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EMBODIED SIMULATION AND TOUCH: THE *SENSE* OF TOUCH IN SOCIAL COGNITION

abstract

This paper explores the sense of touch in relation to social cognition offering a new take on multisensory integration in the brain, within the framework of Embodied simulation (ES) theory. ES provides a new empirically based notion of intersubjectivity, viewed first and foremost as intercorporeality. In relation to touch, by means of ES we do not just "see" a sensation experienced by someone else and then understand it through an inference by analogy. By means of ES we can map others' sensations by re-using our own motor, somatosensory and viscero-motor representations. ES provides an original and unitary account of basic aspects of intersubjectivity, demonstrating how deeply our making sense of others' living and acting bodies is rooted in the power of re-using our own motor, somatosensory and viscero-motor resources.

keywords

Empathy, embodied simulation, mirror neurons, multisensory integration, social cognition, touch

EMBODIED SIMULATION AND TOUCH: THE SENSE OF TOUCH IN SOCIAL COGNITION

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1. Introduction

In our title "The *sense* of touch" the word 'sense' is written in italic to emphasize how the sensory modality of touch is crucially involved in the constitution of the sense we attribute to the world.

In his *The Visible and the Invisible* (1968) the French philosopher Merleau-Ponty wrote: "What there is then are not things firs identical with themselves, which would then offer themselves to the seer [...] – but something to which we could not be closer than by palpating it with our look, things we could not dream of seeing 'all naked' because the gaze itself envelopes them, clothes them with its own flesh" (p. 131). In this famous passage Merleau-Ponty notably emphasizes, on the one hand, the haptic quality of our gaze and, on the other, the intrinsic motor nature of our sensory explorations of the world. As aptly noted by Derrida (2005, p.143), Merleau-Ponty when writing about touch was influenced, beside Husserl, also by the French philosopher Maine de Biran (1766-1823) to whom he devoted a series of lectures in 1947-48.

Maine de Biran, whose philosophy challenged the standard *sensist* notion of the senses and consciousness as mere passive perceptions, emphasizing instead the central role of effort and motor will, indeed wrote: "It is only, therefore, as a motor organ that touch contributes essentially to putting the individual in communication with external nature; it is because it combines the two faculties in the most exact proportion that it is susceptible of such nice, such detailed, such persistent impressions; in short, it is in virtue of this that it opens a feeding ground for intellect and furnishes it with its more substantial nourishment" (1929, p. 61). And two pages later continues: "For that matter, we can apply to sight almost all that we have said of touch. In the natural state and in the ordinary exercise of the organ, the two functions – sensory and motor – correspond with and balance each other with no mutual disturbance" (ibid., p. 63).

As we show in the present article, Maine de Biran's words are not metaphors, since they envisage what cognitive neuroscience has demonstrated during the last two decades: the pervasiveness of multimodal integration in our brain and the crucial role of action and of the motor system in enabling multimodal sensory integration. The results of the empirical brain research we present here demonstrate how vision, touch and action are inextricably related, so that our visual perception of the tactile experience of others systematically leads to the activation of our motor and somatosensory systems. Before addressing these issues, however, we offer a brief overview of how the cortical somatosensory system is organized and how such organization relates to the notions of unimodality and multimodality.

2. The Somatosensory System and Multimodality

‘Tactile stimuli’, like a caress on our hand or a slap on our face, are indeed mechanical events occurring at the periphery of our body, where specialized neurons, called receptors, transduce mechanical energy into action potentials. Several pathways originating by somatosensory receptors variously distributed all over the body travel within the central nervous system and the third cranial nerve. After several relays at the level of the brainstem and of specific thalamic nuclei, they reach the neocortex. The human neocortex is traditionally subdivided in different, functionally and anatomically segregated regions. Behind the central sulcus sits the primary somatosensory area, also known as SI composed of 4 distinct cytoarchitectonic areas, Brodmann’s Area (BA) 3a, 3b, 1 and 2. The secondary somatosensory area, SII, is buried within the depth of the lateral sulcus. Both SI and SII receive the somatosensory-related thalamic inputs, and are traditionally considered to be unimodally related to the processing of somatosensory stimuli, like touch, proprioception, pain and temperature. As we show in the present article, this unimodal modular view doesn’t hold anymore.

