

The body in the brain revisited

Giovanni Berlucchi · Salvatore M. Aglioti

Received: 2 July 2009 / Accepted: 24 July 2009 / Published online: 19 August 2009
© Springer-Verlag 2009

Abstract Corporeal awareness is a difficult concept which refers to perception, knowledge and evaluation of one's own body as well as of other bodies. We discuss here some controversies regarding the significance of the concepts of body schema and body image, as variously entertained by different authors, for the understanding of corporeal awareness, and consider some newly proposed alternatives. We describe some recent discoveries of cortical areas specialized for the processing of bodily forms and bodily actions, as revealed by neuroimaging, neurophysiological, and lesion studies. We further describe new empirical and theoretical evidence for the importance of interoception, in addition to exteroception and proprioception, for corporeal awareness, and discuss how itch, a typical interoceptive input, has been wrongly excluded from the classic concept of the proprioceptive–tactile body schema. Finally, we consider the role of the insular cortex as the terminal cortical station of interoception and other bodily signals, along with Craig's proposal that the human insular cortex sets our species apart from other species by supporting consciousness of the body and the self. We conclude that corporeal awareness depends on the

spatiotemporally distributed activity of many bodies in the brain, none of which is isomorphic with the actual body.

Keywords Body schema · Body image · Corporeal awareness · Extrastriate body area · Insula · Itch

Introduction

Awareness of one's own body is a very special form of cognition, and the scientific study of its experiential components and physiological underpinnings is fraught with considerable theoretical and practical difficulties. From a neuroscientific perspective one can assume that the problem boils down to understanding what kind of messages the brain receives from the rest of the body, and how such messages are integrated by appropriate cerebral mechanisms into organized experiences of one's body and oneself. However, such mechanisms and experiences are also likely to be involved in the ability to perceive and know the structure and movements of the bodies of other individuals, in order to understand their actions and to interpret their gestures for social communication. One can thus postulate the existence of a cognitive category for the human body whose components include one's own body as well as the bodies of other humans.

Nearly a century ago the British neurologists Head and Holmes (1911/12) attempted to tackle the basic problem of how the brain processes its own body by emphasizing the primary role of proprioception and touch, and by proposing one body schema for the appreciation of posture or passive movement and another body schema for the localization of stimulated spots on the skin. In their conception, schemas or schemata are instant-by-instant proprioceptive and surface

G. Berlucchi
National Institute of Neuroscience-Italy,
University of Verona, Verona, Italy

G. Berlucchi (✉)
Department of Neural and Visual Sciences, Physiology Section,
University of Verona, Strada Le Grazie 8, 37134 Verona, Italy
e-mail: giovanni.berlucchi@univr.it

S. M. Aglioti
Department of Psychology and Study Center for Mental
Functions, La Sapienza University of Rome and Santa Lucia
Foundation, IRCCS, Rome, Italy

“plastic models of oneself” against which all subsequent changes in posture, movement and tactile stimulation can be measured. Against this view another British neurologist, Macdonald Critchley (1979), addressed the justifiable complaint that the “not very clear language” of Head and Holmes “had opened a Pandora’s box which let loose a spate of metaphysics, much of it sheer verbiage... Terminology blossomed so that terms like “body image”, “body schema”, “corporeal schema”, “*image de soi*” were employed more or less interchangeably. It soon became obvious that thinking was becoming so muddled that the various expressions were made to stand in the literature for different ideas at different times by different writers. At one moment the idea was perceptual; at another it was a conceptual one. Part of the trouble was due to a lack of clear definition, the one put forward by Head and Holmes being more elucidatory than hermeneutic.... Clearly an all-embracing term is needed, one which combines conceptual with the more tangible perceptual components” (Critchley 1979).

Twelve years ago, in writing about the body in the brain, and realizing that the “chaotic state of affairs” and the confusion of terms lamented by Critchley had by no means dissolved, we adopted his all-embracing term of corporeal or body awareness, with the addition of emotional and affective components to the more obvious perceptual and conceptual ones (Berlucchi and Aglioti 1997). We felt that a discussion of body knowledge as a unitary mental category could help the analysis and description of the available scientific evidence, in correspondence with Melzack’s notion of a neuromatrix, a distributed but functionally integrated brain system that acts as a whole and produces a feeling of the body as a unity, though with different qualities at different times (Melzack 2005). Perhaps it was unwise of us to use the terms “body schema” and “body image” as interchangeable and as more or less synonymous of body awareness, in order to avoid too many repetitions of the latter term. Nevertheless it remains true in 2009 as it was in 1997 and in many previous years that repeated attempts to fractionate body awareness into different cognitive components have largely failed to arrive at universally accepted conceptions and definitions. In particular, the terms body schema and body image continue to be used by different authors in different manners, sometimes even with opposite meanings (for recent publications see Paillard 1999; Graziano and Botvinik 2001; Reed 2002; Holmes and Spence 2004, 2006; Haggard and Wolpert 2005; Gallagher 2005; de Vignemont 2007; Giummarra et al. 2008; Mayer et al. 2008). It is not our aim to review here the various positions in detail, but rather to point to some weaknesses of some of them, as well as to try and relate findings from the rapidly growing literature on various brain–body interactions in humans to some of the proposed neurocognitive operations for the processing of one’s own body and other bodies.

Body schema versus body image in body processing and other dichotomies

Supporters of a dichotomous distinction between body image and body schema have endeavoured to furnish a neural basis to it by referring to more general neurocognitive dichotomies and by exploiting double dissociations in clinical deficits following neurological lesions. Two of the most systematic attempts along these lines are those of Paillard (1999) and Gallagher (2005). By defining the body schema as a sensorimotor map of the body space mainly based on proprioception, and the body image as a pictorial description of the body based on a mainly visual exteroception, Paillard (1999) has linked this body schema/image dichotomy with two interrelated anatomo-functional dichotomies: the what–where dichotomy of Ungerleider and Mishkin (1982), which sets apart object perception and spatial localization, and Milner and Goodale’s dichotomy between vision-for-perception and vision-for-action (Milner and Goodale 1995). Gallagher (2005) has similarly advocated a principle distinction between a body schema, conceived as a system of postural and sensory–motor capacities that usually functions without perceptual monitoring, and a body image broadly envisaged as a system of perceptions, attitudes and beliefs pertaining to one’s own body. The body schema would be involved in action and interaction with the environment, with the body providing the material perspective on the outside world, whereas the body image would be involved in the sense of body ownership and self-consciousness. According to both Paillard (1999) and Gallagher (2005), one’s body image is present to consciousness, whereas the body schema is usually not, although inputs from the body schema to the body image can affect spatial perception, the perception of objects and intentional action. In Gallagher’s words (2005), “preoietic performances of the body schema...operate as constraining and enabling factors that limit and define the possibilities of intentional consciousness”.

