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Types of Body Representation

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Abstract

Our body is an essential component of our sense of self and the core of our identity as an individual. Disorders of body representation, moreover, are a central aspect of several serious clinical conditions. A large and growing literature has therefore investigated the cognitive and neural mechanisms by which we represent our bodies and how these may become disrupted in disease. In this chapter I will give a brief overview of six types of body representation: (1) the *body image*, a conscious image of the size, shape, and physical composition of our bodies; (2) the *body schema*, a dynamic model of the body posture underlying skilled action; (3) the *superficial schema*, mediating localisation of stimuli on the body surface; (4) the *body model*, a model of the metric properties of the body underlying perception; (5) the body as a distinct semantic domain; and (6) the *body structural description*, a topological model of the locations of body parts relative to each other.

Our body is an essential component of our sense of self and the core of our identity as an individual. Distortions and misperceptions of the body are a central part of serious psychiatric conditions such as body dysmorphic disorder (Phillips, Didie, Feusner, & Wilhelm, 2008) and eating disorders (Treasure, Claudino, & Zucker, 2010), as well as other seemingly bizarre conditions, such as *asomotagnosia* in which half the body is perceived as absent (Critchley, 1953), *somatoparaphrenia* in which patients insist that one of their limbs belongs to somebody else (Vallar & Ronchi, 2009), *phantom limbs* in which in amputated limb is perceived as continuing to exist (Melzack, 1990), and *body integrity identity disorder* in which people express desire to have part of their body amputated (First, 2005). The way we represent our body has thus become an increasing focus of research in psychology, neuroscience, and psychiatry.

In thinking about body representation it is important to note that our body has a fundamentally dual character. On one hand, our body is the origin of our first-person perspective, the seat of our sensations, and an omnipresent feature of our perceptual field. In this sense, we have immediate, knowledge of our body from the inside as an object of direct perception. On the other hand, our body is a physical object like any other, subject to gravity and affected by external forces the same as other objects. In this sense, we can reflect cognitively on our body from the outside as a physical or biological object. In a recent review paper, my colleagues and I used this distinction between two modes of thinking about our body to distinguish two broad classes of body representations (Longo, Azañón, & Haggard, 2010). In analogy to the term somato*sensation*, which refers to the basic sensory mechanisms underlying the bodily senses (touch, pain, proprioception, etc.), we divided body representations into those mediating somato*perception*, the construction of higher-level percepts about the body or objects in the world, and somato*representation*, abstract knowledge about one's own body and about bodies generally.

In this chapter I will briefly review research on six types of body representation. The first four representations I will discuss are aspects of somatoperception: the *body image*, the *body schema*, the *superficial schema*, and the *body model*. The final two are aspects of somatorepresentation: *semantic knowledge about the body* and the *body structural description*. My description of each type of representation is illustrative and makes no attempt at an exhaustive review of the literature. In each case, I start with brief description of the type of representation and give two examples of research investigating that representation, where possible combining examples from research on clinical populations and on healthy individuals.

The different representations have emerged at different times, in different literatures, and on the basis of different types of evidence. There is not currently any general theory of the overall relations or connections between the different representations. As a speculative way of conceiving of the overall nature of body representations, however, Figure 1 shows the six representations placed in a two-dimensional space formed by orthogonal axes indicating, on the one hand how *perceptual* vs. *conceptual* the representation appears to be, and on the other how *implicit* vs. *explicit* the representation in. The perceptual/conceptual axis organises representations in somatoperceptual varieties on the left, and somatorepresentational varieties on the right. The implicit/explicit axis organises representations into those accessible to conscious introspection on the top, and those operating as part of the cognitive unconscious on the bottom.

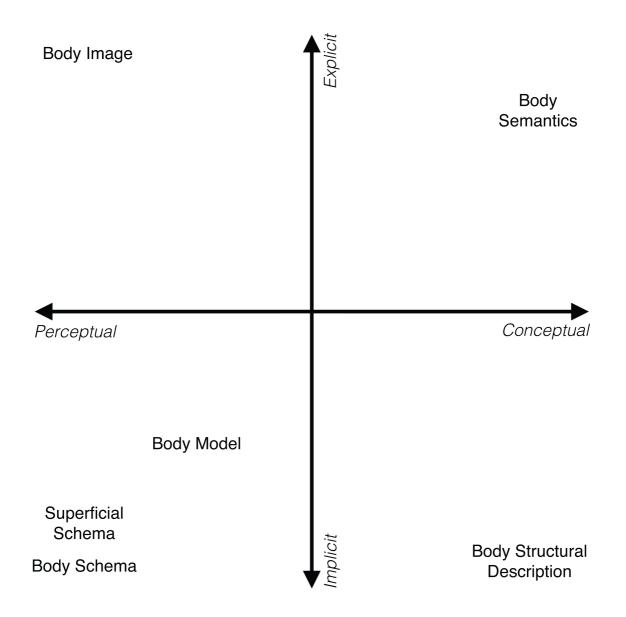


Figure 1: A speculative model of the relations between body representations.

