windt 2010). In fact, vestibular hallucinations systematically preceded OBEs in patients with sleep paralysis, i.e., a motor paralysis characterised by the transient inability to execute bodily actions when waking up from sleep (Cheyne & Girard 2009), showing further dissociations of the spatial location of the bodily self and the physical body and links to sensory processing. These studies seem to suggest that the first-person perspective and self-location may depend on different neural mechanisms (Blanke 2012).

OBE in epileptic patients can be induced by subcortical electrical stimulation of a specific intensity at the TPJ. However, stimulating the same brain region with either lower or higher stimulation intensity induces bodily sensations (including vestibular, visual, somatosensory, kinesthetic sensations) without inducing an OBE (Blanke et al. 2002). These observations gave rise to the idea that the spatial aspects of the bodily self are based on the accurate integration of multisensory signals (i.e., which was perturbed by electrical stimulation in the patient in Blanke et al. 2002, which are sensory signals from personal space to sensory signals from the external environment Blanke et al. 2004).

These clinical observations in patients were corroborated by different full-body illusion experiments in healthy subjects, such as the so-called "body-swap illusion" (Petkova & Ehrsson 2008; Petkova et al. 2011; van der Hoort et al. 2011), the "full-body illusion" (Ionta et al. 2011; Lenggenhager et al. 2009; Lenggenhager 2007; Pfeiffer et al. 2013; Pfeiffer, Schmutz & Blanke 2014), and the "out-of-body illusion" (Ehrsson 2007; Guterstam & Ehrsson 2012). In these experiments, healthy subjects receive conflicting signals about the spatial location of their body and of the temporal synchrony of exteroceptive and interoceptive signals, including somatosensory, cardiac, and vestibular signals that at the same time are applied to a virtual or fake body seen by the subject (Aspell et al. 2013; Ionta et al. 2011; Pfeiffer et al. 2013; Pfeiffer et al. 2014). For example, in the *full-body illusion*, synchronous stroking of a virtual or fake body seen from a distance can induce the feeling in participants that they are more closely located to the position of the virtual or fake body, and that they experience and increase of ownership for the seen body. The brain regions involved in these spatial experimental manipulations of the experienced bodily self most consistently involve the right TPJ region, but also draw on somatosensory and visual regions that process the sensory inputs (Blanke 2012; Ionta et al. 2011; figure 1b in black). Recently, several studies have manipulated visual and vestibular signals about the direction of gravity, affecting self-location and perspective and thus showing that those visual spatial cues affect our subjective experience of the first-person perspective (Ionta et al. 2011; Pfeiffer et al. 2013). These authors presented images on virtual-reality goggles showing visual gravitational cues, similar to the visual perspective during an OBE showing a scene from an elevated spatial location and a visual viewpoint directed downwards into the room. At the same time the somatosensory and the vestibular signals received by the participant, who was lying on the back, suggested that the physical body was oriented upwards with respect to veridical gravity. Thus the visual gravity cues (i.e., downwards) and the vestibular gravity cues (i.e., upwards) were in directional

conflict. When the full-body illusion was induced under these conflicting conditions, participants reported subjective changes in their experienced direction of the first-person perspective (upward or downward) in line with experimentally-induced multisensory conflict (Ionta et al. 2011; Pfeiffer et al. 2013).

3.2 Brain mechanisms of body ownership

A different brain network encodes experimental manipulations of another aspect of the bodily self: body ownership. This was shown by the *body-swap illusion* (Petkova & Ehrsson 2008; Petkova et al. 2011), during which the participant views from a first-person visual viewpoint the body of a mannequin or another person. Thus no conflict between the visual spatial coordinates of the participant's physical body and the visually-perceived location of the mannequin is presented. However, conflicting sensory information about the shape, gender, size, or overall spatial context surrounding the virtual body were presented that typically prevented feeling ownership of the virtual body. If under these conditions visuo-tactile stroking on the abdomen of the participant and the virtual body was synchronously administered, an illusion of ownership for the body emerged, reflected in increased responses to threatening the mannequin. In different variants of the body-swap illusion subjects reported experiencing and adopting different sizes of both the virtual body and the contextual environment (Petkova & Ehrsson 2008; Petkova et al. 2011; van der Hoort et al. 2011). Neuroimaging experiments of the body-swap illusion show activation of the vPM and IPS regions, notably without involving actions made by subjects or performed by the virtual body (Petkova et al. 2011). These brain regions are key nodes of the mirror mechanism network of ES (see Serino et al. 2013). For a recent review see figure 1b.

3.3 A shared brain network of bodily self and social cognition

Although the neuroimaging evidence so far suggests that distinct brain regions encode the spa-

tial aspects of the bodily self and body ownership (Blanke 2012; Serino et al. 2013), the ensemble of those bodily self-encoding regions closely matches the brain regions relevant for social cognition (compare in figure 1a with figure 1b). These empirical data indeed suggest that the bodily self and social cognition are encoded by at least overlapping neural circuits supporting the proposal of ES that neural capacities to control and monitor the own body are used in understanding others.

