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RUNNING HEAD: Body Beyond SI

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. *Somatoception* refers to the process of perceiving the body itself, and particularly of ensuring somatic perceptual constancy. We review three key elements of somatoception: (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.

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 *somatosensation* (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 *somatoperception*, and (2) abstract knowledge, beliefs, and attitudes about bodies generally and one's own body specifically, which we term *somatorepresentation*. 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 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 *illusions*, not *delusions*). The double-dissociation indicated by the two illusions justifies our distinction between somatoperception and somatopresentation, which has, however, rarely been made in the literature (e.g., Lhermitte, 1942; Werner, 1965).

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.

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 of the body itself, particularly but not solely in those skin regions that contact the object.

Figure 1 shows a model of somatoperceptual information processing. In addition to the sensation of tactile quality, there are four basic processes we will discuss, each of which requires mediation by at least one type of body representation. These processes include: (1) localisation of touch on the body surface, (2) perceiving the metric properties (i.e., size and shape) of objects touching the skin, (3) perceiving the location of body parts in external space, (4) perceiving the location of objects touching the body in external space (i.e., *remapping* into external space). We suggest that underlying these processes are three classes of body representations. The first two were first described by Head and Holmes (1911): the *postural schema*, a dynamic representation of the position of the body in space, and the *superficial schema*, mediating localisation of somatic sensations on the body surface. The third body representations is a model of metric

properties of the body, such as body part size. In the following sections, we describe each of these processes and the fundamental role of body referencing in each of them.

*** INSERT FIGURE 1 ABOUT HERE ***

Localisation of touch on the body surface

Perhaps the most fundamental of somatic abilities is the localisation of where on the body touch has occurred (*topognosis*). On some skin surfaces, such as the glabrous skin of the palmar hand, this ability is extremely acute, and can even be specified by activations of single mechanoreceptive afferents (Schady, Torebjörk, & Ochoa, 1983). Head and Holmes (1911) first reported a number of patients who, following cortical lesion, were unable to indicate where they had been touched (*atopognosia*), though their ability to detect that they had been touched was apparently unimpaired. Several authors have suggested that localisation errors mainly involve shifts of perceived location proximal to the actual location of touch (e.g., Critchley, 1953; Halligan et al., 1995; Rapp, Hendel, & Medina, 2002). A more complex pattern of mislocalisations, however, was reported by Denny-Brown, Meyer, and Horenstein (1952) who found in one patient that the perceived locations of touches were funnelled towards the wrist and the ankles, resulting in effective foreshortening of the upper arm and leg. Head (1918) reports several cases in which patients were clearly able to determine *which* finger was touched, but completely unable to indicate *where* on that finger they were touched. Several of his patients reported experiencing the touch “spread out” across the whole of the finger, and even experienced sensations of movement from a single punctuate touch. On the basis of such

observations, Head and Holmes (1911) proposed that the ability to localise stimuli on the body was subserved by a mental representation of the body surface, the superficial schema.

Intriguingly, there are also reports of patients who are able to localise touches they are unable to detect (Paillard, Michel, & Stelmach, 1983; Rossetti et al., 1995), a condition known – by analogy to blindsight – as *numbsense*. Numbsense and atopognosia, then provide an effective double-dissociation between the ability to detect and to localise tactile stimuli. The dissociation, however, is not perfect. Localisation in numbsense, unlike detection in atopognosia, is inaccessible to conscious awareness. Furthermore, preserved localisation in numbsense appears to occur only when participants respond by actively pointing (Rossetti et al., 1995); patients perform at chance when asked to respond by pointing to a location on a schematic drawing, the classic test of atopognosia (Head & Holmes, 1911). Indeed, Anema and colleagues (2009) recently reported a double-dissociation between the ability to indicate on a schematic drawing where one was touched and the ability to point to the location of touch on the body surface itself. Nevertheless, there is clearly some degree of dissociation between detection and localisation, and the former does not imply the latter, as has often been presumed (cf. Bender, 1952).

Poeck and Orgass (1971) criticised the concept of the superficial schema, writing “[i]t is difficult to see the difference between the superficial schema as an organized model and the “homunculus” of the cortical sensorimotor representations” (p. 258). Indeed, several studies have elegantly demonstrated how the brain represents tactile location via population coding within somatotopic maps (e.g., Ghazanfar, Stambaugh, & Nicolelis, 2000; Koerber, Hobbs, & Brown, 1993; Nicolelis et al., 1998). But localising a stimulus within a somatotopic map is not by itself sufficient to localize the stimulus on the body surface. There is no intrinsic, hard-wired, link between a location in a somatotopic map and a body location. This is especially true given

the clear plasticity of somatotopic maps following peripheral trauma (Merzenich et al., 1984; Pons et al., 1991) and learning (Elbert et al., 1995; Pascual-Leone & Torres, 1993). While some referral of sensation between skin surfaces may occur following massive cortical reorganisation (e.g., Ramachandran, Rogers-Ramachandran, & Stewart, 1992) or in plasticity induced by simultaneous tactile co-activation of skin surfaces (Schweizer et al., 2001; Sterr et al., 1998), in most cases plastic changes in somatosensory cortex do not lead to mislocalisation of touch. For example, while mislocalisation of touch between fingers has been reported in three-finger Braille readers (Sterr et al., 1998), similar errors were not found for single-finger Braille readers (Sterr et al., 1998), who nevertheless show large plastic changes of somatosensory cortex (Pascual-Leone & Torres, 1993). The specificity of localisation errors to situations involving tactile co-activation (e.g., Schweizer et al., 2001; Sterr et al., 1998) suggest that they result from a blurring of the representations of skin surfaces, which is not a general consequence of somatosensory plasticity.

That localisation errors are not ubiquitous following plastic changes in somatosensory maps implies that there can be no hard-wired connection between location within a somatotopic map and location on the body surface, since the body part represented by any specific bit of cortex may change. To localise a stimulus on the skin, then, an additional linking function is required which connects locations within a neural map to skin regions overlying particular body parts, and is updated to reflect plastic changes to primary somatotopic maps. The superficial schema is perhaps best viewed as the process that provides this link. Thus, we suggest that localising a touch on the body surface is a two-stage process. First, the stimulus must be localised within a somatotopic map. This involves identifying its *relative* position with respect to other locations in the map. We suggest this relative position computation is a purely

somatosensory process, making no reference to the physical body as an object in the world, potentially being computed entirely within a single map in primary somatosensory cortex or even subcortically (e.g., in the superior colliculus; Clemo & Stein, 1984). Second, this somatotopic location must be mapped onto a corresponding bodily location; this is an essentially somatoperceptual process, referenced to a representation of the body (the superficial schema).