Both Paillard (1999) and Gallagher (2005) assume that the dichotomy between body schema and body image, as defined above, is justified by evidence of double dissociations in patients with neurological lesions. After a left parietal infarct, one of Paillard’s patient had a complete sensory paralysis of her right hand, yet when blindfolded she could touch with the left hand the precise spot which had been touched by the examiner on the insensible hand, in spite of verbally denying any corresponding sensation. This is an instance of blind touch (Paillard et al. 1983), so called by analogy with Weiskrantz’s blindsight (Weiskrantz 2009). Another patient deprived of proprioception and fine touch in the four limbs by a large-fibre peripheral neuropathy could consciously identify body parts touched out of sight, but could not point to them unless aided by vision. Paillard (1999) attributed the performance of the first case

to disruption of the body image (the what/conscious perception system) and preservation of the body schema (the where/unconscious action system), and the performance of the second case to disruption of the body schema and preservation of the body image.

Gallagher (2005) has described a similar double dissociation between hemineglect patients and a patient without proprioception below the neck because of a large-fibre peripheral neuropathy. Some hemineglect patients appear to expunge their left limbs from their body boundaries, but in absence of paralysis they can use those limbs proficiently in motor behaviour and bilateral coordination, presumably because of an intact body schema. In contrast, and in accord with Paillard (1999), patients without proprioception appear to suffer from a faulty body schema and to depend on a mainly visual body image plus attention for making goal-directed movements. Such movements are slow and inefficient compared to those normally controlled by the body schema in an automatic and unattended manner (Gallagher 2005).

These dissociations can be summarized by stating that body schema is generally for unconscious action, and body image is generally for perception and conscious action. Dijkerman and de Haan (see 2007 and related commentaries) have recently supported and qualified such distinction by proposing that somatosensory processing is carried out by two at least partly divided anatomical and functional systems, in analogy with the two-system visual processing proposed by Milner and Goodale (1995). According to them, the somatosensory system responsible for the immediate guidance of action has its main terminal in the posterior parietal cortex, whereas the somatosensory system responsible for conscious perception and memory has its main terminal in the insula. However, neuronal components of the posterior parietal cortex, possibly distinct from those guiding action, would also be involved in conscious somatosensory perception, and in particular in high-level visuo-spatial and semantic internal representations of the body. Dijkerman and de Haan (2007) also reiterate the distinction between a body schema for action and a body image for perception by referring to a double dissociation in somatosensory processing recently published in extenso by Anema et al. (2009). Two patients with lateralized central stroke lesions, one in the thalamus and the other in the supply area of the middle cerebral artery, showed an intact tactile detection, along with deficits in tactile localization which differed between the two patients. One patient was poor at identifying on a line drawing of a hand the position of a tactile stimulus delivered to his hand, but could accurately point to the actual stimulated position. The reverse pattern was observed in the other patient. Anema et al. (2009) attribute the performance of the former patient to preservation of the body

schema and disturbance of the body image, and the performance of the latter patient to preservation of the body image and disturbance of the body schema. However, both patients could perform at some level of efficiency the task on which they were impaired, and in each patient the differences in performance between the two tasks, though significant, were quite small. In addition, the lesion was in the left hemisphere in one patient and in the right hemisphere in the other, so that the double dissociation might have been caused by some interhemispheric difference in the performance of the tasks that was independent of body processing.

Itch and the body schema

The sensory information underlying the body schema concept originally proposed by Head and Holmes (1911/12) is essentially limited to proprioception, that is to postural and kinaesthetic information, and to localized tactile information. These kinds of information are carried by the relatively large afferent fibres belonging to the dorsal column–medial lemniscus system, which are selectively damaged in some patients with peripheral neuropathies and a lack of a body schema according to Paillard (1999) and Gallagher (2005). But these same patients still possess intact small-fibre afferent systems from the body which subserve pain, itch, thermoception and certain kinds of touch. For example, selective activation of a system of unmyelinated fibres from the hairy skin by light mechanical stimuli can evoke sensations of pleasant or sensual touch (Löken et al. 2009), in keeping with the role played by this afferent system in behaviours, such as grooming, search for affective bodily contacts and parental care in non-human primates (Craig 2009).

The concept of the body schema as an exclusively postural, kinaesthetic and tactile basis for action disregards the potential participation of the small-fibre afferent systems to action control, and particularly to actions directed towards the body. Bermúdez (2009) has pointed out that just like actions aimed at extracorporeal objects, actions aimed at the body are made possible by current information about the relative positions of different body parts. Such afferent information can include itch and pain, which are subserved by small-fibre afferent systems and can evoke adapted body-directed actions, such as scratching the itching body part or removing an irritating stimulus from a skin area. The basic neural machinery for these movements is laid down in the reflex circuits of the spinal cord, and voluntary execution of scratching and nocifensive actions in response to the appropriate bodily sensations is basically a release of such adapted reflexes (Sherrington 1906). Neuroimaging studies have identified activations of limbic structures (anterior cingulate and insular cortex) and

ventral prefrontal cortex during experimentally induced itch sensations and as a result of the consequent motivation to relieve such sensations by scratching (Leknes et al. 2007).

In his *Phénoménologie de la Perception*, Merleau-Ponty (1945) reported that the famous brain-damaged patient Schneider of Gelb and Goldstein (see Goldenberg 2002), who suffered from several cognitive disorders, including an absence of the classic body schema, could not localize a tactile stimulus on his body but could promptly move his hand to the skin site of a mosquito sting. As mentioned, patients with large-fibre peripheral neuropathies and absent proprioception and fine touch can still receive information about localized itch and pain stimuli through intact small-fibre afferent systems. Arguably, their ability to scratch an itching body part, if any, would demonstrate the existence of a body schema for action which is independent of the classic, postural-tactile body schema. Although clinical and experimental evidence on this point is quite meagre, an unpublished result of great interest has been obtained in a test on one patient with an extensive peripheral large-fibre deafferentation below C3 (H. Olausson, Personal Communication). This patient (IW), described by Gallagher (2005) as an emblematic case without a body schema and a partial and imperfect substitution of a body image for the missing body schema, has been studied with neuroimaging techniques by Olausson et al. (2008a, b). In an unpublished experiment, IW felt itch when histamine was applied by means of iontophoresis into his skin, and relief when he scratched the skin at the place of histamine application (H. Olausson, Personal Communication). This finding strongly suggests that itch, and probably pain and sensuous touch, have the potential to guide motor actions, more specifically actions aimed at the body itself, in absence of proprioception and fine touch. More generally, if the concept of the body schema is to be retained for denoting bodily information guiding current action, it should include all sensory inputs that have the body as their intentional content, in terms of both localized bodily sensations and adaptive body-directed reactions to them.