These neuroimaging data suggest particular functional associations between different aspects of social cognition and the bodily self. In particular, the brain network of ES anatomically overlaps with regions encoding experimentally-induced changes in body ownership during the body-swap illusion (figure 1a–b in gray), which involves spatial congruence of the observational viewpoint and position of the fake body and the participant's body. A second association can be observed between the brain network of AS and the brain regions encoding spatial aspects of the bodily self, as manipulated during the full-body illusion (figure 1a–b in black). During the latter, the position and observational viewpoints of the virtual body and the participant's body are in spatial conflict, and thus closely resemble social interaction settings.

Based on these functional and neuroanatomical observations, I propose that ES seems to contribute to the bodily self and social cognition in a way primarily related to the sense of body ownership and agency. However, ES does not account for multisensory spatial representations that relate the physical body to the bodily self in space. These spatial aspects of the bodily self are encoded by brain regions outside of the brain network of ES, and rather resemble those brain regions relevant for coding the spatial configuration of attention (or awareness, according to AS).

Because two crucial aspects of the bodily self, i.e., self-location and the first-person perspective, are encoded in the TPJ region, and full-body illusions show that they can be manipulated without action or motor manipulations, it seems implausible that ES as based on

motor resonance is the primary brain mechanism underlying the bodily self. Instead, the brain networks coding self-location and the first-person perspective, which overlap with brain regions proposed to encode spatial aspects of an attention schema (see figure 1), seem to contribute to at least an equal degree to both the bodily self and social cognition. Thus, ES seems to be a necessary but insufficiently "primary" brain mechanism underlying the bodily self and social cognition.

I do not mean to imply that these are independent processes, because it is possible that they cooperatively work together (Graziano & Kastner 2011). However, I think that Gallese and Cuccio's claim of a primacy of motor resonance underlying the multifaceted aspects of the bodily self and social cognition is questionable on empirical and theoretical grounds.

4 Vestibular contributions to the bodily self and social cognition

In the previous sections I have provided theoretical considerations and empirical evidence assigning a critical role to multisensory spatial processing in the neural computations underlying representations of the bodily self and social cognition. This section will further examine the multisensory mechanisms relating the space of the bodily self to other individuals and the external world. I propose that important contributions to the brain's multisensory spatial coding might come from a particular sensory system, i.e., the vestibular system, which has often been neglected in studies of higher brain functions related to subjectivity and intersubjectivity. I will ask: What might be the functional contribution of the vestibular system to pre-reflective representations of the bodily self and social cognition? How does the human vestibular cortex relate to the neural networks of the bodily self and social cognition?

The *vestibular system* consists of sensory organs in the inner ear that sense accelerations of the head in space, including rotational and linear movement of the head and whole body and the constant acceleration of gravity on earth (Day & Fitzpatrick 2005). Vestibular sig-

nals are processed by subcortical and cortical structures (Angelaki & Cullen 2008; Cullen 2012; Lopez & Blanke 2011). Research initially focused on subcortical processing as related to gaze control, postural stabilization, and neural computations of head motion directions (Fernandez & Goldberg 1971; Goldberg & Fernandez 1971). More recently, studies have revealed the contribution of vestibular cortical processing to spatial cognition, body perception, and the bodily self (see Lenggenhager & Lopez this collection; Lopez & Blanke 2011; Pfeiffer et al. 2014 for reviews). These studies show that vestibular cortical processing is based on a neural network of distinct, distributed, and multisensory cortical regions. In distinction from any other sensory modality, there is no primary vestibular cortex that processes purely vestibular signals. Instead, a core vestibular cortical input region, the human parieto-insular vestibular cortex (PIVC; Lopez et al. 2012; zu Eulenburg et al. 2012), processes vestibular, somatosensory, and visual signals and is connected to a number of multisensory brain regions in the parietal, temporal, cingulate, and frontal regions (figure 1c).

The vestibular system contributes to spatial aspects of the bodily self. For instance, OBEs were associated with vestibular sensation, such as floating in elevation (Blanke et al. 2004; Blanke & Mohr 2005; Blanke et al. 2002), and vestibular sensations preceded OBEs in persons with sleep paralysis (Cheyne & Girard 2009). Other studies presented conflicting visual and vestibular signals about earth gravity during the full-body illusion and induced changes in the subjectively-experienced spatial direction of the first-person perspective and self-location (Ionta et al. 2011; Pfeiffer et al. 2013). Thus, it has been argued that vestibular cortical processing does not merely signal the motions of the own body and the external world, but is also constitutive of spatial aspects of the bodily self (Lopez et al. 2008; Pfeiffer et al. 2014).

Previously, Lopez et al. (2013), Deroualle & Lopez (2014), and Lenggenhager & Lopez (this collection) have argued that the vestibular system probably contributes to social cognition. I will briefly summarize their main ar-

guments and complement them with own points:

First, because the human species evolved under the steady influence of the earth's gravitational field, adaptation to gravity also framed and affected action, perception, and social interaction. More recently, research has shown that the brain hosts internal models of gravity, representing the effects of gravity on the motion of objects under the influence of gravity, of self-motion, of bodily actions, and of the direction of the gravitational acceleration. Those internal models of gravity strongly overlap with the vestibular cortex (Indovina et al. 2005; Indovina et al. 2013; McIntyre et al. 2001; Sciutti et al. 2012). More evidence for a vestibular contribution to social perception comes from studies showing the effects of gravitational signals on the perception of emotional faces (Thompson 1980) and the perception of the spatial orientation of bodies (Lopez et al. 2009).