Thus, sensory and motor circuits in the brain that directly guide the interactions between our body and the external world through action and perception also likely contribute to the conceptualization of what we observe in the world around us (Gallese and Lakoff 2005; Gallese and Sinigaglia 2011). In other words, they are supposed to neurally generate bodily formatted representational content about what we perceive in that world.

The body typified by the German philosopher Edmund Husserl as “a thing inserted between the rest of the material world and the subjective sphere” (1989, p.161), clearly accentuates the unique and central position of the *lived body* between the mental/subjective and the physical/objective (Husserl, 1989). Or, as put by Merleau-Ponty (1962), “I perceive with my body” (p. 326), “we are in the world through our body and in so far as we perceive the world with our body [...] perceiving as we do with our body, the body is a natural self and, as it were, the subject of perception” (p. 239). Consequently, the body overcomes the divide between the physical and the mental “if we introduce the phenomenal body beside the objective one, if we make a knowing body of it” (p. 278).

At the neural level, a necessary condition to meet for sensory and motor systems in order to serve our knowledge of the world is multimodality (e.g., Gallese and Lakoff 2005). That is, in order to entertain the capacity to generate knowledge, like knowledge about others' mental states and behaviors, neurons should respond to more than one modality. This view is completely different from the still dominant view in classic cognitive science, according to which our conceptual knowledge of the world is supported by amodal representations that result from abstract, symbolic computation (Fodor 1975, 1983). Traditionally, a clear distinction was made between modular structures for action and perception, and supramodal association areas linking different modality specific areas. However, accumulating empirical evidence suggests that sensory and motor systems are multimodal and directly linked systems, responding to and processing information associated with multiple modalities. Not coincidentally, the interactions of our body with the external world, including other living bodies, are actually multimodal. For instance, in the case of action, one could argue that action performance contains motor components as well as various perceptual contents, like vision (what does the action look like, what are the visuospatial characteristics of the object), sounds (what kind of sound accompanies a particular action), somatosensations (body-object interaction, proprioception) and localization in space. The same applies to ouch. In the following sections we show how the sensory modality of touch, both when subjectively experienced and when observed being experienced by others, relies on dynamic processes of multimodal integration, encompassing the activation of somatomotor and visceromotor cortical networks.

3.
Multimodal Processing in Sensory and Motor Systems

Empirical evidence consistently supports multimodal properties of sensory and motor systems as they appear not exclusively dedicated to inputs from a specific modality. By contrast, they rather tend to respond to more than one modality. Concerning somatosensory systems, a number of studies showed that tactile processing is not confined to somatosensory cortex, but that other brain regions, traditionaly thought to subserve sensory modalities other than touch, are indeed involved in somatosensory processing too. For instance, Bolognini et al. (2010) demonstrated by means of transcranial magnetic stimulation (TMS) that the cortical region of the superior temporal gyrus, generally considered an auditory modality-specific area, is involved not only in auditory processing, but also in temporal aspects of somatosensory processing. Furthermore, a functional magnetic resonance imaging (fMRI) study reported that also primary visual cortex responds to tactile input (Merabet et al. 2007). In addition, by using neural tracers, it was shown that the primary visual cortex of macaques receives both direct and indirect connections from auditory and somatosensory cortices, providing an anatomical basis for a highly integrative functioning among sensory systems (see Borra and Rockland 2011).

Likewise, also the motor system is endowed with multisensory properties. Several studies consistently showed that premotor and parietal areas contain neurons that perceptually respond to visual, auditory and somatosensory inputs (Fogassi et al. 1992, 1996; Gentilucci et al. 1983, 1988; Rizzolatti et al. 1988, 1997; Graziano et al. 1994, 1997, 1999).

A peculiar example in this context is ventral premotor area F4 in macaque monkeys' agranular frontal cortex (Matelli et al. 1985), part of a circuit that maps specific sensory events in the space near the body onto arm and head movements (Rizzolatti and Luppino 2001). A large proportion of F4 neurons has bimodal properties responding to both somatosensory and visual stimuli (Fogassi et al. 1996). Visual receptive fields of F4 neurons are mostly located in the space near the monkey (peripersonal space) and typically extend in the space adjacent to the tactile receptive fields of the same neurons.