New dichotomies versus multiple levels in body processing

The difficulties inherent in the definition and distinction of the concepts of body schema and body image have prompted new theoretical and practical approaches to the analysis of body awareness. Carruthers (2008a, b) has proposed a new dichotomy which avoids the traditional schema/image contraposition and maintains that all representations of the body are available to consciousness. Online (synchronic) body representations, which are newly constructed moment by moment to afford a perception of

the body as it is *currently*, are distinguished from offline representations which are relatively stable and describe the body as it is *usually* like. Online representations are supposed to be constructed from extant sensory inputs, including vision, and to have explicitly conscious contents, such as a movement made now. Offline representations are supposed to be constructed in part from present sensory inputs, in part from stored memories, and to be available to explicit consciousness both immediately or after memory retrieval. The concept of an offline representation of the body which is updated diachronically may be useful for explaining the inclusion into the body boundaries of non-corporeal objects that bear a systematic relation to the body itself (Aglioti et al. 1996; Maravita and Iriki 2004; Cardinali et al. 2009), as well as a number of disorders of body awareness. For example, phantom limb phenomena and anosognosia for hemiplegia may both depend on a failure to record the amputated or plegic limb into the offline body representation, and procedures which at least temporarily suppress these pathological phenomena can possibly operate by updating the offline representation. An example for this is the use of mirrors for relieving phantom pain or improving hemiparesis (Fotopoulou et al. 2009; Ramachandran and Altschuler 2009). Further, an innate offline representation of the whole body might account for the existence of phantom limbs phenomena in congenital limb aplasia, in the obvious absence of an online representation of the missing limb or limbs (Carruthers 2008a, b; Tsakiris and Fotopoulou 2008). However, evidence for specific neural mechanisms subserving this postulated innate offline body representation is still lacking.

A multicomponent organization of body knowledge above and beyond the schema-image dichotomy has been proposed by various authors (e.g. Sirigu et al. 1991; Coslett et al. 2002; Slaughter and Heron 2004; Schwoebel and Coslett 2005; Giummarra et al. 2007, 2008). Sirigu et al. (1991) have argued that body knowledge involves semantic and lexical information about body parts, category-specific visuospatial representations of one's own and other bodies, a dynamic current body representation constructed from various sources of sensory information (called image but compared to Head and Holmes' postural schema), and concrete as well as symbolic representations of actual or potential motor programs and performances. Schwoebel and Coslett (2005) also propose a multiple representation system of the body which includes: (1) a body schema, conceived as a dynamic internal representation of bodily parts based on proprioception as well as on information based on motor commands; (2) a body structural description, derived primarily from vision and (3) a body image representing semantic and lexical information about the human body. Evidence from neurological patients has been offered in support of these hypothesized multiple

representations of the body, but the extent to which such representations map onto specific brain operations is still to be determined.

The existence of multiple levels in the perception and knowledge of the body is also suggested by developmental evidence. With regard to awareness of one's own body, co-perceived flows of multisensory information, including visual, tactile, proprioceptive and vestibular inputs as well as other bodily inputs, enable individuals from their earliest infancy to gain a realistic and accurate perception of the relations between their body and their physical environment (Neisser 1993). But it appears that even before experiencing contacts with the environment, humans are equipped with a rudimentary "knowledge" about the dynamic organization not only of their own body, but also of its relations to that of other bodies. Humans show a strong innate tendency to mimic sounds and motor acts, and even minutes after birth neonates can imitate oro-facial movements performed by adult models in front of them (Meltzoff and Moore 1977). This deceptively simple performance indicates that neonates can visually identify a movement of at least some specific parts of the adult body and produce a similar movement in the corresponding part of their own anatomy. This is perhaps the most compelling indirect evidence for an innate presence of mirror neurons (Rizzolatti and Craighero 2004) in the human brain (Gallagher and Meltzoff 1996). Imitation is likely to provide a basis for a precocious apprehension of reciprocated relations between one's own behaviour and that of other persons, eventually leading to the sense of the self as an agent and target of social interactions. During affective social exchanges with their mothers, babies a few weeks old vocalize in response to heard language and most probably pay attention to the mother's oro-facial territory as a source of emotional visual and acoustic signals much more than to her body. Indeed before one year of age infants can distinguish between canonical and scrambled images of faces, but not between canonical and scrambled images of bodies, attesting to a slower build-up of non-facial body knowledge compared to face knowledge (Slaughter and Heron 2004). Visual recognition of the typical spatial configuration of the human body below the face matures after one year of age, followed by the ability to identify and name body parts, which goes in parallel with full language acquisition (Slaughter and Heron 2004). It is around this time that the child begins to recognize his or her face and body in a mirror, an emergent ability restricted to a very few mammalian species with large brain size and a complex social organization which some regards as an objective index of self-consciousness (Keenan et al. 2003; but see Prior et al. 2008 for a possible mirror self-recognition in a bird).

The body in the occipito-temporal cortex

It is well established that there exist in the human brain category-specific cortical regions which respond in a selective manner to the visual presentation of different objects like tools, houses, places, animals, faces and so forth (e.g. Culham and Kanwisher 2001). Perhaps the most important discovery about the body in the brain in the last decade has been the identification of cortical areas specifically activated by vision of total or partial images of the body except the face. Using fMRI Downing et al. (2001) found a region in the right lateral occipitotemporal cortex which yielded a significantly stronger response when subjects viewed images of human bodies and body parts than when they viewed various inanimate objects and object parts, or faces and face parts. They named the area extrastriate body area (EBA), and the selectivity of such area for the body excluding the face has been repeatedly confirmed with the same or different experimental approaches (review in Peelen and Downing 2007). Indeed EBA activation may be diminished when the body is exposed along with the face compared to stimulation with the sole body (Morris et al. 2006).

A second body-selective area was then discovered, again with fMRI, in the middle fusiform gyrus and named fusiform body area (FBA). FBA responds about as selectively as EBA to faceless images of human bodies compared to tools and scenes, and more to line depictions of bodies than to scrambled rearrangements of them (Peelen and Downing 2005). Both EBA and FBA respond also to light-point animations portraying human motion, with a voxel-by-voxel correlation between body selectivity and human motion selectivity (Peelen et al. 2006). According to Schwarzlose et al. (2005), FBA abuts and in most subjects partly overlaps with the well known face-specialized area in the middle of the fusiform gyrus (FFA of Kanwisher et al. 1997), whereas EBA is contiguous to, but does not overlap with, the occipital face area named OFA by Gauthier et al (2000) (Peelen and Downing 2007). EBA seems to be biased towards the analysis of individual body parts, including small parts like single fingers, instead of the whole body (Taylor et al. 2007). In contrast FBA appears more interested in processing the unified body or its largest parts like the torso or the limbs (Taylor et al. 2007), in analogy with the respective roles of the face selective areas OFA and FFA in processing the face and its parts (Liu et al. 2009). The following description will be limited to EBA.