The dissociation between somatotopic localisation and localisation onto the body surface is demonstrated by the study of Rapp and colleagues (2002). They reported two patients with left hemisphere lesions who showed distorted, but highly structured, errors of tactile localisation. These patients' localisation errors preserved the somatotopic arrangement of the hand, but systematically misplace each point onto the body surface. This suggests that their deficit does not involve somatotopic representation as such, since the somatotopy is preserved. That is, their responses preserve the relative location of touches with respect to other touches. Rather, their deficit appears to involve a distortion in the way locations in such a map are related to the body surface.

Other evidence suggests that the superficial schema involves both the somatotopic maps in the primary somatosensory cortex (SI), and additional processes in parietal areas posterior to SI. For example, the ability to localise touch on the skin can be impaired by transcranial magnetic stimulation (TMS) applied to primary sensorimotor cortices. Seyal et al. (1997) found that TMS over the sensorimotor cortex disrupted both tactile detection and localisation, but found more profound and long-lasting deficits for localization than for detection. A more selective deficit in localisation was reported by Porro et al. (2007). These authors asked participants to make forced-choice judgments of tactile or painful stimuli delivered at one of four locations on the dorsum of the hand. They found that three-pulse trains of 25 Hz TMS applied to

the anterior parietal cortex starting 150 ms (but not 300 ms) after touch selectively impaired the ability to localise the touch on the skin, with no apparent affect on stimulus detection. One fMRI study comparing judgments of location to judgments of form (i.e., grating orientation) found activation of the right temporoparietal junction (TPJ) selective for localisation (Van Boven et al., 2005). It is possible that this TPJ activity may reflect the process of linking somatotopic and body-surface localisation.

Proprioceptive localisation of body parts in external space

Head and Holmes (1911) introduces the notion of the postural schema to refer to a continuously updated representation of the posture of the body:

“By means of perpetual alterations in position we are always building up a postural model of ourselves which constantly changes. Every new posture or movement is recorded on this plastic schema, and the activity of the cortex brings every fresh group of sensations evoked by altered posture into relation with it. Immediate postural recognition follows as soon as the relation is complete.” (pg. 187)

This construct is now often referred to as the *body schema*, and related to the control of action. The term body schema, however, has a long history of inconsistent and contradictory usage (for reviews see Gallagher, 2005; Poeck & Orgass, 1971). Thus, we use the less ambiguous term postural schema.

Proprioceptive afferent information comes from mechanoreceptors in joints, muscles, muscle tendons, and stretch-sensitive receptors in the skin. Together with efferent signals from the motor system specifying movements, these describe the configuration of the body in terms of the degree of flexion or extension of each joint (Burgess, Wei, Clark, & Simon, 1982). There is, however, no afferent signal, or combination of afferent signals, analogous to a global-positioning

system (GPS) signal, specifying the absolute location of body parts in external space. In order to determine the location of a body part or skin surface in external space, information about the configuration of the body (joint angles) must be combined with information about the length of the segments connecting those joints, and about the width of each body part. No afferent information provides such information about body size; it must be provided by a pre-existing body representation.

Therefore, locating body parts in space requires a combination of afferent information and stored representations of the body. Head and Holmes (1911) recognised that this is a complex and vulnerable computational process:

“Inability to recognize the position of the affected part in space is the most frequent sensory defect produced by lesions of the cerebral cortex. In some cases, this and the allied faculty of recognizing passive movement may be the only discoverable abnormalities. Whenever sensation is disturbed at all, these two forms of spatial recognition will be certainly affected.” (p. 157)

Given its disruption by widespread lesions throughout the parietal lobes, it is difficult to specifically localise the postural schema in the brain. Areas of the superior parietal cortex have been found to encode arm position in monkeys (area 5; Graziano, Cooke, & Taylor, 2000; Sakata et al., 1973) and to maintain and update the postural representation of the current body's state in humans (Wolpert et al., 1998; PelliJeff et al., 2006; Filimon, Nelson, Huang, & Sereno, 2009). Other studies have implicated the lateral intraparietal area (LIP) in coding of head posture; Snyder, Grieve, Brotchie, & Andersen, 1998; Fasold et al., 2008). Furthermore, deficits of

position sense are on average more severe following PPC lesions in the right than the left hemisphere (Sterzi et al., 1993; Vallar, Antonucci, Guariglia, & Pizzamiglio, 1993).

The need for veridical body models for accurate proprioception is shown by the widely-reported clumsiness seen in adolescents (Tanner, 1962), often claimed to be related to the ‘growth spurt’ in which rapid changes in body size occur. These changes may outpace the ability of somatoperception to update the body model used for proprioceptive localisation in adolescents. This would produce systematic misjudgments about the location of body parts in external space. Indeed, recent studies have shown that the onset of coordination difficulties is temporally tightly locked to the onset of increased growth velocity (Visser, Geuze, & Kalverboer, 1998; Hirtz & Starosta, 2002). Similarly, systematic changes in locomotor coordination were recently observed in an achondroplastic patient following surgical extension of the limbs, as well as in healthy adults wearing stilts (Dominici et al., 2009).

Little is known, however, about the specific nature of the body model underlying external localisation of the body. Indeed, it is not even clear whether this body model is the same as underlies perception of the size and shape of tactile objects (see below). One interesting observation was reported by Gurfinkel and Levick (1991), who found that participants asked to indicate the perceived location joints tended to underestimate the distance between them. This raises the possibility that the body model mediating proprioceptive localisation may be systematically distorted. This is an important issue for future research.

Perceiving the metric properties of tactile objects

There are multiple ways of perceiving the size of objects via passive touch. For example, we can perceive the size of an object touching two different skin surfaces (e.g., during precision grip) by determining proprioceptively how far apart the finger and thumb are. Such perception

requires reference to a model of the metric properties of the body for the reasons described in the previous section. We can also perceive the size of objects touching a single skin surface on the basis of the extent of skin surface touched (or the distance between two touches). This too must be referenced to a representation of bodily size. For example, if I feel that an object covers half the width of my hand, I can only form a representation of the object's size if I know how wide my hand is.

Such problems do not arise only in perceiving the absolute size of objects; even determining the *relative* size of objects touching the skin poses a similar computational problem. Somatosensory representations are massively distorted at all levels of the nervous system that have been studied. This distortion derives ultimately from the density and receptive field sizes of mechanoreceptors in the skin, but it is also seen in receptive field size of cortical units, and over-representation of skin regions such as fingers and lips in cortical sensory maps. It also has important effects on perception. For example, Weber (1834/1996) reported an illusion in which the perceived distance between two points on the skin increases as the points are moved from a region of low to one of higher sensitivity (*Weber's illusion*). Subsequent quantitative studies confirmed Weber's observation, and showed that perceived tactile distances are, indeed, tightly related to tactile sensitivity and cortical magnification (Cholewiak, 1999; Goudge, 1918).