Based on their somatocentered receptive fields (RFs), neurons in F4 are suggested to be involved in space perception. In particular, their RFs are anchored to a particular body part and when the body part is moved, the RF moves along with it (Fogassi et al. 1996; Graziano and Gross 1998). Hence, it has been proposed that area F4 could be involved in the integration of multisensory information from vision, touch and proprioception onto the motor representations of different body parts (Fogassi et al. 1996; Graziano 2001; Rizzolatti et al. 2002).

Several studies identified a putative human homologue of monkey area F4 in premotor cortex. With respect to its multisensory properties, Bremmer et al. (2001) demonstrated by means of fMRI that the ventral aspect of human premotor cortex responds to visual, auditory and tactile stimuli. More recently, a repetitive TMS study showed a specific disruption of audio-tactile interactions around the hand, showing the crucial role of human premotor cortex in the processing of multisensory stimuli within peripersonal space (Serino et al. 2011).

Beside providing evidence for multimodal processing in the sensory-motor system, these findings bear more general significance. Let's ask the following question: how do premotor F4 neurons "perceptually" work? A likely and intriguing answer to this question is, by means of embodied simulation. That is, perceiving an object or event through one of the senses at a given location within peripersonal space evokes the motor simulation of the most appropriate actions towards that very same spatial location (Rizzolatti et al. 1997; Gallese 2005).

The embodied simulation hypothesis is supported by the fact that F4 neurons discharge not only when an object is present in the peripersonal space, but also when the monkey *believes* the object is still present, while the object has been removed without the knowledge of the monkey (Graziano et al. 1997). Thus, space representation in the premotor cortex can be generated not only as a consequence of an external, multisensory stimulation, but also internally on the basis of previous experience.

4. Mirror Mechanisms and Embodied Simulation

Although the recognition of the contribution of first-person bodily experiences to consciousness and knowledge can be traced back in modern times to the philosophical school of phenomenology (e.g., Edmund Husserl, Merleau-Ponty), or to 19th century psychology (e.g., William James), it is mainly since the discovery of mirror neurons in area F5 within the ventral premotor cortex of macaque monkeys (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996) that the idea of understanding the world around us in terms of the way we function with our bodies in that world gained wide attention in neuroscience. Neurons in premotor area F5 are known to code goal-related motor acts, like hand and mouth grasping. Surprisingly, many of these neurons (called, mirror neurons) were found to be activated not only when the monkey performed a particular object-related action, but also when the monkey observed someone else performing the same action. Neurons with similar mirror properties were later on also found in regions of the inferior parietal lobe reciprocally connected with area F5 (Fogassi et al. 2005; Petrides & Pandya 1984; Rozzi et al. 2006).

In accordance with these findings in monkeys, a similar mirror mechanism mapping action perception on motor representations of the observer's brain was revealed in humans by many studies through different methodologies, including fMRI, PET, MEG, EEG, TMS (Rizzolatti et al. 1996; see for reviews Rizzolatti and Sinigaglia 2010; Rizzolatti and Craighero 2004; Gallese and Sinigaglia 2011). It was proposed that the mirror mechanism might underpin basic aspects of social cognition and empathy (Gallese 2003; Gallese et al. 2004) on the basis of its documanted involvement in the understanding of action goals (Umiltà et al. 2001, 2008; Rizzolatti and Sinigaglia 2007; Gazzola et al. 2007) and basic motor intentions (Iacoboni et al. 2005; Fogassi et al. 2005), with behaviors like imitation (Iacoboni et al. 1999; Rizzolatti et al. 2001), complementary actions (Newman-Norlund et al. 2007) and with the semantics of action-related words and sentences (Hauk et al. 2004; Tettamanti et al. 2005; Aziz-Zadeh et al. 2006; Pulvermuller et al. 2005).