The neuroimaging evidence for a specialization of EBA for body recognition is strongly supported by complementary evidence that functional interference with neural activity in EBA impairs visual processing of human body parts. Urgesi et al. (2004) were the first to show that

temporary inactivation of EBA with repetitive transcranial magnetic stimulation (rTMS) induces a significant decrease in reaction speed, but not in accuracy, for performance on a delayed matching-to-sample visual task with non-facial body parts as stimuli. The specificity of the interference effect was demonstrated by absence of effects from rTMS of EBA on a similar task with facial and non-corporeal stimuli, and by absence of effects on the task with body parts from rTMS applied outside EBA. Effective rTMS was applied between 150 and 250 ms after the presentation of the sample, suggesting an early involvement of EBA in visual information processing. This suggestion is in keeping with intracranial subdural recordings from EBA, showing that its body-selective electrophysiological responses start at 190 ms and peak at 260 ms after stimulus onset (Pourtois et al. 2007). The finding that rTMS of EBA selectively impairs discrimination of bodies but not faces or objects has been recently replicated in the context of a study also demonstrating the selectivity of the right OFA for faces and the right LO for inanimate objects. Unlike Urgesi et al. (2004), Pitcher et al. (2009) found that impairments caused by rTMS were decreases in accuracy (d' measures) rather than increases in RT.

Other rTMS have further qualified certain functional features of EBA. Urgesi et al. (2007) have reported that functional interference with EBA, but not with ventral premotor cortex (vPMC), impairs the visual distinction between slightly different configurations of the same body part in the same posture, whereas interference with vPMC, but not with EBA, impairs the distinction between pictures representing slightly different actions performed by the same body part. This double dissociation between body form (or identity) and body action on one hand, and differential effects from functional interference with EBA and vPMC on the other, has received support from a lesion study by Moro et al. (2008). Patients with anterior brain lesions including either left or right vPMC were impaired in the visual processing of bodily actions but not bodily forms, whereas patients with posterior lesions including either left or right EBA showed an opposite pattern of deficits. According to Candidi et al. (2008), an additional specialization of vPMC is indicated by the finding that functional inactivation of this area with rTMS impairs the visual discrimination of biomechanically possible actions but not impossible actions, unlike functional inactivation of EBA which has no effect on discrimination of either type of action. If EBA takes part in the perception of action, it does so by coding the static structure, rather than dynamic aspects, of the human form (Peelen et al. 2006).

On the other hand EBA (along with FBA) does appear to be sensitive to actual bodily actions expressing emotions. Short movie clips of expressions of anger, disgust, happiness and fear by faceless bodies have proven apt to activate

EBA more than matched emotionally neutral bodily movements. The specificity of the effect at a presumably neuronal level was demonstrated by the coincidence between voxels selective for the body independent of emotional expression and voxels modulated by emotional displays. A positive correlation between amygdala activation and modulation of EBA and FBA suggests that emotional signals are transmitted to the body-selective areas from the amygdala (Peelen et al. 2007). Perhaps viewing actual bodily movements is the crucial factor for the emergence of EBA modulation by emotional expressions, given that EBA has been found to be insensitive to emotions expressed by static body images (van de Riet et al. 2009) or to pictures of noxious stimuli inflicted to bodily parts (Lamm and Decety 2008).

EBA's processing of the body extends beyond the visual modality. An fMRI study (Kitada et al. 2008) found that recognition by touch of human faces and other body parts like hands and feet activated FFA and EBA independent of vision. In particular EBA activation was higher during haptic identification of non-facial body parts than of non-biological control objects, supporting a general role of EBA in processing static configurations of the human body through non-visual as well as visual inputs. However, haptic exploration of bodily parts was also shown to activate cortical sites near EBA but clearly distinguishable from it. Sensorimotor influences on EBA had already been shown by an earlier fMRI study by Astafiev et al. (2004), in which EBA responded to own goal-directed bodily movements even in the absence of visual feedback from the moving body part. This raises the question of whether EBA may respond differentially to signals from one's own body and signals from other bodies, either visual or non-visual, thus contributing to the self/non-self distinction. Experimental evidence related to this question is contradictory. Recent fMRI studies by Hodzic et al. (2009) have reached the conclusion that EBA is only involved in the analysis of body-related information but not in the assignment of body identity, insofar as it shows no differential activation to the presentation of unfamiliar or familiar bodies, including one's own body. Other studies have suggested that EBA is activated more by allocentric than egocentric views of body parts (Chan et al. 2004; Saxe et al. 2006), and more by one's own hand than by a stranger's hand (Myers and Sowden 2008).

Two studies have examined the relations between EBA and the correspondence or non-correspondence between self-generated movements and the attendant visual feedback. In an fMRI study subjects performed joystick movements while the visual feedback could be congruent or incongruent with the subjects' own generated movements. EBA was found to distinguish between the two conditions because it was more active with incongruent

than congruent feedbacks (David et al. 2007). In another study by the same group, observers had to discriminate between visual feedbacks congruent and incongruent with their own movements. rTMS applied over the left EBA increased the reaction time of the discrimination without affecting its accuracy, suggesting that EBA plays some role in monitoring the sensory consequences of one's own movements and thus may participate in the sense of agency and the self/other distinction (David et al. 2008). Yet other cortical regions, such as the insula, are probably more important than EBA for the sense of agency and the sense of body ownership, both of which are probably essential for self-consciousness.

In many of the above studies of EBA the area on the right side has been given more importance than its counterpart on the left. Exceptions to this apparent right dominance of EBA are represented by the study by David et al. (2007) on the distinction between self-generated and non-self-generated visual feedbacks, where rTMS effects were obtained from the left EBA (see above), and a single case with body part anomia and a left occipital lesion including EBA (Kemmerer and Tranel 2008). Recently Aleong and Paus (2009) have shown that the right EBA and FBA are indeed more responsive than their left counterparts to bodily images, yet this difference is significant in females but not in males. Clearly various aspects of the laterality of body-selective areas in the human cortex are still in need of specific analyses.