Second, the vestibular system might contribute to social cognition because it detects head motions in space and hence directly enables us, when compared to other sensory signals, to discern movements made by our own body from motions of other individuals and motions of the external environment (Deroualle & Lopez 2014).

Third, mental spatial transformation of the own visual viewpoint to that of another person presents an important underlying cognitive aspect of social cognition (Furlanetto 2013; Hamilton 2009; Newen & Vogeley 2003; also cited by Gallese & Cuccio this collection, pp. 9–11). More direct evidence supporting this hypothesis comes from a recent study that showed that physical whole-body rotations, which stimulate the vestibular sensory organs, affected the ability of participants to perform mental spatial transformations (van Elk & Blanke 2013).

Fourth, I have argued in previous sections of this commentary that multisensory spatial coding is a critical prerequisite that underlies pre-reflective brain mechanisms of the bodily self and social cognition. Because the vestibular cortical processing has been strongly associated with multisensory integration (for review see Lopez & Blanke 2011), it is likely that vestibu-

lar signals shape multisensory spatial coding relevant to the bodily self and social cognition (Deroualle & Lopez 2014; Pfeiffer et al. 2014).

Fifth, the distributed multisensory vestibular cortical network clearly overlaps with the neural structures involved in social cognition and the bodily self, which suggests that there is a functional contribution on the part of vestibular processing to these phenomena (compare figure 1c to 1a and 1b; compare also to Deroualle & Lopez 2014).

Together, these five points suggest that the vestibular system may be a promising candidate for future studies of the sensorimotor mechanisms of social cognition, which should motivate research on the intersection of vestibular cortical processing, mirror mechanisms, and intersubjectivity. These studies may, for instance, question how vestibular stimulation affects our ability to reconstruct the process of attention of another person, a function critical in the AS framework. Although the vestibular system is related to reflexive motor control, it is not clear whether it also affects motor resonance (see Deroualle & Lopez 2014 for a related proposal). One might ask whether vestibular processing facilitates or inhibits motor resonance and our understanding of intentional action observed in others. How about vestibular contributions to theory of mind and reasoning? On the other hand, does social interaction modulate vestibular functions, such as self-motion perception, postural stabilization, and gaze control? These questions address the role of vestibular processing in functional mechanisms relevant to the AS and ES frameworks. Furthermore, empirical research addressing the causal relationship between the AS and ES brain mechanisms and the bodily self and social cognition are needed, for instance by brain lesion analysis or direct brain stimulation.

5 Conclusion

At the beginning of this paper I asked which brain mechanisms underlie pre-reflective representations of the bodily self and social cognition. ES, based on motor resonance, substantially contributes to the representation of the bodily

self and social cognition. However, a unified theory of the neural basis of these target phenomena cannot assign a primary role to motor resonance. I have argued that multisensory spatial coding is at least of equal importance and probably more basic than ES in contributing to several key aspects of the bodily self and social cognition.

Specifically, I have argued that:

(1) Social cognition and the bodily self depend on multisensory spatial coding, which is distinct from motor resonance. Thus, motor resonance may be a necessary but insufficiently "primary" brain mechanism of social cognition and the bodily self (cf. section 1, 2).

(2) The brain networks underlying social cognition and the bodily self largely overlap. Specific functional associations exist (a) between motor resonance and body ownership/agency and (b) between multisensory spatial coding and self-location/the first-person perspective (cf. section 2).

(3) The vestibular system, i.e., the sensory system encoding head motion and gravity, might provide unique information used for multisensory spatial coding that relates the bodily self to other individuals and the external world. This is further suggested by the large overlap existing between the human vestibular cortex and the brain networks underlying the bodily self and social cognition (cf. section 3).

A unifying theory of pre-reflective brain mechanisms of the bodily self and social cognition must be able to account for the empirical evidence reviewed here; and it seems that such a theory cannot exclusively depend on motor resonance. Multisensory spatial coding, motor mechanisms, but also representations of the process of attention appear highly relevant to bodily self and social cognition.

I agree with Gallese & Cuccio (this collection, pp. 3–7) that cognitive neuroscience cannot fully explore these exciting topics by limit-

ing itself to a specific neuroimaging method, such as functional magnetic resonance imaging. Instead, we should exploit multi-method approaches in search for correlative and causal evidence relating brain function and anatomy to the phenomenology of the bodily self and social cognition. The body, but also the spatial representation of the world around us, are relevant to understanding brain function, and when taken into account can lead to novel approaches to phenomenal analysis of subjective experience. But we should be careful in assigning priority to a single brain mechanism when aiming to explain the human self and intersubjectivity. Scrutiny and dialogue at the intersection of philosophy of mind and cognitive neuroscience are necessary in order to advance our understanding of the nature of the human mind.

Acknowledgments

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