The multisensory properties of mirror neurons are highlighted by studies showing that they not only respond to visual input, but also to the sounds of specific actions (Kohler et al. 2002; Keysers et al. 2003; Gazzola et al. 2006). The relevance of this discovery is that it allows a direct mapping of the perception of an action onto the perceiver's motor representation of the same action. The sensory representation of another's action is mapped onto one's own motor representation of the same action (e.g., Rizzolatti et al. 2001). In other words, one's own motor knowledge is used to understand the action of another agent by means of embodied simulation (see Gallese 2003 2005; Gallese and Sinigaglia 2011).

Probably, mirror neurons for action are just the tip of the iceberg, representing one specific aspect of a more general mirror mechanism (MM) that uses bodily formatted representations of goals, emotions, body states and sensations to map the same states in other individuals (Goldman and Gallese 2000; Gallese 2003, 2005; Gallese et al. 2004; Gallese and Sinigaglia 2011). Indeed, empirical evidence from numerous neurophysiological, neuroimaging and behavioral studies confirmed this initial hypothesis that a similar mirror mechanism could be applied to the social perception of other mental states and bodily experiences as well (see Keysers and Gazzola 2009; Gallese and Sinigaglia 2011).

By using different techniques and methodologies, a vast series of studies corroborates this conclusion by showing that the same cortical regions underlying the first-person experience of emotions and sensations are also activated when witnessing others' emotions (Carr et al. 2003; Wicker et al. 2003; Leslie et al. 2004; Pfeifer et al. 2008) and sensations, like touch (see Keysers et al., 2010), pain (Hutchison et al. 1999; Morrison et al. 2004; Singer et al. 2004; Botvinick et al. 2005; Jackson et al. 2005; Avenanti et al. 2005) and pleasant touch (McCabe et al. 2008).

The theory of embodied simulation (Gallese 2003, 2005; Gallese and Sinigaglia 2011) provides a unified theoretical framework for all of these phenomena. It proposes that our social perceptions become meaningful by means of re-using our own mental states or processes in functionally attributing them to others. Here, we refer to simulation as an automatic, unconscious, pre-reflective mechanism of the brain-body system, whose function is to model, objects, agents and events, and which is triggered by perception (Gallese 2005), although is plastically modulated by contextual, cognitive and personal identity-related factors. This neurobiological perspective on the notion of simulation holds that the same neural structures involved in our own bodily self-experiences are also involved with the pre-reflective understanding of the behaviors and of some mental states of other individuals.

5. Tactile Sociality

The tactile dimension, i.e., touch, plays a peculiar role in our interaction with the external world. The sense of touch is the first to develop before all other senses, and is the most important sense allowing infants to initially learn about their inanimate and animate environment, and their bonds with it. Concerning the animate world, touch plays a pivotal role in social interactions subserving a nonverbal communication of intentions and affect through somatosensory stimulation of another individual. In contrast to the other senses, it is present all over the body. Moreover, it is crucial for the awareness of our own body in relationship with the external world based on both external perceptions (i.e., touch) and internal perceptions (i.e., proprioception). As posited by Edmund Husserl, everything we see, we also see it as a tactile object, as something directly related to the *lived body*, and not just by virtue of its visibility (Husserl 1989).

A substantial amount of studies points to manifold functions accommodated by the somatosensory system. For example, Zhou and Fuster (2000) found that monkeys' SI neurons responded also to visual stimuli, if these were previously associated with tactile experiences. A very recent study revealed within macaque monkeys' area SII the presence of purely motor, hand grasping-related neurons (Ishida et al. 2013). Since lesion of SII produces tactile agnosia (Caselli 1991; Reed and Caselli 1994, 1996), that is, the inability to recognize objects by means of their haptic exploration (Valenza et al. 2001), these newly discovered neurons might likely provide the somato-motor binding principle enabling the translation of diachronic somatosensory inputs fed by peripheral receptors into a coherent image of the explored object. Indeed, the German philosopher Hans Jonas (1973) posited that tactile qualities like roughness and smoothness, in order to be experienced, require a series of dynamic somatosensory sensations obtained by means of friction and pressure of the fingers, that is, by means of movement.