The body in the insula

In the nineteenth century, neurological thinking about the means by which the body communicates with the brain emphasized the importance of the concept of coenesthesia, a mainly unconscious sense of the normal functioning of the body and its organs which emerges to full consciousness only when one is unwell. Recently the concept has been revived, renamed interoception, and given scientific status by defining its experiential components and anatomophysiological underpinnings. Interoception, defined as a sense of the physiological (homeostatic) condition of the body, is subserved by dedicated neural pathways from spinal cord and brain stem to the cortex, and includes such feelings such as pain, temperature, itch, sensual touch, muscular, visceral sensations, vasomotor activity, hunger, thirst and air hunger. Sensual or pleasant touch is caused by stimulation of an afferent system of small unmyelinated fibres projecting to the posterior insular cortex rather than to the primary somatosensory area in the parietal cortex. Neuroimaging evidence from patients lacking myelinated tactile afferents shows that residual tactile experiences are indeed associated with activation of the posterior insular cortex in absence of activation in somatosensory cortices

(Löken et al. 2009). Interoception works along with proprioception and exteroception to provide the brain with a complete information about the rest of the body, and its cortical representation in the insula is thought to be part of a system for emotional expression and self-consciousness (Craig 2009). Direct stimulation of the human insular cortex with implanted electrodes causes somatosensory, viscerosensory, motor, auditory, vestibular and speech effects (Nguyen et al. 2009), in keeping with a broad spectrum of functional localizations in this part of the brain.

The insular cortex is organized in a hierarchical fashion in a caudal–rostral direction, whereby primary sensory inputs projecting to the posterior insula, including gustatory, somatosensory, vestibular and visceral inputs, are progressively elaborated and integrated across modalities in the middle and anterior insula (Craig 2009). The highest integrative level in the anterior insula is tightly interconnected with the anterior cingulate cortex to form an emotional network in which the limbic insular component is involved in sensory reception and conscious feelings, and the cingulate cortex is the motivational and motor component for the behavioural expression of the feelings (Critchley 2005). The anterior insula–cingulate network is also credited with the specific function of self-recognition (Devue et al. 2007). Craig (2009) maintains that the anterior insular cortex is a peculiarly human brain structure which is crucial for integrating all subjective feelings related to the body, and especially to its homeostatic conditions, into emotional experiences and conscious awareness of the environment and the self.

The insula has been strongly implicated in neurological disorders concerning anosognosia for hemiplegia, the sense of body ownership, the sense of agency and out-of-body experiences. Anosognosia for hemiplegia, either motor or sensory or both (Marcel et al. 2004; Orfei et al. 2007; Spinazzola et al. 2008), is the failure of some patients to realize that they are paralyzed on one side of the body. The right posterior insula is commonly damaged in paralytic patients with anosognosia for left hemiplegia, while it is usually spared in similar hemiplegic patients without anosognosia (Karnath et al. 2005). Anosognosia for hemiplegia may be accompanied by the disownership by the patient of the paralyzed body parts (Aglioti et al. 1996), or even the attribution of ownership of the disowned parts to other people (Vallar and Ronchi 2009). In a recent neuroimaging study comparing lesions of anosognosic patients with or without bodily disownership, lesions of the right posterior insula were identified as a crucial determinant of the association of anosognosia for hemiplegia with disorders of sense of ownership of the paralyzed parts (Baier and Karnath 2008).

The sense of ownership of a body part is normally associated with a sense of agency accompanying voluntary movement of that part. Patients with personal hemineglect

who deny ownership of a non-paralytic body part also deny to be the agent of goal-directed movements of that part in spontaneous behaviour. Similarly, schizophrenic patients who do not feel in control of their intentional movements are led to believe that their actions are caused by someone else (Frith 2005). Neurological investigations on the sense of agency in normal participants have shown an activation in the anterior insula when participants knew that the movement of a cursor on a screen was caused by them, whereas there was an activation in the inferior parietal cortex when they knew that the movement was caused by another person rather than by themselves (Farrer and Frith 2002). The anterior insula may be essential for detecting the coincidence of the multisensory feedbacks generated by volitional movements, whereas the inferior parietal cortex may differentially code for self-generated actions as well as for actions of others. Spengler et al. (2009) have recently reported that the intensity of activation in the temporal–parietal junction matches the degree to which one can attribute an action to another rather than to himself. It must be recalled that other cortical areas, such as EBA (David et al. 2007, 2008), have been implicated in the distinction between self-generated actions and actions generated by others, so that the sense of agency is likely to be sustained by a distributed brain system rather than by a single brain centre.

The body in the parietal cortex

As previously mentioned, disownership phenomena typically occur after lesions involving the right parietal lobe. Visual illusions during which people have the clear impression of seeing a second own body in extrapersonal space are broadly defined autoscopic phenomena. These range from the feeling that the centre of self-awareness is outside the physical body (Out-of-body experiences, OBE) to the condition in which a double of themselves is seen in the extrapersonal space without the experience of leaving one's body (autoscopic hallucinations). The main difference between these two experiences is the sense of disembodiment present in the former but not in the latter (Blanke and Mohr 2005). Recent studies demonstrate that such bizarre experiences result from a disturbance of multisensory integration in right temporo-parietal cortex and in the vestibular representation in the posterior insula, though probably frontal areas and fronto-parietal connections are also involved (Blanke and Metzinger 2009).

Neuropsychological studies indicate that left parietal lesions are implicated in autotopagnosia, a typical alteration of body awareness, in which patients are unable to point to parts of their own body on verbal command, in spite of being able to carry out successfully verbal commands unrelated to the body, such as “touch the pedal of a

bicycle”. These patients also have difficulties in describing the spatial relations between body parts: for example they may say that the mouth is between the nose and the eyes. Lesions associated with autotopagnosia typically affect the left posterior parietal lobe and fMRI studies in normals point to the angular gyrus and the intraparietal sulcus as critical areas for dealing with body parts and their relations (Corradi-Dell'Acqua et al. 2008). Autotopagnosia is usually associated with heterotopagnosia insofar as affected individuals are unable to point to their own as well as to other people's body parts. Recently, however, cases of pure autotopagnosia and pure heterotopagnosia have been observed, with the causative lesion being in the inferior parietal lobe in the former case and in the superior parietal lobe in the latter case (Felician et al. 2009). Further, long lasting pure heterotopagnosia has been reported in two cases with joint parietal and insular lesions (Claret de Langavant et al. 2009). Therefore, a possible role of the insula in classic autotopagnosia is not supported by the available evidence, and the evidence for a role of the insula in pure heterotopagnosia is very limited.

Persisting ignorance about the neural bases of various body-related disorders

Virtually nothing is known about the derangements in brain organization leading to the depersonalization syndrome, characterized by a persistent feeling of living outside one's own body, and the Cotard's syndrome, in which patients entertain a nihilistic delusion about the body to the point of denying its existence. Equally disappointing is our ignorance about the neural underpinnings of the body dysmorphic disorder, an enduring excessive concern with a selective bodily flaw which is totally imaginary or grossly exaggerated, or about the eating disorders anorexia nervosa and bulimia nervosa which are thought by most to depend on deviant attitudes towards body weight and shape, or about the body integrity disorder, a psychological condition in which non psychotic individuals exhibit, early in childhood, the persistent desire to have one or more limb amputated, in the attempt to match their physical body with an idealized body. Although neuroscientists are becoming more and more interested in these mysterious conditions, knowledge about them remains thus far elusive.