The Body Image

The *body image* refers to our subjective experience of the physical structure of our body in terms of its size, shape, and physical composition. The body image has been the subject of intense research across several disciplines, such as cognitive neuroscience and neurology (e.g., Berlucchi & Aglioti, 1997; Critchley, 1953; Schilder, 1935/1950) and psychiatry (e.g., Ben-Tovim, Walker, Murray, & Chin, 1990; Bruch, 1978; Cash & Deagle, 1997). In the clinical literature on body image disturbances in eating disorders and other

conditions such as body dysmorphic disorder (Phillips et al., 2008), the concept of body image typically also incorporates a broader set of issues such as attitudes towards the body. The examples I discuss here, however, focus on the perceptual body image, which has been the focus of research on body image in neurology and cognitive neuroscience.

Most of the time in healthy people, our body image provides a generally accurate impression of the true structure of our body. However, as will be familiar to anyone unfortunate enough to have undergone dental anaesthesia, which makes it feel as if the entire mouth has swollen in size (Türker, Yeo, & Gandevia, 2005), our subjective experience of our body can sometimes prove inaccurate. In the case of dental anaesthesia, this results in a conflict between our immediate subjective experience of our body ("it feels like my mouth has become swollen and gigantic") and our actual beliefs ("of course, I know my mouth is actually it's normal size"). In some cases, however, distortions of body image can become genuinely delusional, for example in somatoparaphrenic patients who vehemently insist that one of their limbs actually belongs to somebody else (Vallar & Ronchi, 2009), or in people with anorexia nervosa who insist that they are fat despite being severely underweight (Treasure et al., 2010).

Example 1: Phantom limbs

As briefly mentioned above, phantom limbs refer to the subjective experience of a body part that no longer physically exists or, in the case of congenital limb absence, a limb that never existed. Phantom experiences occur in the large majority of cases of amputation (Melzack, 1990; Ramachandran & Hirstein, 1998), and less commonly in congenital limb absence (Brugger et al., 2000). The experience of limb presence is frequently so vivid that people may try to walk using their phantom leg (Melzack, 1990). Nevertheless, it is important to emphasise that the phantom experiences are not delusional: the limb is perceived to be present, although the patient knows perfectly well that it is not.

Phantom experiences have fascinated people for centuries. Admiral Horatio Nelson (hero of the Nile and Trafalgar), who lost his right arm leading a commando raid on the island of Tenerife, considered his phantom arm to be proof of the immaterial soul. There is a certain elegance to Nelson's logic, for if the experience of his arm could survive its physical annihilation, why should we think that the rest of his body is any different? Nevertheless, from the perspective of the body image, phantom experiences have a very different interpretation: though there has been a change to the physical body, there has *not* been a corresponding change to the central body image in the person's brain. Phantom limbs thus demonstrate a remarkable resilience of the body image to alteration, even in the face of massive alteration of the true physical structure of the body.

Nevertheless, the experience of phantoms does change over time. In particular, the limb tends to 'telescope' into the stump over months or years, with the experience of the fingers or toes remaining vivid, while the middle portion of the limb fades from awareness (Riddoch, 1941). Interestingly, while telescoping is common in phantoms following limb amputation, it is not found in phantom experiences following spinal cord injury (Evans, 1962). As both amputation and spinal cord injury result in deafferentation, this pattern suggests that telescoping results from conflict between the body image and visual experience of limb absence.