Weber's illusion suggests that the perception of tactile size is not, in fact, veridical. Nevertheless, the magnitude of Weber's illusion is less than 10% of what would be predicted on the basis of tactile acuity or cortical magnification alone (Taylor-Clarke et al. 2004). This suggests an additional process of tactile size constancy which corrects for distortions inherent in primary representations to produce (approximately) veridical percepts of size (cf. Taylor-Clarke, Jacobsen, & Haggard, 2004), that would require a representation of the actual metric properties

of the body. There are no afferent signals, however, that directly specify bodily size or shape. Rather, current tactile input must be scaled by a pre-existing body model in order to compute size of the objects touching the skin. Indeed, several recent studies have demonstrated that manipulating the perception of body form produces corresponding alterations in the perception of tactile size.

Taylor-Clarke and colleagues (2004) investigated the effects of vision of the body on the perception of tactile size. Participants judged whether the distance between two touches on the index finger was bigger or smaller than a distance presented on the forearm. A classic Weber illusion was found, with identical touches being perceived as larger on the finger. Using a video camera and magnifying mirrors, they then presented participants with the visual percept of their hand reduced in size by half, and of their forearm doubled. As expected, following such vision, the magnitude of Weber's illusion between the finger and forearm was significantly reduced. These results suggest that visual experience of the body serves an important function in shaping the body model underlying tactile size constancy.

A similar result was reported by de Vignemont, Ehrsson, and Haggard (2005a) who used the logic of the Pinocchio illusion to alter the perceived length of the finger. By having participants hold onto their left index finger with their right hand while vibrating the biceps or triceps tendons of the right arm, de Vignemont and colleagues produced the illusion that the left index finger was either lengthening or shrinking, depending on which muscle was stimulated (cf Lackner, 1988). This illusion of finger lengthening in turn induced a significant modulation of Weber's illusion measured between the index finger and forearm; participants were more likely to judge identical touches as bigger on the index finger when that finger was perceived as being longer. This result echoes the findings of Taylor-Clarke and colleagues (2004), showing that

alterations to the perceived metric properties of the body affect tactile perception of metric properties of external objects.

Although no peripheral receptors specify the size of body parts, alterations of perceived body size can also be induced by peripheral deafferentation. Gandevia and Phegan (1999) found that complete anaesthesia of the thumb induced via digital nerve block led to a 60-70% increase in its perceived size. Interestingly, Berryman, Yau, & Hsiao (2006) found a 28% increase of perceived size of objects held between the fingertips when cutaneous afferents were blocked by anaesthesia. The difference between their 28% effect and the 60-70% effect of Gandevia and Phegan may arise because cutaneous afferents are only one source of information about the size of objects held in the hand: proprioceptive signals from the muscles also contribute.

Perceiving the location of tactile objects in external space

Consider the ability to use your right hand to swat a fly crawling on your left hand. Such computation of the external spatial location of an object touching the skin is perhaps the most computationally demanding of somatoperceptual tasks, requiring the use of all three body representations. First, the location of the touch on the body surface must be determined, implicating the superficial schema. Second, the configuration of joints must be determined, implicating the postural schema. Lastly, the external spatial location of the touched body surface must be established by combining information about joint configurations with representations of the length of body segments connecting joints, implicating a model of the metric properties of the body. This process of converting tactile location from a somatotopic to an external frame of reference is referred to as the *remapping* of touch.

A curious failure of remapping in the case of fingers was first described by Aristotle (1924). The main characteristic of this *Aristotle illusion* is an erroneous perception of two objects when a single object is placed between crossed fingers (Benedetti, 1985). Under this unusual posture, tactile spatial information is processed as if fingers were in the usual, uncrossed posture. Only after months of adaptation to crossed fingers, which presumably modifies the postural schema representation, remapping seems to be accurately achieved (Benedetti, 1991). Thus, manipulating limb positions, and in particular crossing body parts, has become a main tool in the study of tactile spatial encoding (Bolognini & Maravita, 2007; Röder, Rösler, & Spence, 2004; Yamamoto & Kitazawa, 2001). Yamamoto and Kitazawa (2001) for example, found that crossing the hands impaired judgments of the temporal order of tactile stimuli delivered in rapid succession to homologous fingers of the two hands. This effect was interpreted as a failure to process the external position of touch when a second stimulus is presented before the first stimuli is adjusted for the crossed posture of the hands. Similar disruption of temporal order judgments has been also found by placing uncrossed hands close together as compared to far apart (Shore, Gray, Spry, & Spence, 2005), even when the separation is apparent, visually introduced by mirrors, but the actual position of the hands is kept constant (Gallace & Spence, 2005). Such results have been reported even when non-homologous body parts (e.g., one hand and one foot) are crossed (e.g., Schicke & Röder, 2006). Such findings demonstrate the obligatory nature of remapping touch into external space, even when this is maladaptive for the current task. If tactile representations were encoded solely in terms of the localisation on the skin surface, posture should not have affected performance at all.

Yamamoto and Kitazawa's (2001) study also pointed to a plausible time course of these spatial transformations, suggesting that spatial encoding takes approximately 300 ms, given that

systematic reversals of temporal order were observed at shorter intervals. Similarly Groh and Sparks (1996a) found that saccades to tactile stimuli with hands crossed were initially directed towards the wrong hand, but corrected online approximately 265 ms after initiation. Similarly, Azañón and Soto-Faraco (2008) found an inversion of spatial cueing effects of touch on vision when the hands were crossed. When the interval between tactile cues and visual targets was less than about 180 ms spatial cueing effects appeared to be determined by somatotopic representations that were later replaced by an external representation of touch. These results suggest that immediately following stimulation, touch is remapped into external space not on the basis of a percept of the actual current posture of the body, but rather on the basis of a stored representation of the canonical, or default, posture. Intriguingly, the canonical posture suggested by these studies is similar to that reported by individuals following deafferentation of the arm by brachial plexus anaesthesia (Bromage & Melzack, 1974), in which a stereotyped arm posture is perceived, independent of the actual posture of the arm before anaesthesia. Bromage and Melzack (1974) suggested that this posture, with the shoulder and elbow joints approximately midway through their range of motion, constitutes the “position of orthopaedic rest” (p. 271) at which subsequent changes of joint position are maximally informative.

As described above, the representation of current limb position has been linked to the superior parietal lobule (Filimon et al., 2009; Pellijeff et al., 2006; Wolpert et al., 1998), as well as the lateral intraparietal area (Fasold et al., 2008; Snyder et al., 1998). Putative sites mediating the further remapping process include areas within the parietal and the premotor cortex, as well as subcortical areas such as the putamen (Graziano & Gross, 1993). For example, the ventral intraparietal area (VIP) contains neurons representing visual, vestibular, tactile and auditory information (Schlack et al., 2002, 2005; Bremmer et al., 2001) and responds both to stimuli on

the skin and the surrounding peripersonal space (Duhamel, Colby, & Goldberg, 1998). The ventral premotor cortex also contains neurons highly responsive to arm position responding to both touch and visual input in peripersonal space (Graziano, Yap, & Gross, 1994), and together with VIP has been suggested to constitute a multisensory representation of peripersonal space in monkeys (Graziano & Cooke, 2006) and in humans (Lloyd, Shore, Spence, & Calvert, 2003).

