Neuropsychologia 48 (2010) 756–762

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

# Body and movement: Consciousness in the parietal lobes

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ARTICLE INFO

*Article history:*
Received 20 April 2009
Received in revised form 6 October 2009
Accepted 8 October 2009
Available online 27 October 2009

*Keywords:*
Consciousness
Action monitoring
Body representation
Parietal cortex
Self-recognition
Egocentric reference
Sense of body

ABSTRACT

A critical issue related to the notion of identity concerns our ability to discriminate between internally and externally generated stimuli. This basic mechanism likely relies on perceptual and motor information, and requires that both motor plans and the resulting activity be continuously mapped on a reliable body representation. It has been widely demonstrated that the parietal cortices of the two hemispheres play a crucial role, albeit differently specialized, in both monitoring internal representation of our own actions and sustaining body representation. Ample neuropsychological evidence indicates that while damage to the left parietal cortex affects the ability to generate and/or monitor an internal model of one's own movement, lesions of the right parietal lobe are largely responsible for severe perturbations of the internal representation of one's own body. In the present paper, we discuss the processes involved in body perception and self-recognition and propose a tentative model describing how the right and left parietal cortices contribute in integrating various sources of information to produce the unique, elementary experience of one's own body in motion. The ecological value of this process in constructing identity and autobiographical experience will be discussed.

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## 1. Introduction

Successful interaction with the environment requires integration of the continuous flow of information that arises from sensory organs, in order to keep track of external stimuli and constantly monitor body status. In addition, interacting within the external world further requires planning, monitoring and executing the appropriate motor acts. Although distinctly processed, sensory information and motor responses are not entirely separable events. Sensory inputs often drive motor behaviour, and planning a movement generates sensory consequences that must be anticipated for actions to be properly carried out. In a cognitive perspective, these processes imply both an immediate elementary analysis of incoming and efferent information, and the possibility of representing inner and outer reality, thus allowing the individual to construct models (or images) of sensations, perceptions and actions.

Conscious behaviour further requires that sensorimotor representations be overtly accessed at will, i.e. the ability to "observe" oneself while acting. At the behavioural level, this capacity is expressed through (at least) two major processes aiming, respectively, at consciously exploring internal and external reality, and planning motor activities. The former goal is accomplished by voluntarily (top-down) directing attention towards salient stimuli (Hopfinger, Buonocore, & Mangun, 2000; Taylor, 2003; Vidyasagar, 1999), the latter through the creation of intentional motor plans (Haggard, 2005; Jeannerod, 2001). Both processes directly stem from the ability of the brain to represent space and movement.

The representation of corporeal space constitutes the basis for acting. All motor activities are necessarily centred in egocentric reality, and incoming sensory information is also conveniently framed (automatically) in egocentric coordinates (Nico & Daprati, 2009). This organization clearly facilitates anticipation of the sensorimotor consequences of the actions, as any new input will automatically receive an egocentric, expected, localization. Attention can thus be directed towards the relevant area of corporeal space prior to action. When motor activity comes into play, a variety of representations would be prompted, spanning from knowledge about tool use to procedural motor competences, motor imagery and, critically, the explicit perception of being the source of a given action (sense of agency, Gallagher, 2000; Marcel, 2003).

Many studies in the domain of neuropsychology and neurophysiology indicate a crucial role for the parietal cortex of the two hemispheres in supporting the representation of corporeal space and action. Specifically, the right parietal lobe would contribute to provide a spatial description of incoming sensations (Burgess, 2008; Tsakiris, Costantini, & Haggard, 2008), while the left parietal cortex would maintain the ability to generate and/monitor an inter-

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0028-3932/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2009.10.008

nal model of the required movement (Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999).

Here, we propose that integration of the information processed by these brain areas contributes to construct a fundamental aspect of consciousness, namely, the sense of the body in action. By this term we will refer to the awareness of being both the agent of a motor act, and the owner of the body parts that carries it out. This knowledge would be supported by the brain areas that are specialized for two complementary cognitive operations that define voluntary behaviour: spatial attention and motor intention.

## 2. Corporeal identity in the right parietal lobe

The feeling of our body is a crucial element in determining motor behaviour in the environment. Based on the effects of brain lesions, it was suggested (Berlucchi & Aglioti, 1997; Melzack, 1990) that corporeal awareness is supported by the activity of a composite network that includes the parietal and insular cortex. In agreement with neuropsychological evidence, neuroimaging studies have recently emphasised involvement of the primary and secondary somatosensory cortex (Corradi-Dell'Acqua, Tomasino, & Fink, 2009; Hari et al., 1998; Schaefer, Haaland, & Sainburg, 2007, 2009; Schwartz, Assal, Valenza, Seghier, & Vuilleumier, 2005; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007), insula (Baier & Karnath, 2008; Berti et al., 2005; Craig, 2002, 2009; Karnath, Baier, & Nägele, 2005; Lopez, Halje, & Blanke, 2008; Tsakiris et al., 2007), and posterior parietal cortex (Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004; Farrer et al., 2003; Fink et al., 1999; Kammers et al., 2009) in sustaining the feeling of the body, each area playing a different, albeit coordinate, role (Berlucchi & Aglioti, 1997; Dijkerman & De Haan, 2007; Melzack, 1990). Specifically, while higher order somatosensory areas have been mainly related to body schema and perceived changes in location and size of body parts, the insular cortex has been often linked to an ample variety of bodily sensations. In agreement with the rich associated circuitry, it has been shown that insular cortex represents a multifaceted sensory area involved in processing visceral, somatosensory and vestibular information (see for instance Augustine, 1996; Craig, 2009). Unsurprisingly, activation of the insular cortex has thus been related to various aspects of self-related information, and particularly to both the sense of agency during active hand movements (Farrer & Frith, 2002; Farrer et al., 2003) and the (passive) sense of body ownership in the absence of motor activity (Tsakiris et al., 2007), the latter hypothesis being further supported by data from neuropsychology (Baier & Karnath, 2008; Fotopoulou et al., 2008; Karnath et al., 2005). The possibility that segregated parts of the insular cortex would contribute to either perception has recently been raised (Mutschler et al., 2009).