How many bodies in the brain?

The scientific understanding of the body in the brain has still a long way to go. The field is not helped by the persistent use of vague concepts like body schema and body image the definition of which varies conspicuously and confusingly from author to author. The confusion is particularly evident when one tries to use the two concepts for

categorizing a variety of neurological disorders which share some evidence for a defective knowledge of the anatomical and functional reality of the body. Among autotopagnosia, finger agnosia, phantom and supernumerary limbs, anosognosia for hemiplegia, somatoparaphrenia, allesthesia, the dismorphophic body disorder, the eating disorders, and the body integrity disorders, which are disorders of the body schema and which of the body image? The difficulty of assigning these disorders to one or the other concept is made obvious by the fact that what is a body schema disorder for one author is a body image disorder for another author, or all body-related disorders are collectively labelled as body schema disorders by some and body image disorders by others. Such inconsistency and variability in definition make a good case for giving up the terms body image and body schema completely.

The identification of body-related cortical areas, such as the extrastriate body area and the fusiform body area and their roles in body processing have brought considerable empirical and theoretical contributions to the field, and so has the recognition of an heretofore underrated importance to the insular cortex in linking bodily sensations and feelings with organized conscious awareness of the outside world and the self. Yet to think that corporeal awareness and self-recognition may map onto a single cortical area, be it the insula or any other area, seems way too simplistic in view of the general evidence for a cerebral organization based on a variety of distributed systems constituted by specifically interconnected areas in multiple locations (Fig. 1).

The subjectively experienced unity, continuity, and constancy of most mental images are rarely, if ever, duplicated in the causative brain processes which by their nature are scattered, disparate and spatiotemporally fractured. Although there is a great deal of somatotopy in the

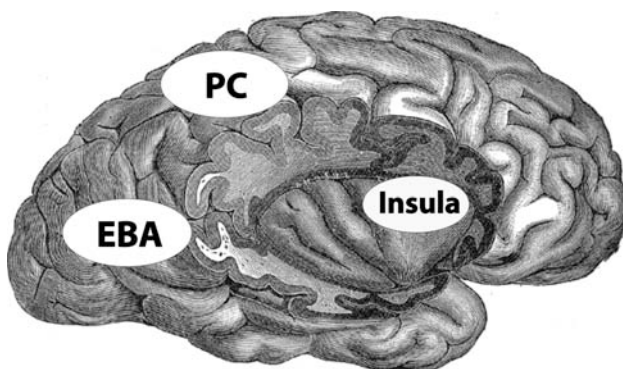


Fig. 1 The figure shows three cortical regions which have attracted most attention recently as possible brain sites specialized for different aspects of bodily awareness: the posterior parietal cortex (PC), the anterior insula and the extrastriate body area (EBA). These body-related cortical regions are present in both cerebral hemispheres, but here they are shown in the right hemisphere because most studies have provided evidence for a right-sided dominance in many facets of bodily awareness

brain, mostly due to neurogenetic rather than representational constraints (Sperry 1952), the “body in the brain” sustaining corporeal awareness is extremely unlikely to be isomorphic with the body itself, as instead implied by the body schema and body image concepts. Indeed the body-related brain areas already known and those which assuredly will be discovered in the near future argue for the existence of many bodies in the brain. Understanding the brain processes of corporeal awareness will require to know the contributions of each of these bodies in the brain as well as their interactions.

Acknowledgments G.B. is funded by Ministero Università e Ricerca of Italy. S.M.A. is funded by Ministero Università e Ricerca of Italy, by Sapienza University of Rome and by IRCCS Fondazione Santa Lucia.

References

- Aglioti S, Smania N, Manfredi M, Berlucchi G (1996) Disownership of left hand and objects related to it in a patient with right brain damage. *NeuroReport* 8:293–296
- Aleong R, Paus T (2009) Neural correlates of human body perception. *J Cogn Neurosci* (Epub ahead of print)
- Anema HA, van Zandvoort MJ, de Haan EH, Kappelle LJ, de Kort PL, Jansen BP, Dijkerman HC (2009) A double dissociation between somatosensory processing for perception and action. *Neuropsychologia* 47:1615–1620
- Astafiev SV, Stanley CM, Shulman GL, Corbetta M (2004) Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neurosci* 7:542–548
- Baier B, Karnath HO (2008) Tight link between our sense of limb ownership and self-awareness of actions. *Stroke* 39:486–488
- Berlucchi G, Aglioti S (1997) The body in the brain: neural bases of corporeal awareness. *Trends Neurosci* 20:560–564
- Bermúdez JL (2009) Self: body awareness and self-awareness. In: Banks W (ed) *Encyclopedia of consciousness*. Elsevier Academic Press, Amsterdam, pp 289–300
- Blanke O, Metzinger T (2009) Full-body illusions and minimal phenomenal selfhood. *Trends Cogn Sci* 13:7–13
- Blanke O, Mohr C (2005) Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin implications for neurocognitive mechanisms of corporeal awareness and self-consciousness. *Brain Res Brain Res Rev* 50:184–199
- Candidi M, Urgesi C, Ionta S, Aglioti SM (2008) Virtual lesion of ventral premotor cortex impairs visual perception of biomechanically possible but not impossible actions. *Soc Neurosci* 3:388–400
- Cardinali L, Frassinetti F, Brozzoli C, Urquizar C, Roy AC, Farnè A (2009) Tool-use induces morphological updating of the body schema. *Curr Biol* 19:R478–R479
- Carruthers G (2008a) Types of body representation and the sense of embodiment. *Conscious Cogn* 17:1302–1316
- Carruthers G (2008b) Reply to Tsakiris and Fotopoulou “Is my body the sum of online and offline body representations?” *Conscious Cogn* 17:1321–1323
- Chan AW, Peelen MV, Downing PE (2004) The effect of viewpoint on body representation in the extrastriate body area. *NeuroReport* 15:2407–2410
- Cleret de Langavant L, Trinkler I, Cesaro P, Bachoud-Lévi AC (2009) Heterotopagnosia: when I point at parts of your body. *Neuropsychologia* 47:1745–1755