The conscious body image

Is the body model used for scaling tactile percepts the same as the conscious body image? The presence of Weber's illusion suggests it is not. This illusion demonstrates that the body model underlying tactile rescaling preserves (in attenuated form) distortions characteristic of the somatosensory homunculus. In contrast, such distortions do not appear to be part of the conscious model of our body: although our fingers have high receptor density and high sensitivity, we do not perceive them as distorted. This dissociation suggests the existence of both implicit and explicit body models, the former retaining homuncular distortions characteristic of primary somatosensation and being used for scaling tactile percepts, the latter being approximately veridical and underlying our conscious perception of body form. It is clear, however, that these implicit and explicit body models interact. For example, changes in the conscious perception of body size, induced with visual (Taylor-Clarke et al., 2004) or proprioceptive illusions (de Vignemont et al., 2005a) influence tactile perception. Furthermore, modulations of somatosensory input alter the conscious body image (Gandevia & Phegan, 1999).

Several lines of evidence suggest that the conscious body image is not directly linked to primary somatosensory activity, but arises from activity in the posterior parietal cortex (PPC).

Thus, while both phantom limb *pain* (Flor et al., 1995; Grüsser et al., 2001; Knecht et al., 1995) and referred sensations elicited by *painful* stimuli (Knecht et al., 1996; Grüsser et al., 2001) are closely correlated with plastic changes in SI following amputation, *non-painful* phantom phenomena, such as referred sensations of touch and the perceived telescoping of phantom limbs into the stump, are more closely related to changes in PPC (Flor et al., 1995, 2000; Knecht et al., 1995, 1996; Grüsser et al., 2001). Similarly, subjective experiences of phantom limbs are not strongly related to sensory thresholds or tactile acuity on the stump (Hunter, Katz, & Davis, 2005). Furthermore, Kew et al. (1994) found abnormal increases in the posterior parietal cortex activity related to movements of the phantom arm. Furthermore, while ablation of SI has remarkably little effect on phantom limbs (White & Sweet, 1969), some authors have reported that lesions of the posterior parietal cortex can suppress the experience of phantom limbs (Berlucchi & Aglioti, 1997). Thus, while SI may be involved in the generation of pain related to phantom limbs, it does not appear to be fundamentally involved in the generation of the phantom limb as such, a function more clearly related to the PPC.

Consistent with this interpretation, lesions of the PPC (usually in the right hemisphere), can induce the condition of *asomatagnosia*, in which the left side of the body feels as if it has disappeared (Critchley, 1953). This condition is an interesting and strange inversion of the phantom limb situation (Arzy, Overney, Landis, & Blanke, 2006; Critchley, 1953). Following a lesion of the left PPC, the patient of Wolpert, Goodbody, and Husain (1998) found that her right arm and leg would gradually fade from consciousness, but would return when she looked at them. Similarly, surgical section of the non-dominant PPC frequently induced various disturbances of the conscious body image, such as perceived absence of body parts (Salanova et al., 1995). Related to such phenomena of perceived absence is personal neglect following right

PPC lesion, in which patients do not report their left arm as missing, but nevertheless fail to attend to or use it (Bisiach, Perani, Vallar, & Berti, 1986; Critchley, 1953; Guariglia & Antonucci, 1992).

Where does the conscious body image come from? The most obvious source of information about the form of one's body is vision. In patients with phantom sensations following spinal cord injuries, sensations of *increased* body part size are common, but sensations of *decreased* body part size are conspicuously absent (Bors, 1951; Conomy, 1973; Evans, 1962). This is in striking contrast to the common phenomena of shrinkage and telescoping of phantom limbs following traumatic amputation (Henderson & Smyth, 1948; Riddoch, 1941). Since deafferentation is common to both situations, this suggests an important role of visual feedback in calibrating the conscious model of the body. Telescoping, then, can be considered a result not of deafference as such, but of the conflict between the premorbid body image and vision (or, possibly, touch) of the body which occurs in amputees, but not in paraplegics.

On the other hand, telescoping of phantom limbs is generally a gradual process, occurring gradually over months or years (Riddoch, 1941). This is in contrast to the nearly instantaneous modulations of perceived body form induced by acute deafferentation following cutaneous anaesthesia (Gandevia & Phegan, 1999; Paqueron et al., 2003; Türker, Yeo, & Gandevia, 2005), or proprioceptive illusions (Ehrsson et al., 2005; Lackner, 1988; de Vignemont et al., 2005a). It is not clear why acute deafferentation should have more striking effects on the body image than chronic deafferentation. Nevertheless, such findings suggest that vision is not entirely dominant in the formation of the conscious body image, which appears to reflect a combination of several

sources of input, including proprioceptive and tactile afferent inputs (e.g., Lackner, 1988) as well as thermal and nociceptive ones (e.g., Paqueron et al., 2003).

Emotion-in-body

Dijkerman and de Haan (2007) drew a distinction between emotional experience related to the body, which they related to processing in the insula, and metric properties of body representation, which they related to processing in the posterior parietal cortex. We suggest that our distinction between somatoperception and somatorpepresentation applies to bodily emotions, in the same way as we have applied it above to metric perception. Therefore, we distinguish between the somatoperceptual processes related to experienced emotion *in* the body from emotional states and attitudes *about* the body. The latter cases are best described as representations *of* one's own body, and attitudes *towards* one's own body that have emotional significance. Examples might include the feeling of distaste generated by looking at one's hand after bruising, bleeding or touching offensive objects, or disliking a particular feature of one's body that one judges unaesthetic. This distinction is important, because the two situations have very different implications for body representation. The first case, which we call *emotion-in-body* has well-characterised neurophysiological correlates, generally involves specific stimulus and response events, and involves the body as a vehicle rather than content of mental representation. The second case, which we call *emotion-about-body* (discussed later), has less clear neural correlates, generally involves contexts, attitudes and states, rather than single stimulus or response events, and involves the body as a direct content of mental representation.

The connections between mental representation of one's own body and emotion have long been recognised. To give one classical example, Descartes in his Sixth Meditation (1641/1989, pp. 113-114) notes:

Nor was I altogether wrong in likewise believing that that body which, by a special right, I called my own, pertained to me more properly and strictly than any of the others; for in truth, I could never be separated from it as from other bodies; I felt in it and on account of it all my appetites and affections, and in fine I was affected in its parts by pain and the titillation of pleasure, and not in the parts of the other bodies that were separated from it.

Descartes not only stresses the obvious link between self and body, but also notes that affect and emotion play an essential role in making that link. Emotional states have a clear grounding in the body, and are often linked to specific body locations (pain) or to more diffuse but readily identifiable systems (fear, stress). At the same time, they provide a dominant and immediate tone of mental life.