Moreover, if we move to the domain of social cognition, a series of fMRI studies demonstrated activation of a shared neural circuitry in primary (SI) and secondary (SII) somatosensory cortices, which is normally involved in our experience of touch, during the observation of another person being touched (Keysers et al. 2004; Blakemore et al. 2005; Ebisch et al. 2008, 2011; Schaefer et al. 2009; Meyer et al. 2011; Kuehn et al. 2012, 2013). The involvement of somatosensory cortex in touch observation was subsequently replicated by means of somatosensory-evoked potentials (Bufalari et al. 2007), magnetoencephalography (Pikho et al. 2010) as well as TMS and lesion studies (Bolognini et al. 2011, 2012; Rossetti et al. 2012). Whereas MEG provides a more direct, but still correlational measure of neural activity related to a given function at a high temporal resolution, TMS and lesion data suggest a causal role of brain regions in specific functions.

Keysers et al. (2004) additionally demonstrated that activation of this shared mechanism for touch in SII also occurred for the sight of an object being touched. Thus, in order to activate a shared neural circuitry for touch by vision, it does not matter what is being touched (animate or inanimate) as long as touch occurs. In accordance with the latter finding, action observation studies consistently show somatosensory activation when witnessing bodies interacting with objects (Gazzola et al. 2009; Ramsay et al. 2011; Turella et al. 2012).

Although not systematically investigated, psychological evidence supports a role of mental simulation also in the predictive coding of others' peripheral sensations (Bosbach et al. 2005). Neuroimaging studies suggested that predicting the consequences of observed object-directed actions involves the somatosensory cortex (Ramsey et al. 2011; Morrison et al. 2012). Further studies using fMRI showed that SI is activated both when participants view a hand being stimulated by an object as well as when an object is moving in the space close to the hand, but not when moving far from the hand (Schaefer et al. 2012). One independent set of data further support the notion that predictive responses of multimodal somatosensory-related areas map the augmented probability for touch to occur for movements within others' peripersonal space, on the basis of embodied simulation. Indeed, single neurons recordings in macaque monkeys showed that parietal area 7b and the ventral intraparietal area (VIP), contain visuo-tactile neurons that respond both to visual stimuli moved within monkeys' peripersonal space, approaching tacile RFs on the monkey's body and to the observation of similar stimuli approaching equivalent parts of the experimenter's body (Ishida et al. 2010).

In another fMRI study, when directly contrasting the observation of animate and inanimate touch, stronger SI responses were detected by fMRI for the sight of intentional, animate touch, compared to accidental, inanimate touch (Ebisch et al. 2008). The intensity of neural activation in this area significantly correlated with the degree of intentionality of the observed touching stimuli as rated by participants, even when intentionality only was assumed by the observer. This finding suggests that SI, in addition to simulation of others' tactile experiences, could also be involved in the simulation of the proprioceptive aspects related to the act of touching. Indeed, Brodmann's area 2 in SI has been associated with proprioceptive functions, in addition to tactile perception (Gardner and Kandel, 2000).

With respect to more affective aspects of social perception, somatosensory cortex function has also been linked to empathic ability (Zaki et al. 2009; Schaefer et al. 2012) or the recognition of emotional expressions (Adolphs et al. 2000; Pitcher et al. 2008). Few studies reported modulation of the activation either of SI (Bufalari et al. 2007; Bolognini et al. 2013) or of posterior SII (Ebisch et al. 2011) by the affective valence or intensity of observed social touch.

Finally, few studies further supported the hypothesis that embodied simulation processes in somatosensory cortex contribute to the conceptualization of our perceptions in the external world, even in the absence of animate involvement. Ebisch et al. (2008) showed that an automatic tendency to activate brain areas involved in the processing of our own experience of touch applies to the observation of any touch. Specifically, SII activation occurred independently of whether the observed touch was intentional or accidental, and independent of whether an observed touched object was animate or inanimate. This may suggest that embodied simulation principles apply to the understanding of more abstract events, too (see Keysers et al. 2004; Gallese 2005; Ebisch et al. 2008). Accordingly, an fMRI study by Lacey et al. (2012) provided evidence for activation in somatosensory cortex associated with the processing of metaphors from the domain of texture, suggesting that comprehension of metaphors could be perceptually grounded by means of embodied simulation in sensory systems. These findings therefore support the activation of an ‘‘abstract’’ notion of touch in somatosensory cortices, building on the neural mechanisms for interpreting actual touch even for inanimate contact and metaphors, where abstraction is the likely prelinguistic outcome of a multimodal integration mechanism (see Lakoff and Gallese 2005; Gallese 2008). It is worth noting that already in the XVIII century the Italian philospher Gianbattista Vico wrote that “...n’tutte le lingue la maggior parte dell’espressioni d’intorno a cose inanimate son fatte con trasporti del corpo umano e delle sue parti e degli umani sensi e dell’umane passioni” (1725-1744, p. 284).[1]