- Corradi-Dell'Acqua C, Hesse MD, Rumiati RI, Fink GR (2008) Where is a nose with respect to a foot? The left posterior parietal cortex processes spatial relationships among body parts. *Cereb Cortex* 18:2879–2890
- Coslett HB, Saffran EM, Schwoebel J (2002) Knowledge of the human body: a distinct semantic domain. *Neurology* 59:357–363
- Craig AD (2009) How do you feel-now? The anterior insula and human awareness. *Nat Rev Neurosci* 10:59–70
- Critchley M (1979) Corporeal awareness: body image; body scheme. In: Critchley M (ed) *The divine banquet of the brain*. Raven Press, New York, pp 92–105
- Critchley HD (2005) Neural mechanisms of autonomic, affective, and cognitive integration. *J Comp Neurol* 493:154–166
- Culham JC, Kanwisher NG (2001) Neuroimaging of cognitive functions in human parietal cortex. *Curr Opin Neurobiol* 11:157–163
- David N, Cohen MX, Newen A, Bewernick BH, Shah NJ, Fink GR, Vogeley K (2007) The extrastriate cortex distinguishes between the consequences of one's own and others' behavior. *Neuroimage* 36:1004–1014
- David N, Jansen M, Cohen MX, Osswald K, Molnar-Szakacs I, Newen A, Vogeley K, Paus T (2008) Disturbances of self-other distinction after stimulation of the extrastriate body area in the human brain. *Soc Neurosci* 21:1–9
- De Vignemont F (2007) Habeas corpus: the sense of ownership of one's own body. *Mind Lang* 22:427–449
- Devue C, Collette F, Balteau E, Degueldre C, Luxen A, Maquet P, Brédart S (2007) Here I am: the cortical correlates of visual self-recognition. *Brain Res* 1143:169–182
- Dijkerman HC, de Haan EH (2007) Somatosensory processes subserving perception and action. *Behav Brain Sci* 2:189–201 Discussion 201–239
- Downing PE, Jiang Y, Shuman M, Kanwisher N (2001) A cortical area selective for visual processing of the human body. *Science* 293:2470–2473
- Farrer C, Frith CD (2002) Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. *Neuroimage* 15:596–603
- Felician O, Anton JL, Nazarian B, Roth M, Roll JP, Romaiuguère P (2009) Where is your shoulder? Neural correlates of localizing others' body parts. *Neuropsychologia* 47:1909–1916
- Fotopoulou A, Rudd A, Holmes P, Kopelman M (2009) Self-observation reinstates motor awareness in anosognosia for hemiplegia. *Neuropsychologia* 47:1256–1260
- Frith C (2005) The self in action: lessons from delusions of control. *Conscious Cogn* 14:752–770
- Gallagher S (2005) *How the body shapes the mind*. Oxford University Press, New York
- Gallagher S, Meltzoff AN (1996) The earliest sense of self and others: Merleau-Ponty and recent developmental studies. *Philos Psychol* 9:211–233
- Gauthier I, Tarr MJ, Moylan J, Skudlarski P, Gore JC, Anderson AW (2000) The fusiform “face area” is part of a network that processes faces at the individual level. *J Cogn Neurosci* 12:495–504
- Giummarra MJ, Gibson SJ, Georgiou-Karistianis N, Bradshaw JL (2007) Central mechanisms in phantom limb perception: the past, present and future. *Brain Res Rev* 54:219–232
- Giummarra MJ, Gibson SJ, Georgiou-Karistianis N, Bradshaw JL (2008) Mechanisms underlying embodiment, disembodiment and loss of embodiment. *Neurosci Biobehav Rev* 32:143–160
- Goldenberg G (2002) Goldstein and Gelb's case Schn.—a classic case in neuropsychology? In: Code C, Wallech CW, Joannette Y, Roch-Lecours A (eds) *Classic cases in neuropsychology*, vol 2. Psychology Press, Hove, pp 281–299
- Graziano M, Botvinik M (2001) How the brain represents the body: insights from neurophysiology and psychology. In: Prinz W, Hommel B (eds) *Common mechanisms in perception and action, attention and performance XIX*. Oxford University Press, Oxford, pp 136–157
- Haggard P, Wolpert DM (2005) Disorders of body scheme. In: Freund H-J, Jeannerod M, Hallett M, Leiguarda R (eds) *Higher-order motor disorders: from neuroanatomy and neurobiology to clinical neurology*. Oxford University Press, Oxford, pp 261–272
- Head H, Holmes G (1911/12) Sensory disturbances from cerebral lesion. *Brain* 34:102–254
- Hodzic A, Kaas A, Muckli L, Stirn A, Singer W (2009) Distinct cortical networks for the detection and identification of human body. *Neuroimage* 45:1264–1271
- Holmes NP, Spence C (2004) The body schema and the multisensory representation(s) of peripersonal space. *Cogn Process* 5:94–105
- Holmes NP, Spence C (2006) Beyond the body schema. In: Knoblich G, Thornton IM, Grosjean M, Shiffrar M (eds) *Human body perception from the inside out*. Oxford University Press, Oxford, pp 15–64
- Kanwisher N, McDermott J, Chun MM (1997) The fusiform “face area” is part of a network that processes faces at the individual level. *J Neurosci* 17:4302–4311
- Karnath HO, Baier B, Nägele T (2005) Awareness of the functioning of one's own limbs mediated by the insular cortex? *J Neurosci* 25:7134–7138
- Keenan JP, Gallup GG, Falk D Jr (2003) *The face in the mirror: the search for the origins of consciousness*. Harper Collins, New York
- Kemmerer D, Tranel D (2008) Searching for the elusive neural substrates of body part terms: a neuropsychological study. *Cogn Neuropsychol* 25:601–629
- Kitada R, Johnsrude IS, Kochiyama T, Lederman SJ (2008) Functional specialization and convergence in the occipito-temporal cortex supporting haptic and visual identification of human faces and body parts: an fMRI study. *J Cogn Neurosci* (Epub ahead of print)
- Lamm C, Decety J (2008) Is the extrastriate body area (EBA) sensitive to the perception of pain in others? *Cereb Cortex* 18:2369–2373
- Leknes SG, Bantick S, Willis CM, Wilkinson JD, Wise RG, Tracey I (2007) Itch and motivation to scratch: an investigation of the central and peripheral correlates of allergen- and histamine-induced itch in humans. *J Neurophysiol* 97:415–422
- Liu J, Harris A, Kanwisher N (2009) Perception of face parts and face configurations: an fMRI study. *J Cogn Neurosci* (Epub ahead of print)
- Löken LS, Wessberg J, Morrison I, McGlone F, Olausson H (2009) Coding of pleasant touch by unmyelinated afferents in humans. *Nat Neurosci* 12:547–548
- Maravita A, Iriki A (2004) Tools for the body (schema). *Trends Cogn Sci* 8:79–86
- Marcel AJ, Tegnér R, Nimmo-Smith I (2004) Anosognosia for plegia: specificity, extension, partiality and disunity of bodily unawareness. *Cortex* 40:19–40
- Mayer A, Kudar K, Bretz K, Tihanyi J (2008) Body schema and body awareness of amputees. *Prosthet Orthot Int* 32:363–382
- Meltzoff AN, Moore MK (1977) Imitation of facial and manual gestures by human neonates. *Science* 198:75–78
- Melzack R (2005) Evolution of the neuromatrix theory of pain. The Prithvi Raj Lecture: presented at the third World Congress of World Institute of Pain, Barcelona 2004. *Pain Pract* 5:85–94
- Merleau-Ponty M (1945) *Phénoménologie de la Perception*. Gallimard, Paris
- Milner D, Goodale MA (1995) *The visual brain in action*. Oxford University Press, Oxford
- Moro V, Urgesi C, Pernigo S, Lanteri P, Pazzaglia M, Aglioti SM (2008) The neural basis of body form and body action agnosia. *Neuron* 60:235–246