It is widely recognised that emotions involve a tight coupling between subjective experiences and widely-distributed bodily reactions to external stimuli. According to the James-Lange theory of emotions (James, 1884, 1890), the emotion of sadness is a psychological sequela of the physiological response of crying, the feeling of fear is a response to visceral changes in fight/flight situations etc. The somatic marker hypothesis (Damasio, 1994, 1999) agrees on the basic body-emotion direction of causation, but stresses the role of emotions in guiding behaviour, through influencing decision-making and behavioural control. Emotions thus form a key part of the homeostatic design principle.

Most neuroscientific work in this tradition has focussed on identifying the brain mechanisms linking emotion to voluntary behaviour, and more specifically the key role of orbitofrontal cortex (Rolls, 2004). These functions reflect a form affective-cognitive control rather than body representation. However, a second aspect of the homeostatic view of emotion refers to the role of somatosensory cortices in sensory simulation of affectively-significant states. On this view, emotion processing involves neural body representations directly, because the anterior brain circuits for emotion may reactivate somatosensory-based memories of previous bodily experiences through an “as-if body-loop” (Damasio, 1994). For example, an emotion of sadness may simulate or recall a previous somatosensory experience of convulsive sobbing. This view receives some support from studies in which simply viewing the bodies of others can activate the somatosensory cortex. For example, rTMS applied to the face region of SI impaired recognition of facial emotional expressions, but not of face identity (Pitcher, Garrido, Walsh, & Duchaine, 2008). Conversely, viewing stimuli such as erotic images or mutilated bodies produced an activation of right SI and SII in a MEG study, relative to viewing neutral material (Rudrauf et al., 2009). These activations could be interpreted as increased attention to one’s bodily states resulting from increased arousal due to emotional stimuli. However, this would not explain their clear lateralisation in the brain. Alternatively, they might reflect a somatosensory simulation triggered by the viewed material, and linked to previous somatic experience. In either case, neural representation of the experiencing subject’s body is a vehicle of their emotional experience triggered by the stimulus (which in this case is the body of another person).

Avenanti and colleagues (2007) found direct causal evidence for somatosensory cortex involvement in body-related processing. When people view either possible or impossible (and painful-looking) manual actions, the excitability of the motor cortex to TMS is increased relative

to viewing a static hand. However, previous temporary disruption to SI using rTMS prevented this excitability increase for impossible actions only. This result suggests that the somatosensory cortex plays a necessary role in regulating cortical excitability as a function of viewing body parts. Future research might use the same paradigm compare body and non-body stimuli, and explicitly manipulate the emotional valence of the stimuli presented.

A second type of emotion-in-body has focussed on the brain pathways that carry signals of potentially affective significance from the body periphery. Here the focus has generally been on nociceptive inputs to the insula. While visceral inputs to the insula are strong and important (e.g., Critchley et al., 2004; Mehnert et al., 2008; Wang et al., 2008), most research has focussed on tactile and thermal inputs (e.g., Craig, Chen, Bandy, & Reiman, 2000; Olausson et al., 2002), which are methodologically easier to study. Craig (2009), reviewing a wide range of human studies, noted that anterior insular activation is repeatedly associated with awareness of one's own body in general, and with awareness of the emotional significance of bodily events in particular. For example, stimulation of the anterior insula evokes feelings of nausea and sickness (Penfield & Faulk, 1955), and it is activated both by the first-person experience of disgusting tastes (Small et al., 2003) and smells (Royet et al., 2003), as well as by the perception of disgust in others (Phillips et al., 1997; Krolak-Salmon et al., 2003; Wicker et al., 2003). Further, Tsakiris et al. (2007) found that insular activation increased in proportion with a measure of body ownership in the Rubber hand illusion (RHI). Interestingly, this form of bodily awareness is related to specific sensorimotor events, such as the correlated visual-tactile inputs that induce the RHI, rather than having continuity through time. The insula may house the bodily awareness required to pass a rouge test (Gallup, 1970), rather than the continuous bodily self of autobiographical memory (Conway, 2001).

The emotional, rather than purely sensory, aspects of the insular representations of somatic information are very clearly demonstrated in the context of touch. Recent neurophysiological studies suggest the existence of two parallel touch systems. Most skin mechanoreceptors project via myelinated afferents to the thalamus and primary somatosensory cortex (Johnson & Hsiao, 1992; Mountcastle, 2005). However, a distinct subgroup of tactile mechanoreceptors project via unmyelinated afferents to the insula (Olausson et al., 2002; Vallbo, Olausson, & Wessberg, 1999). The unique contribution of these tactile C-fibres was elegantly shown by Olausson and colleagues (2002) in a study with an individual lacking myelinated afferents. Gentle stroking of the skin produced a faint, pleasant sensation, and activation of the insular cortex, but no activation in classical somatosensory cortical areas SI and SII. This parallel system for “affective touch” (Essick, James, & McGlone, 1999) may play a particular role in social bodily interactions such as grooming and caressing that are characterised by their strong emotional associations. Similarly, the anterior insular cortex codes the affective component of pain, both as experienced oneself (Kong et al., 2006; Schreckenberger et al., 2005), and in others (Singer et al., 2004).

Somatorepresentation

Somatoperception involves the on-line construction of higher-level percepts related to the body, building on the unique status of the body as a source of private first-person experience. In contrast, somatorepresentation emerges from the body’s character as a physical object in the external world, just like any other. At a general level, the body, like all objects, is subject to physical laws such as gravity, and shares the same types of features (e.g., mass, volume, solidity). More specifically, our body is a specific instance of various biological categories (e.g.,

human bodies, mammals, etc.) about which we have various types of knowledge. For example, we each believe that we have various internal organs (e.g., a spleen) on the basis of general knowledge about humans (or animals), though we usually lack direct evidence of the existence and nature of our personal organs. Somatopresentation, then, involves abstract knowledge, beliefs, and attitudes related to body as an object of third-person perception, categorisation, and cognitive reflection.

Knowledge about the body

Bodies, whether our own or others', are among the most salient objects we encounter in daily lives. As such, we have a tremendous amount of knowledge about bodies. Kemmerer and Tranel (2008) suggest four main components of semantic knowledge about bodies: (1) knowledge about typical shape of body parts, (2) knowledge of the spatial location of a body part within the body as a whole, (3) knowledge of the characteristic functions of body parts, and (4) knowledge of the cultural associations of body parts. We also have general, or encyclopaedic, knowledge about bodies. Furthermore, in addition to general knowledge about bodies as a category, we also have specific knowledge about our own body and those of people we know, as specific instances of this category.