Thus, although the somatosensory system is obviously endowed with tactile properties (e.g., Kaas 1983; Ferretti et al. 2003), the data here concisely reviewed suggest that its functions extend well beyond its classic role in the personal

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[1] “Thus we discover the important principle that every language, no matter how copious and learned, encounters the hard necessity of expressing spiritual things by means of relationships with corporeal things.”

perception of somatic sensations. Regarding the social domain, a somatosensory mirror mechanism may allow individuals to map others' bodily experiences on their own bodily formatted somatosensory representations. In other words, by exploiting the same neural circuits as those recruited for first-person bodily experiences, a direct inter-subjective link is established between self and other allowing an experiential understanding of others bodily feelings (Gallese 2003).

6. Self Versus Other in (Tactile) Social Perception

Although a vast amount of empirical studies shows that neural circuits allowing first-person bodily experiences contribute to the understanding of similar experiences in other individuals (Keysers and Gazzola 2009; Gallese 2003, 2005), an intriguing, but poorly investigated issue remains how a self-other distinction is established. In addition to the importance of a pre-reflective, experiential understanding of others' by re-using our own mental states and processes, one could argue that it would be equally crucial to discriminate to whom these feelings and experiences belong (e.g., Banissy et al. 2009; Eisenberg et al. 1989; Batson et al. 1987). In other words, in functional empathic experiences, there is no complete overlap between one's own and others' mental states. Others' experiences, which are empathically shared, nevertheless are experienced as belonging to the other.

From a phenomenological perspective, such self-other discrimination is considered constitutive for the perception and understanding of others' behavior and mental states, a crucial aspect of empathy. For instance, Edith Stein (1989) defined **empathy as "the experience of foreign** consciousness in general" (p. 11). Here, she not solely emphasized the experiential aspect of empathy, like an intersubjective sharing of the experiences of others as similar to us, but she also emphasized the preservation of otherness. As stated by Stein (1989), "the subject of empathizing is not the subject empathizing, but another, a foreign mind" (p.10) and so "the experience of foreign consciousness can only be the non-primordial experience which announces a primordial one" (p. 14). Thus, unlike our own experiences, which are primordially given, empathy does not have this primordiality. As further emphasized by Zahavi (2010, 2001), it is because of this asymmetry, that the minds we experience are experienced as *other minds*. Also according to Husserl, "had one had the same access to the other's consciousness as to one's own, the other would have ceased being another, and would instead have become a part of oneself" (Husserl 1973, p. 139, transl. Zahavi 2010). Thus, empathy does not consist of experiencing the other's behaviors and mental states in the same way as the other does. Others' mental states are essentially experienced as belonging to a foreign mind, without being in the same state as the other. In other words, we do not necessarily experience the specific contents of others' (tactile) experiences, but experience others as having (tactile) experiences similar to ours.

How can this self-other discrimination be reconciled with an empathic sharing of others' states based on vicarious brain activity in the sensory-motor system and be translated into brain function? Part of the answer can be found in the intensity of vicarious activity. Blakemore and colleagues (2005) investigated by means of fMRI scanning brain activation for the observation of touch in a case of vision-touch synaesthesia, that is, a person for whom the observation of another person being touched is experienced as tactile stimulation on the equivalent part of her own body. The sensory-motor system including somatosensory cortex, premotor cortex and anterior insula, responsible for first-person tactile experiences, showed stronger activation for the vision of touch in the case of vision-touch synaesthesia, compared to participants not affected by this condition. This led the authors to conclude that an abnormal intensity of vicarious activation may lead to the actual experience of first-person bodily experiences, even though not primordially given.