While not questioning the contribution of a larger network in constructing the sense of an embodied self, for the purpose of this paper we will limit our discussion to the role of the parietal cortex. In agreement with what reported in the literature, we will specifically refer to the posterior parts of this brain region, and mainly consider the inferior parietal lobule (IPL), which has been often associated to own-body perception (Berlucchi & Aglioti, 1997). In recent years, many studies have further analysed this area in humans with respect to self-other distinctions (Farrer et al., 2003; Preston & Newport, 2008; Uddin, Molnar-Szakacs, Zaidel, & Iacoboni, 2006), and interestingly, out-of-body experiences have been found to emerge following direct cortical stimulation of the right IPL (Blanke, Ortigue, Landis, & Seeck, 2002). In addition to contributing to body perception, it has been widely demonstrated that the posterior areas of the brain in the right hemisphere drive voluntary attention both in response to an external change and when actively searching the environment (Behrmann, Geng, & Shomstein, 2004; Fan, McCandliss, Fossella, Flombaum, & Poster, 2005). Due to the functional requirement of integrating internal and external experiences related to body states, attentional processes largely depend on a distributed network that includes the insular cortex (Berthier, Starkstein, & Leiguarda, 1987; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991).

From a functional perspective, attentional and perceptual abilities have a neural counterpart in the anatomical location of the parietal cortex. Critchley describes the parietal cortex as located at the "crossroads of the brain" (Critchley, 1953). Indeed, due to numerous connections with cortical areas and subcortical regions related to sensory analysis and motor activity, parietal cortex plays a pivot role in integrating multisensory information that are used when performing actions (Dijkerman & De Haan, 2007). This process relies on the spatial coherence between the representation of both sensory and motor reality, which is obtained by referring to a unique coordinate system centred on the body. In fact, albeit many representations of the incoming sensory information can co-exist (retinotopic, eye/head-centred, etc.), the most salient is body centred. It has been shown that the centre of mass of the body (i.e. the trunk) constitutes a "physical anchor" according to which external reality and movements required to explore it are represented (Karnath, Schenkel, & Fischer, 1991).

The role played by the body as a spatial reference for organizing stimulus detection emerges even at neural level (for reviews see Holmes & Spence, 2004; Maravita, Spence, & Driver, 2003). Multisensory neurons have been described in the monkey brain that show overlapping visual and tactile receptive fields, the former being typically anchored to the tactile one. These cell types have been identified in subcortical and cortical regions, including putamen (Graziano & Gross, 1993), premotor cortex (Fogassi et al., 1996; Graziano, Hu, & Gross, 1997; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997) and posterior parietal lobe (Colby & Duhamel, 1996; Colby, Duhamel, & Goldberg, 1993). In functional terms, they describe a complex network that permits spatial coding of incoming information in a system of coordinates centred on the body part directly involved by motor responses. A comparable system likely exists in humans, as various behavioural and neuropsychological studies have shown (Làdavas, 2002, for a review).

In a broader perspective, body perception further depends on the physical reference to earth gravity, a process that likely recruits a complex neural network. Indeed, illusory perceptions about the body are more common in the supine position, suggesting that gravitational information might participate to embodiment; in addition, vestibular stimulation can evoke abnormal bodily sensations (see Lopez et al., 2008, for a brief review). Hence, it is reasonable to suppose that the parieto-insular vestibular cortex could represent another important node in the process of integrating signals about the body in space, in addition to the well-established role of posterior parietal cortex in multisensory integration (Fasold, Heinau, Trenner, Villringe, & Wenzel, 2008).

In this context, we will consider corporeal identity as the conscious experience of one's body in space as derived from afferent sensory information pertaining to the body (i.e. proprioception, interoception, vestibular inputs). This, in turn, would generate the feeling of being a functional unit separate from the environment in which one operates. In this view, corporeal identity implies the ability to self-represent, namely the ability of directing attention towards oneself. As such, we consider this form of consciousness as a cognitive function that cannot be ascribed to a single brain region, but would rather represent an "attribute of network activity" (Kinsbourne, 2006). Being aware of one's body part or spatial location would depend on the ability to represent it internally, namely representational abilities would make consciousness possible (Kinsbourne, 2006).

At least two cognitive operations would contribute to conscious perception of the body. A process of multisensory integration

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