In many semantic domains, categorical knowledge is organised into hierarchical structures (taxonomies), in which subordinate nodes inherit properties of superordinate nodes (Collins & Quillian, 1969). The relation between a node in a taxonomy and its immediately superordinate node is characterised by 'type of' relations (e.g., a robin is a type of bird). In contrast, several authors have described knowledge about body parts as being organised into a structure called a *partonomy* (Brown, 1976; McClure, 1975), in which the relation between

subordinate and superordinate elements is characterised by ‘part of’ relations (e.g., an arm is *part of* a body, but is not a *type of* body). While a parthood is a specific type of data structure, representing the structural organisation of bodies, the more general process of segmenting the body into parts is known as *body mereology* (de Vignemont, Tsakiris, & Haggard, 2005b).

It is commonly assumed that while the nature of the connection between levels differs between taxonomies and parthoods, these are essentially similar types of data structure. Nevertheless, there do seem to be differences in the patterns of inference drawn from taxonomies and parthoods. For example, transitivity across levels is characteristic of taxonomies: if an X is a type of Y and a Y is a type of Z, then an X is a type of Z (e.g., a robin is both a type of bird and a type of animal); conversely, many speakers of English (and other languages) agree that a finger is part of a hand, but not that a finger is part of an arm. Indeed, even more problematic for the concept of parthood is the hesitance of many speakers to admit the validity of the ‘part of’ relation even to an immediately superordinate node. For example, many English speakers are not comfortable with the claim that ‘a hand is part of an arm’, preferring to say that ‘a hand is *connected to* an arm’ (Brown, 1976; McClure, 1975). From such observations, Palmer and Nicodemus (1985) argued that contiguity and spatial relations, rather than part-whole relations, underlie semantic knowledge about bodies. Alternately, Warrington and McCarthy (1987) suggest that functional information is central to the organisation of body semantics, to the point that bodies are more tightly linked as a semantic domain to man-made artefacts than to other types of living things. Given the complexity and salience of body parts, and their numerous social and cultural associations, however, it seems unlikely that any single type of hierarchical structure could mediate such semantic knowledge. Indeed, both spatial and functional errors are characteristic of deficits both of lexical-semantic and structural knowledge of bodies (see below).

Furthermore, Majid (2006) reports evidence that within a single language (Punjabi), the relations between different body parts are conceptualised using either part-whole relations and others through spatial relations (e.g., ‘in’, ‘on’, ‘attached-to’, etc).

Lexical-semantic knowledge about bodies

Early linguistic studies of body-part nomenclature (e.g., Andersen, 1978; Brown, 1976; McClure, 1975) focussed on the idea that cultural and linguistic universals in body part terms could be described, analogous to the universals found to underlie domains such as colour (Berlin & Kay, 1969) and folk biology (Berlin, Breedlove, & Raven, 1973). For example, while all languages studied had verbal labels for ‘fingers’ and ‘toes’, several languages (e.g., Romanian) did not have a label for ‘hand’ (McClure, 1975). Indeed, as far as McClure was able to determine in her interviews, many Romanian speakers made no conceptual distinction at all between the hand and the rest of the arm (analogous, for example, to the way that English speakers are unlikely to conceptually distinguish that portion of the finger distal to the first interphalangeal joint). If, however, a language did label ‘hand’, then the label was a primary lexeme (i.e., is not derivative from another term, as with, for example, ‘fingernail’). Conversely, while always labelled, terms for fingers and toes were often secondary (i.e., derivative) lexemes (Brown, 1976). While subsequent studies have called the literal universality of some such rules into question (e.g., Enfield, Majid, & van Staden, 2006; Palmer & Nicodemus, 1985), there are, nevertheless, striking regularities in the organisation of body part terms.

This suggests that the body is a distinct, and well-organised, lexical-semantic domain (cf. Coslett, Saffran, & Schwoebel, 2002). Indeed, several researchers have reported cases of patients with selective impairment (e.g., Dennis, 1976; Goodglass, Klein, Carey, & Jones, 1966;

Laiacona, Allamono, Lorenzi, and Capitani, 2006; Suzuki, Yamadori, & Fujii, 1997) of lexical-semantic knowledge related to the body following brain damage. For example, the patient described by Dennis (1976), with a left anterior temporal lesion, showed a delimited body part anomia, impaired in naming body parts, or in pointing to body parts that were verbally named, despite being able to point to the corresponding part on her own body. Nevertheless, naming errors for body parts never involved providing a word for a non-body part, nor were body part words given when she was asked to name other types of objects. This pattern suggests that she was able to correctly categorise objects as body parts, but had lost the finer lexical organization within that category. Similarly, the patient described by Suzuki and colleagues (1997) was unable to point to a verbally named body part, but was able to point to body parts described functionally (e.g., ‘with which organ do you see?’) or associated with another objects (e.g., ‘which parts do you put your socks on?’). This pattern suggests that information about functions and cultural associations was preserved, and the deficit was specific to lexical information about the names of body parts.

Other studies have reported selective sparing of lexical-semantic knowledge about bodies (e.g., Coslett et al., 2002; Shelton, Fouch, & Caramazza, 1998), providing clear double-dissociations between knowledge about bodies and other domains. Nevertheless semantic knowledge about the body may be unusually resilient to impairment (e.g., Capitani, Laiacona, Mahon, & Caramazza, 2003; Gainotti, 2004; Kemmerer & Tranel, 2008). Indeed, in a large study of 104 patients with brain lesions, Kemmerer and Tranel (2008) found 10 patients with difficulty in verbal naming of body parts, but only a single case of (extremely mild) impairment for comprehension of body parts terms. The confirmatory factor analysis conducted by Barbarotto, Capitani, and Laiacona (2001) on 57 patients confirmed that semantic knowledge

about body parts was unusually resilient to impairment, and also supported the proposed link between body part semantics and artefacts, rather than living things (cf. Warrington & McCarthy, 1987). The patient studied by Shelton and colleagues (1998), though unable to name pictures of everyday objects such as tools, fruits, vegetables and animals, was nevertheless incredulous at the idea that she might have difficulty in naming body parts, “everyone knows what a hand is” (pg. 342).

Structural knowledge about bodies

There is also evidence for a dissociation of lexical-semantic knowledge and knowledge about topological relations among body parts. For example, Benedet and Goodglass (1989) found no relation between two measures of body topology (figure drawing and placement of parts in relation to a face) and two auditory measures of body part comprehension. Similarly, Schwoebel and Coslett (2005), in a principal components analysis of a number of tasks given to stroke patients, found distinct latent variables reflecting performance on tasks requiring lexical-semantic knowledge vs. knowledge of the location or configuration of body parts. The most dramatic deficit in structural knowledge of the body is seen in the condition of *autotopagnosia* (not to be confused with *atopagnosia*, the inability to localise touch on the skin surface, described above). For example, the autotopagnosic patient of Sirigu, Grafman, Blessler, and Sunderland (1991) was unable to point to parts of her body on verbal command, nor to verbally indicate the spatial relations between body parts (e.g., “is the wrist next to the forearm”), though she was unimpaired in verbally indicating the functions of body parts (e.g., “what are the eyes for?”). Buxbaum and Coslett (2001), furthermore, described an autotopagnosic patient who was able to point on his own body to the part associated with seen objects (e.g., shown a picture of a

shoe, he was able to point to his foot), though he was unable to point to parts that were cued directly, whether verbally or visually. Such findings suggest a selective impairment of a structural representation of the topological relations among body parts, preserving semantic knowledge about the functions of parts and their cultural associations. Coslett and colleagues (e.g., Buxbaum & Coslett, 2001; Schwoebel & Coslett, 2005) have referred to this representation as the *body structural description*.