Furthermore, it has been proposed that the extent of vicarious activity could contribute to the distinction between self and other as well. Usually, there is no complete overlap between first-person tactile experiences and the observation of similar experiences in other individuals. Studies showed that witnessing others being touched only activated part of somatosensory cortex that is activated when actually experiencing touch (Keysers et al. 2010). In particular, neuroimaging studies reviewed by Keysers et al. (2010) show vicarious activation in SII as well as in BA 1 and 2 (part of SI), while BA 3 seems to be reserved for processing tactile perceptions of one's own body. The absence of vicarious activation in certain regions of primary sensory cortex could be co-responsible for the absence of real bodily perceptions when just witnessing them in others.

Finally, this issue was recently more specifically addressed by means of fMRI (Ebisch et al. 2011). In this study, healthy participants watched other individuals being touched on their hands in different ways and, at the end of the experiment, were touched on their hands themselves. The results demonstrated overlapping activation for the experience and observation of touch in several sensory-motor regions, including SII and premotor cortex. However, differential activation was found for the experience and observation of touch in the posterior insular cortex (pIC). Specifically, neural activation in pIC was positively modulated when participants were touched themselves, but negatively modulated (i.e., suppressed compared to baseline) when they observed social-affective touch in other individuals. pIC is considered central to interoceptive functions (Craig 2002). Anatomically, thalamo-cortical pathways that provide afferent information to pIC, and interactions with limbic, somatosensory and motor regions could be at the basis of the role of pIC in the awareness of bodily feelings, including threatening or comforting information from the skin (Augustine 1996; Saper 2002; Critchley 2005; Craig 2009; Olausson et al. 2002; Loken et al. 2009).

In accordance with the idea of pIC as a central cortical node in a system constituting a neural representation of 'the material me' (Craig 2002), a series of studies also show that pIC contributes to self-awareness. Tsakiris et al. (2007) found a relationship between neural activation in pIC and the subjective experience of the rubber hand illusion (RHI: a condition in which an observed rubber hand synchronously stroked with participants' unseen hand is subjectively experienced as if it actually were one's own hand).

In line with the proposed pIC function in the awareness of the physiological state of the body, a close link between the awareness of the physical and the physiological self was suggested during the RHI (Moseley et al. 2008). pIC has further been related to the awareness of body parts in anosognosia patients with hemiplegia/hemiparesis (Karnath et al. 2005), and to the sense of agency (Farrer et al. 2003).

Taking into account the view of pIC as a brain region crucially involved with body-related feelings and body awareness, the opposite activation pattern we reported for the experience and observation of touch in pIC (Ebisch et al. 2011) could reflect its role in the differentiation between self and other tactile conditions. Such a function is further corroborated by a recent lesion study investigating the neural basis of illusory own-body perceptions (Heydrich and Blanke 2013). Specifically, heautoscopy, a condition associated with the visual perception of a second own body, a strong self-identification with that second own body, and the experience of existing at and perceiving the world from two places at the same time, could be related to lesions in left pIC. Importantly, autoscopic hallucinations where a second own body is seen without any changes in bodily self-consciousness, are related to lesions in right occipital cortex, but not in pIC.

7.
Conclusions

On the basis of the evidence summarized in this article, it can be proposed that the pre-reflective side of (tactile) social perception as captured by the theory of embodied simulation and by phenomenology may emerge as a rather multifaceted function that relies on a dynamic interaction between, on the one hand, embodied simulation processes within shared neural networks grounding an implicit understanding of others' behaviors and mental states (Gallese, Keysers, and Rizzolatti, 2004; Gallese 2003), and, on the other, processes allowing one to maintain a coherent and unique sense of self, comprising self-other discrimination (Ebisch et al. 2011, 2012; de Waal, 2008; Cheng et al. 2007; Lamm et al. 2007; Batson et al. 1987). According to this perspective, identity and alterity – together with reciprocity – are necessary and intertwined dimensions of intersubjectivity.

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