Example 2: The rubber hand illusion

Phantom limbs are a situation in which an individual knows that the physical structure of their body has changed, though it feels as if their body remains the same. Many recent studies have demonstrated converse effects, showing that people's subjective experience of their body can be altered, even as people know it hasn't (e.g., Botvinick & Cohen, 1998; Lackner, 1988; de Vignemont, Ehrsson, & Haggard, 2005). For example, in the *rubber hand illusion* a prosthetic hand is placed in front of the participant and touched in synchrony with the participant's own unseen hand (Botvinick & Cohen, 1998). Remarkably, many people report feeling like the rubber hand actually is their hand. In contrast, when the two hands are touched asynchronously this effect is not found. Subsequent studies showed similar effects using more objective measures of the illusion, including proprioceptive displacement of the participant's actual hand towards the rubber hand (Tsakiris & Haggard, 2005; Longo et al., 2008), skin-conductance changes when the rubber hand is threatened (Armel & Ramachandran, 2003; Ehrsson et al., 2008), and changes in the temperature of the participant's own hand (Moseley et al., 2008). More recently, the logic of the rubber hand illusion has been generalised to create analogous *full body illusions* in virtual reality (Lenggenhager, Tadi, Metzinger, & Blanke, 2007; Petkova & Ehrsson, 2008; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2009).

In contrast to the rigidity of body image demonstrated by phantom limbs, the rubber hand and full body illusions suggest dramatic body image plasticity. Not only do participants experience body ownership over rubber hands and avatars which are obviously not their own, but the similarity between the hand or avatar and the participant's own body seems to have little impact. For example, in the rubber hand illusion, the similarity in skin colour between the rubber hand and the participant's hand has no apparent effect on the illusion (Holmes, Snijders, & Spence, 2006; Longo et al., 2008), while full body illusions can be produced for avatars of different sex (Slater, Spanlang, Sanchez-Vives, & Blanke, 2010) or weight (Piryankova et al., 2014). Nevertheless, there are limits to body image plasticity. Neither the rubber hand illusion (Tsakiris & Haggard, 2005) nor the full body illusion (Lenggenhager et al., 2007) can be elicited over a non-body object. This suggests that the body image can incorporate anything that looks like *a* body, regardless of whether it looks like *my* body. Such a general template can also potentially account for the lack of plasticity following amputation that results in phantom limbs: while changes in the size or proportions of different body parts will still fit with this template, *deletion* of body parts will not.

The Body Schema

Our body image is generally stable from moment to moment, which makes sense since the size and shape of our body changes only slowly. In contrast, the posture and orientation of our body in space changes constantly as we go about out daily lives. Whereas the body image refers to our conscious image of our body, the *body schema* refers to a more dynamic representation of body posture (Head & Holmes, 1911). The history of research on the body schema has unfortunately been characterised by inconsistent and ambiguous usage of terms. Nevertheless, these concepts have been differentiated both on theoretical (Gallagher, 1986) and empirical (Gallagher & Cole, 1995; Paillard, 1999) grounds. For example, in the condition of *numbsense*, patients are able to actively point towards the location at which a touch was applied, while denying any subjective awareness of having been touched (Paillard, Michel, & Stelmach, 1983; Rossetti, Rode, & Boisson, 1995). This shows a clear dissociation between implicit representations of the body underlying motor control (i.e., the body schema), from more conscious representations (i.e., the body image).

In comparison with the body image, which is intrinsically conscious, the body schema is thought to be less accessible to conscious introspection. Rather, the body schema operates outside of conscious awareness to guide and control our actions in the world. For example, Castiello, Paulignan, and Jeannerod (1991) asked participants to reach for visual objects which were suddenly displaced after reach onset. Kinematic analyses showed that

participants corrected their reach trajectory more than 300 ms before they were consciously aware of the displacement.

Example 1: Extending the body with tools

Tools allow us to act at farther distances and to perform different types of actions that we otherwise could. In a very real sense, the tool becomes a physical extension of our body. Head and Holmes (1911) gave a colourful example which came naturally to the Edwardian mind (pg. 188): "Anything which participates in the conscious movement of our bodies is added to the model of ourselves and becomes part of these schemata: a woman's power of localization may extend to the feather in her hat." Over the past two decades, an increasing literature has provided empirical support for this claim, showing that wielded tools are incorporated into the body schema (for review, see Maravita & Iriki, 2004).

In a seminal study, Iriki, Tanaka, and Iwamura (1996) recorded from neurons in the somatosensory cortex of macaque monkeys with spatially-aligned tactile and visual receptive fields. The neurons fired when visual stimuli were presented in the *peripersonal space*, immediately around the tactile receptive field. When the monkey used a rake to retrieve food pellets, the visual receptive fields extended to include the space immediately surrounding the tool. In contrast, when the monkeys passively held the rake no such extension was found. This suggests that the tool was coded as actually being part of the arm.