De Renzi and Scotti (1970) suggested that autotopagnosia might result from a generalised inability to deconstruct a whole into its component parts, rather than a body-specific deficit. They reported a patient who was unable to point to his own body parts or to parts of a bicycle, despite the ability to name parts presented individually. While this may account for impaired body part localisation in some patients, several subsequent authors reported selective impairment for body-part localisation, without any apparent deficit in point to parts of other types of objects (e.g., Buxbaum & Coslett, 2001; Ogden, 1985; Semenza, 1988). Interestingly, though apparently unimpaired for non-body objects, the patient of Ogden (1985) did make errors when asked to position parts of a face on a model. For example, he placed the ears where the eyes should have gone and the mouth on top of the head. Thus, structural knowledge about bodies can be dissociated both from other types of knowledge about bodies and from structural knowledge about non-body objects.

Many impairments related to the body are commonly selective to specific parts of the body. For example, tactile sensory or proprioceptive deficits are often isolated to body parts or regions of the skin, leaving other parts unaffected. Similarly, Laiacona and colleagues (2006) reported a patient who showed severe impairment of lexical-semantic knowledge related to the

limbs, but only mild impairment for other body parts. In contrast, Kinsbourne (1995) points out that there are no reported cases of local autotopagnosias. Impaired topological knowledge appears to be approximately homogenous across the entire body (finger agnosia being a possible exception to this generalisation). This suggests that, unlike other types of body perception and knowledge, topological knowledge about the body is instantiated in a single, holistic, representation, rather than as a map-like structure of representations of component parts (though, of course, the *content* of this representation is a map).

The literal meaning of the term *autotopagnosia* implies difficulties related to the representation of the topology of *one's own* body, as opposed to other people's bodies or drawings. In most cases, however, patients showing deficits for topological knowledge of their own body are similarly impaired in topological knowledge of human bodies generally (e.g., Gerstmann, 1942; Ogden, 1985; Semenza & Goodglass, 1985; Sirigu et al., 1991), leading Gerstmann (1942) to suggest that the disorder might more properly be termed *somatotopagnosia*. There are, however, reports of dissociations between the ability to point to locations on one's own body and on other people's bodies. Degos and colleagues (1997), for example, studied eight patients with brain lesions of the left posterior parietal lobe who showed a selective deficit in pointing to body parts on other people's bodies, what they termed *heterotopagnosia*. These patients did not have any deficit in pointing to their own bodies, and, indeed, when asked to point to someone else's body part often pointed to the corresponding body part on their own body (self-referencing). Felician and colleagues (2003) reported a clear double dissociation between the ability to point to parts of one's own or someone else's body. Intriguingly, in general, heterotopagnosic patients are also unimpaired in pointing to body parts on *representations* of human bodies, such as photographs or dolls. This suggests that their errors do not result from an

actual loss of topographical knowledge of bodies. Rather, their deficit may have something to do with the social context of pointing towards another person. Indeed, a recent study has reported dissociations of an impaired ability to *point* towards another person's body parts with preserved ability to *grasp* those same body parts (Cleret de Langavant, Trinkler, Cesaro, & Bachoud-Lévi, 2009).

Like lexical-semantic deficits of body knowledge, autotopagnosia is almost invariably associated with lesions of the left parietal lobe. Several neuroimaging studies have found that making judgments about the internal configuration and relative spatial localization of body parts involves the left superior parietal cortex and intraparietal sulcus (Corradi-Dell'Acqua, Hesse, Rumiati, & Fink, 2008; Corradi-Dell'Acqua, Tomasino, & Fink, 2009; Felician et al., 2004; Le Clec'H et al., 2000). These findings are consistent with the localization of lesions resulting in autotopagnosia. Denes and colleagues (2000), however, do report one case resulting from right parietal damage in a left-handed patient with right hemisphere language dominance, suggesting that it is the parietal lobe of the language dominant hemisphere, rather than the left absolutely, that underlies topological knowledge of bodies. This relation to language is supported by the finding of Semenza and Goodglass (1985) that topological errors were inversely correlated with the lexical frequency of body-part words, both in Italian and American-English speaking populations. Thus, while topological body knowledge is clearly doubly-dissociable from lexical-semantic knowledge, it is nevertheless closely related to language.

Emotion about the body

Above, we discussed emotion-in-body, cases in which the body is the vehicle of emotional experiences. This somatoperceptual process was distinguished from the

somatorepresentational process of emotion-about-body, in which one's body is the object of emotion. Two manifestations of emotion about one's own body are encountered fairly frequently in the normal population. One concerns emotions about diseased, damaged, amputated, excised or otherwise abnormal pathological body parts. In general, these seem to represent a combination of possibly altered somatoperception due to organic change in the body part, and affective attitudes based on knowledge of and fears about the disease process. However, the majority of the medical literature on emotional aspects of body has focussed on cosmesis and disfigurement, rather than on emotional attitudes to the affected body part per se (e.g., Fobair et al., 2006). That is, the question is generally "how do I look/how does it look (to others)?" rather than "what emotional response do I have to body part X?"

A second manifestation of emotion-about-body relates to concerns about one's normal physical appearance with reference to how one is perceived by others, and particularly with reference to sexual attractiveness. Many people can experience positive emotions about their body in this context, but negative emotions about the body can have devastating effects on self-esteem, and high social cost. Eating disorders such as anorexia nervosa may include an extreme form of such emotions about the body. Most importantly, the concern with appearance cannot be considered without a social dimension. This social dimension is clearly culture-bound, and strongly linked to cultural expectations about the body, although these norms may vary across cultures (Lee, 1996). This cultural dimension lies outside our current scope, though possible cultural influences mental representation of the individual body may be a fruitful area for future research.

Interestingly, emotional concerns about the body are frequently expressed in terms of body size and body part size. Muscle dysmorphia ("bigorexia"), involves an excessive

preoccupation with one's muscularity, and thus also involves a representation of body size.

Muscle dysmorphia has been less studied than anorexia nervosa, but may be better conceptualised as a compulsive behaviour focussing on the body, rather than as a pathology of emotion-about-body (Chung, 2001).

