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More than skin deep: Body representation beyond primary somatosensory cortex

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ABSTRACT

The neural circuits underlying initial sensory processing of somatic information are relatively well understood. In contrast, the processes that go beyond primary somatosensation to create more abstract representations related to the body are less clear. In this review, we focus on two classes of higher-order processing beyond somatosensation. *Somatoperception* refers to the process of perceiving the body itself, and particularly of ensuring somatic perceptual constancy. We review three key elements of somatoperception: (a) remapping information from the body surface into an egocentric reference frame, (b) *exteroceptive* perception of objects in the external world through their contact with the body, and (c) *interoceptive* percepts about the nature and state of the body itself. *Somatorepresentation*, in contrast, refers to the essentially cognitive process of constructing semantic knowledge and attitudes about the body, including: (d) lexical-semantic knowledge about bodies generally and one's own body specifically, (e) configural knowledge about the structure of bodies, (f) emotions and attitudes directed towards one's own body, and (g) the link between physical body and psychological self. We review a wide range of neuropsychological, neuroimaging and neurophysiological data to explore the dissociation between these different aspects of higher somatosensory function.

1. Introduction

Our body is a unique object in the world. On the one hand, the body is the seat of our sensations and the reference of first-person experience. Sensations on the body surface or from the viscera have a private character, distinct from the public availability of visual or auditory stimuli (Bermúdez, Marcel, & Eilan, 1995; Evans, 1982). On the other hand, one's body is also a physical object, like any other in the external world. This duality suggests two modes by which we can experience and understand our body. On the one hand, we can feel our body pre-reflectively, from the inside, as an object of direct perception; on the other, we can reflect cognitively on our body, from the outside, as a physical and biological object. Thus, it is important to distinguish between how we *perceive* our body to be, and how we *remember* or *believe* that it is (cf. Lhermitte, 1942). A large body of research in experimental psychology, psychophysics, and neurophysiology has investigated basic mechanisms of somato*sensation* (for reviews see, Iwamura, 1998; Johnson & Hsiao, 1992; Mountcastle, 2005; Romo & Salinas, 2001). But much less is known about how the brain goes beyond basic somatosensation to construct (1) higher-level percepts of the body and objects contacting the body, which we term somato*perception*, and (2) abstract knowledge, beliefs, and attitudes about bodies generally and one's own body specifically, which we term somato*representation* (see Table 1). Here, we review these processes of somatoperception and somatorepresentation.

Various illusions illustrate this distinction between on-line perception and off-line representation of the body. In the case of individuals with phantom limbs following amputation, for example, the missing limb is perceived to be present, even though the patient well knows that it is absent (Melzack, 1992; Ramachandran & Hirstein, 1998). Often the phantom sensation is extremely vivid and realistic, to the point that patients may attempt to walk on their phantom leg (Melzack, 1990). This conflict demonstrates the presence of two types of representation: (1) a perceptual representation (what the body is *felt* to be like) which has not been updated to reflect the amputation, and (2) a cognitive representation (what the body is *believed* to be like) which has been updated. Thus, phantom limbs provide an example of an intervention (i.e., amputation) which can induce a selective modification of cognitive – but not perceptual – body representations.

Conversely, other illusions provide evidence for selective modification of perceptual information about the body, without change in body representation. For example, Lackner's (1988) *Pinocchio illusion* relies on vibrating muscle tendons to trigger afferent signals to the brain that the muscle is lengthening. This produces

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Table 1
Major components of somatoperception and somatorepresentation, describing their basic functions and neural bases.