- Morris JP, Pelphey KA, McCarthy G (2006) Occipitotemporal activation evoked by the perception of human bodies is modulated by the presence or absence of the face. *Neuropsychologia* 44:1919–1927
- Myers A, Sowden PT (2008) Your hand or mine? The extrastriate body area. *Neuroimage* 42:1669–1677
- Neisser U (1993) *The perceived self: ecological and interpersonal sources of self knowledge*. Cambridge University Press, New York
- Nguyen DK, Nguyen DB, Malak R, Leroux JM, Carmant L, Saint-Hilaire JM, Giard N, Cossette P, Bouthillier A (2009) Revisiting the role of the insula in refractory partial epilepsy. *Epilepsia* 50:510–520
- Olausson HW, Cole J, Vallbo A, McGlone F, Elam M, Krämer HH, Rylander K, Wessberg J, Bushnell MC (2008a) Unmyelinated tactile afferents have opposite effects on insular and somatosensory cortical processing. *Neurosci Lett* 436:128–132
- Olausson H, Wessberg J, Morrison I, McGlone F, Vallbo A (2008b) The neurophysiology of unmyelinated tactile afferents. *Neurosci Biobehav Rev* (Epub Oct 8 2008)
- Orfei MD, Robinson RG, Prigatano GP, Starkstein S, Rüsç N, Bria P, Caltagirone C, Spalletta G (2007) Anosognosia for hemiplegia after stroke is a multifaceted phenomenon: a systematic review of the literature. *Brain* 130:3075–3090
- Paillard J (1999) Body schema and body image—a double dissociation in deafferented patients. In: Gantchev GN, Mori S, Massion J (eds) *Motor control, today and tomorrow*. Academic Publishing House, Sophia
- Paillard J, Michel F, Stelmach G (1983) Localization without content. A tactile analogue of ‘blind sight’. *Arch Neurol* 40:548–551
- Peelen MV, Downing PE (2005) Selectivity for the human body in the fusiform gyrus. *J Neurophysiol* 93:603–608
- Peelen MV, Downing PE (2007) The neural basis of visual body perception. *Nat Rev Neurosci* 8:636–648
- Peelen MV, Wiggett AJ, Downing PE (2006) Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron* 49:815–822
- Peelen MV, Atkinson AP, Andersson F, Vuilleumier P (2007) Emotional modulation of body-selective visual areas. *Soc Cogn Affect Neurosci* 2:274–283
- Pitcher D, Charles L, Devlin JT, Walsh V, Duchaine B (2009) Triple dissociation of faces, bodies, and objects in extrastriate cortex. *Curr Biol* 19:319–332
- Pourtois G, Peelen MV, Spinelli L, Seeck M, Vuilleumier P (2007) Direct intracranial recording of body-selective responses in human extrastriate visual cortex. *Neuropsychologia* 45:2621–2625
- Prior H, Schwarz A, Güntürkün O (2008) Mirror-induced behavior in the magpie (*Pica pica*): evidence of self-recognition. *PLoS Biol* 6(8):e202
- Ramachandran VS, Altschuler EL (2009) The use of visual feedback, in particular mirror visual feedback, in restoring brain function. *Brain* 132:1693–1710
- Reed CL (2002) What is the body schema? In: Printz W, Meltzoff A (eds) *The imitative mind: development, evolution, and brain bases*. Cambridge University Press, Cambridge, pp 233–243
- Rizzolatti G, Craighero L (2004) The mirror-neuron system. *Annu Rev Neurosci* 27:169–192
- Saxe R, Jamal N, Powell L (2006) My body or yours? The effect of visual perspective on cortical body representations. *Cereb Cortex* 16:178–182
- Schwarzlose RF, Baker CI, Kanwisher N (2005) Separate face and body selectivity on the fusiform gyrus. *J Neurosci* 25:11055–11059
- Schwoebel J, Coslett HB (2005) Evidence for multiple, distinct representations of the human body. *J Cogn Neurosci* 17:543–553
- Sherrington CS (1906) *The integrative action of the nervous system*. Yale University Press, New Haven, CT
- Sirigu A, Grafman J, Bressler K, Sunderland T (1991) Multiple representations contribute to body knowledge processing. Evidence from a case of autotopagnosia. *Brain* 114:629–642
- Slaughter V, Heron M (2004) Origins and early development of human body knowledge. *Monogr Soc Res Child Dev* 69:1–102
- Spengler S, von Cramon DY, Brass M (2009) Was it me or was it you? How the sense of agency originates from ideomotor learning revealed by fMRI. *Neuroimage* 46:290–298
- Sperry RW (1952) Neurology and the mind–brain problem. *Am Sci* 40:291–312
- Spinazzola L, Pia L, Folegatti A, Marchetti C, Berti A (2008) Modular structure of awareness for sensorimotor disorders: evidence from anosognosia for hemiplegia and anosognosia for hemianaesthesia. *Neuropsychologia* 46:915–926
- Taylor JC, Wiggett AJ, Downing PE (2007) Functional MRI analysis of body and body part representations in the extrastriate and fusiform body areas. *J Neurophysiol* 98:1626–1633
- Tsakiris M, Fotopoulou A (2008) Is my body the sum of online and offline body-representations? *Conscious Cogn* 17:1317–1320
- Ungerleider LG, Mishkin M (1982) Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RJW (eds) *Analysis of visual behavior*. The MIT Press, Cambridge, MA, pp 549–586
- Urgesi C, Berlucchi G, Aglioti SM (2004) Magnetic stimulation of extrastriate body area impairs visual processing of nonfacial body parts. *Curr Biol* 14:2130–2134
- Urgesi C, Candidi M, Ionta S, Aglioti SM (2007) Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. *Nat Neurosci* 10:30–31
- Urgesi C, Moro V, Candidi M, Aglioti SM (2006) Mapping implied body actions in the human motor system. *J Neurosci* 26:7942–7949
- Vallar G, Ronchi R (2009) Somatoparaphrenia: a body delusion. A review of the neuropsychological literature. *Exp Brain Res* 192:533–551
- van de Riet WA, Grezes J, de Gelder B (2009) Specific and common brain regions involved in the perception of faces and bodies and the representation of their emotional expressions. *Soc Neurosci* 4:101–120
- Weiskrantz L (2009) *Blindsight: a case study spanning 35 years and new developments*, 2nd edn. Oxford University Press, Oxford