Patients with eating disorders may perceive themselves as "too fat". Several psychiatric studies have considered perceived body size in the context of body image in eating disorders (for review see Skrzypek, Wehmeier, & Remschmidt, 2001). Interestingly, this literature generally distinguishes two components of body image in eating disorders: a perceptual component which overestimates one's actual body size, and a cognitive/evaluative component responsible for emotional attitudes towards one's own body. The perceptual component may relate to the neural mechanisms that represent body part size, discussed above. In essence, the anorexic patient's self-starvation might be an attempt to correct what they perceive to be the excessive size of their own body. Many studies have reported overestimation of body size or body part size in anorexia, notably by measuring biases when patients are asked to adjust a distorting mirror until it showed them their body in its true proportions (Traub & Orbach, 1964). Some studies have found similar results (e.g., Smeets, 1999), while others have failed to replicate the result, or found that it applies only to a small subset of patients (Probst, Vandereycken, Coppinolle, & Pieters, 1998). In contrast, the attitudinal dissatisfaction component is found in more studies and in more patients (Ben-Tovim, Walker, Murray, & Chin, 1990; Skrzypek et al., 2001). For our purposes, the crucial point is that perceptual size estimation and negative emotional attitude are *separable* components in the model. On this view, emotions about the body need not be directly linked to the representations of the body.

Finally, we consider examples of focal pathology of emotion-about-body, body image identity disorder, body integrity identity disorder and misoplegia. These disorders involve strongly negative emotional attitudes to individual body parts, can be found without organic abnormality in the body part in question, and seem to be endogenous, and independent of social evaluation by others. As such, they seem closer to focal delusions rather than evaluative attitudes. As such, they suggest an abnormality in a neural representation of the body that combines somatotopic organisation with emotional significance.

In the condition of *body dysmorphic disorder* (BSD), a patient develops an extreme dislike of a particular part of their body, often during childhood or adolescence (Phillips, 1991). Crucially, the body part is healthy, functions normally, and appears normal to other people. Concerns involving the head and face, specifically, the nose, hair, and skin, are especially prevalent, and are often associated with anxiety, depression, and low self-esteem (Phillips, Didie, Feusner, & Wilhelm, 2008). In the possibly related condition of *body integrity identity disorder* (BIID; also known as *apotemnophilia*), patients report enduring dislike of a particular part of their body, and that they would feel more whole without it (First, 2005). In some cases, they may seek voluntary amputation of the body part. Amputation seems to have a positive effect on well-being, and makes the patient feel whole (First, 2005). Interestingly, while BSD frequently involves the head and face, BIID has been reported almost exclusively in relation to limb extremities, suggesting potentially important differences in underlying etiology. Most discussion of BIID relates to the ethical dilemmas posed by amputation of a healthy limb (Bayne & Levy, 2005; Müller, 2009). Recent studies have begun to investigate perceptual processing and experience on the affected body part. Brang, McGeoch, and Ramachandran (2008), for example, found that skin conductance responses to pinprick were heightened on the affected body part.

Similarly, Blanke and colleagues (in press) found that 65% of their sample of BIID patients reported perceptual abnormalities including pins-and-needles (paraesthesia), sensory deficits (hypoesthesia), impaired sense of ownership over the limb (somatoparaphrenia), and asomatognosia. On one hypothesis, BIID reflects a mismatch between a neural representation of the actual anatomical body, and a second (unidentified) representation of the desired body form (Ramachandran & McGeoch, 2007). Blanke and colleagues (in press) suggest that BIID can be considered a chronic form of asomatognosia, essentially a negative phantom limb. Crucially for our purposes, the disorder seems to involve both a mapped body representation and clear emotional valence assigned to some parts of the map. It thus qualifies as a chronic pathology of the emotion-about-body component.

Some hemiplegic patients, while perfectly *aware* of their deficit, show peculiar lack of *concern* of this inability, what Critchley (1953) termed *anosodiaphoria*. Conversely, *misoplegia* refers to hatred of a limb (Critchley, 1974; Moss & Turnbull, 1996). It is a rare but well-established consequence of right hemisphere stroke causing hemiplegia, and is associated with other disorders of sense of ownership (DSO: Baier & Karnath, 2008), including anosognosia, and somatoparaphrenia. Interestingly, the cluster of DSO was localised to the right insula, consistent with the insular role in both self-awareness and emotion. In most reports of misoplegia, it is not possible to distinguish hatred of the limb itself from hatred of the paralysis affecting the limb. Therefore, a recent case of misoplegia without hemiplegia or sensory loss (Loetscher, Regard, & Brugger, 2006) is of special interest. Their patient showed negative attitude and hatred of her left leg, including striking, following a right temporal/temporoparietal tumour. However, the left leg was atrophic due to poliomyelitis, and the authors hypothesised that the tumour had caused disinhibition of latent negative feelings about the leg.

Conclusion

Uniquely, the body has a dual character, simultaneously the medium of private, internal sensations, as well as a publically perceptible object in the physical world. We have argued that this duality is reflected in two major classes of higher-order representations about the body. On the one hand, somatoperception refers to the essentially perceptual process of constructing perceptual representations of the body and somatic stimuli from perceptual input. On the other, somatrepresentation refers to the essentially cognitive processes of forming abstract knowledge about and attitudes towards the body as a physical object.

Much recent research has focused on identifying dissociations between different body representations (e.g., Dijkerman & de Haan, 2007; Gallagher & Cole, 1995; Kammers, van der Ham, & Dijkerman, 2006; Paillard, 1999; Schwoebel & Coslett, 2005; Sirigu et al., 1991). This poses the problem of how many representations is too many. De Vignemont (2007) identified a risk of “infinite multiplication” of body representations. The present dissociation of somatoperception and somatrepresentation attempts to impose structure upon dissociable representations. We predict that functional interactions between body representations are more likely to occur between two somatoperceptual representations or two somatrepresentational one than between one of each class. This is because somatoperception involves an integrated, on-line percept of the current state of the body, based on integrating the available multisensory input, while somatrepresentation involves knowledge about one's body as a unique, continuous object. For example, while we (following Head & Holmes, 1911) have argued that the superficial and postural schemas represent distinct, potentially dissociable, representations, there are clear interactions between tactile localisation and body posture (e.g., Ho & Spence, 2007; Medina & Rapp, 2008). Analogously, while deficits of lexical-semantic and structural knowledge about

bodies are clearly doubly-dissociable, we suggest that there are nevertheless likely to be important functional relations between them; indeed, Semenza and Goodglass (1985) found that the strongest predictor of errors in patients' pointing to body parts even in non-verbal tasks (the classic index of structural knowledge) was the lexical frequency of the name for that body part. Equally, we would expect few interactions between somatoperception and somatopresentation. For example, we would predict that the accuracy of pointing to body parts in autotopagnosia should be independent of current posture and tactile input to the designated part.

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Figure Captions

Figure 1: A model of somatoperceptual information processing, highlighting the role of body representations in the construction of somatic percepts. Inputs are depicted as diamond shapes, body representations as ovals, and perceptual processes as rectangles.