	Functions	Neural bases
Somatosensation		
	Primary sensory processing of somatic stimuli	Primary somatosensory cortices (Kaas, 1983; Mountcastle, 2005)
Somatoperception		
Superficial schema	Localisation of somatic stimuli on the body surface	Parietal lobes (Denny-Brown et al., 1952), esp. anterior parietal/TPJ (Porro et al., 2007; Van Boven et al., 2005)
Postural schema	Perceiving the current posture of the body	Superior parietal (Pellijeff et al., 2006; Wolpert et al., 1998), and lateral intraparietal (LIP; Fasold et al., 2008; Snyder et al., 1998), esp. in right hemisphere (Sterzi et al., 1993)
Model of body size and shape	Perceiving metric properties of tactile stimuli	Unknown, presumably parietal lobes
Conscious body image	Construction and maintenance of sense of self, self-recognition	PPC (Bisiach et al., 1986; Salanova et al., 1995), esp. in right hemisphere (Critchley, 1953)
Emotion-in-body	Affective processing of and responses to somatic stimuli	Anterior insula (Olausson et al., 2002; Schreckenberger et al., 2005)
Somatorepresentation		
General/encyclopaedic knowledge about bodies	General semantic knowledge	Unknown, likely diffuse
Lexical-semantic knowledge about bodies	Naming and communication	Left hemisphere, esp. inferior parietal (Kemmerer & Tranel, 2008; Laiacona et al., 2006; Suzuki et al., 1997), anterior temporal (Dennis, 1976), and inferior frontal (Kemmerer & Tranel, 2008) cortices
Structural/topological knowledge of one's own body	Semantic knowledge about arrangement of body parts	Left hemisphere, esp. superior parietal cortex (Felician et al., 2004), intraparietal sulcus (Corradi-Dell'Acqua et al., 2008), left temporal lobe (Schwoebel & Coslett, 2005)
Emotion-about-body	Formation of attitudes towards the body	Right hemisphere (Loetscher et al., 2006), esp. parietal and frontal lobes (Blanke et al., 2009; Critchley, 1953)

corresponding illusions of movement and displacement (Goodwin, McCloskey, & Matthews, 1972). For example, vibrating the biceps tendon produces the illusion of elbow extension, while vibrating the triceps tendon produces the illusion of elbow flexion. Lackner (1988) used tendon vibration to induce illusions of elbow flexion or extension while participants held onto their nose with the hand of the stimulated arm. This situation produces a perceptual dilemma, since the hand is perceived to be moving relative to the body, yet maintains continuous contact with the nose. Lackner found that many participants experienced their nose as changing size, shrinking during illusions of forearm flexion, and extending during illusion of forearm extension. Nevertheless, participants were perfectly aware that their nose was not actually changing.

In contrast to the case of phantom limbs in which perception of the body remains relatively constant following an actual change of body form, the Pinocchio illusion provides an example of an intervention (tendon vibration plus self-touch) which, conversely, induces selective modification of perceptual – but not cognitive – body representations. It is worth noting, though, that in both cases beliefs are veridical and percepts mistaken (that is, these are *il*lusions, not *de*lusions). The double-dissociation indicated by the two illusions justifies our distinction between somatoperception and somatorepresentation, which has, however, rarely been made in the literature (e.g., Lhermitte, 1942; Werner, 1965).

2. Somatoperception

Somatoperception refers to the processes of constructing percepts and experiences of somatic objects and events, and of one's own body. Unique among sensory modalities, the somatic receptor surface (the skin) is coextensive with the body surface. This implies that the construction of veridical percepts of touch must be referenced to and informed by pre-existing representations of the body. Similarly, several forms of immediate emotional experience appear to be fundamentally linked to the body. These cases involve body representations *mediating* perception and experience. However, the body can also be a direct *object* of perception. This can be seen in the process of constructing explicit models of body form (the conscious body image, i.e., a percept of *what* my body is), and the configuration of body parts (the *postural schema*, i.e., a percept of *where* my body is). Thus, somatoperception involves some cases in which the body is a vehicle for perception, and others in which it is itself the object of perception. Both cases, however, involve the essentially perceptual process of constructing representations of the present state of the body and tactile stimuli from sensory inputs.

2.1. Body referencing of somatic sensation

Representations of the body must figure in some way in sensory processing in several modalities. For example, auditory localization requires representations of the distance between the two ears, and the shape of the pinna (Aslin, Pisoni, & Jusczyk, 1983; Clifton et al., 1988). Similarly, for binocular disparity to be effective for visual depth perception, the spacing between the two eyes must be taken into account (Banks, 1988). Other types of body representation, such as of eye-height (Warren & Whang, 1987), and arm-length (Longo & Lourenco, 2007), play a role in various aspects of visual perception. Nevertheless, the information about the body required for vision and audition is secondary. In the case of touch, in contrast, models of the body are fundamental. Some qualities of tactile stimuli, such as pressure, tapping, and flutter, may be specified in part by labelled lines (Torebjörk, Vallbo, & Ochoa, 1987) operating independent of body representation. However, to go from pure sensation to tactile perception requires referring to models of one's own body. Veridical perception of the size, shape, location, and identity of objects touching the skin requires that afferent information be informed by representations of the size, shape, configuration, and posture of the body. Perceiving the properties of an external object touching the body depends on perceiving the state