Berti and Frassinetti (2000) investigated this issue in a neurological patient, P.P., who showed neglect in the space near the body, but not for farther away. When bisecting lines with a laser pointer, P.P. erred to the right of centre for lines in near space (50 cm away), but not in far space (100 cm). In contrast, when she used a long stick to bisect lines, neglect was apparent at both distances. This suggests that during tool use the farther distance was recoded as being near the body. Longo and Lourenco (2006) applied a similar logic to address this issue in healthy participants. When participants bisect lines with a laser pointer they show a small leftward bias in near space, known as *pseudoneglect*, but a rightward bias in far space. When participants responded using sticks, however, they showed pseudoneglect at all distances.

Example 2: Loss of Proprioception

Localising the body in external space requires integration of multiple sources of information (as will be discussed in more detail below in relation to the body model). Head and Holmes (1911) noted that loss of proprioception was conspicuously common following brain injury, and often the only apparent perceptual deficit following brain damage. Even more dramatic is selective loss of afferent signals at the spinal level, producing a total loss of proprioception without associated impairment of the ability to send motor commands. Patient I.W. suffered a near complete loss of afferent fibres below the neck at age 19 (Cole, 1995), leaving him with virtually complete lack of proprioception and touch below the neck. While the fibres carrying motor commands to the body were physiologically intact, I.W. was initially almost entirely unable to produce skilled actions. Gallagher and Cole (1995) interpreted I.W.'s condition as reflecting a near total loss of the body schema. Remarkably, through intense practice and force of will, I.W. re-learned to walk and perform many other daily activities using constant and intense visual guidance. In this sense, he uses his conscious body image to achieve the task normally handled by the unconscious body schema. I.W.'s actions thus lack the automaticity of normal action and requires constant attention, leading his neurologist to refer to I.W.'s life as a "daily marathon" (Cole, 1995).

The Superficial Schema

Head and Holmes (1911) introduced the body schema based on patients who could localise touch on their body, but could not localise their limbs in space. They also reported patients with the opposite pattern, *atopognosia*, who were unable to judge *where* on the skin they had been touched, though they could tell *that* they had been touched and perceive limb posture. Given this dissociation, Head and Holmes postulated an additional representation, now generally called the *superficial schema*, mediating the localisation of tactile sensations onto the skin surface.

Some authors have questioned whether tactile localisation requires any additional representation than somatotopic maps in primary somatosensory cortex (e.g., Poeck & Orgass, 1971). However, since patients with atopognosia can detect touch, initial sensory processing must be intact. My colleagues and I (Longo et al., 2010) argued that localising a stimulus within a somatotopic map is not sufficient for localisation on the skin, but requires an additional linking function between locations in a somatotopic maps following perceptual and motor learning (e.g., Elbert et al., 1995) also suggests that there cannot be a one-to-one mapping between locations in a somatotopic maps and bodily locations, as plastic changes in the size or location of skin surfaces in a map would thereby result in perceptual mislocalisations.

Example 1: Disorganisation of localisation after stroke

The exact form of impaired tactile localisation varies widely. Head (1918) described several patients who could indicate which finger had been stimulated, but not where on that finger the touch had been. In some cases, the patients reported that the touch had "spread out" to cover the entire finger. Mislocalisations are more likely involve proximal displacements of stimulus location (e.g., Critchley, 1953; Rapp, Hendel, & Medina, 2002). In these cases, it

does not appear to be primary somatotopic representations of touch that are impaired, as patients can still detect the presence of touch. Rather, it appears to be some subsequent linking function.

A particularly striking example is the two patients described by Rapp and colleagues (2002). These patients localised touch on their hand by pointing with their other hand. They showed large localisation errors of stimuli presented on their right hands, generally misplacing stimuli proximal to actual location. These misplacements, however, were not random or idiosyncratic, but showed highly systematic structure. The pattern of localisation judgments preserved the overall organisation of the skin, but systematically misplaced this pattern onto the actual hand surface. This suggests that primary somatotopic representations were spared, since responses preserved the relative locations with respect to each other. The impairment was in mapping the somatotopic organisation of the skin onto the external structure of the body.

Example 2: A supramodal representation of the body surface

Mislocalisation of touch is not limited to brain injury. Trojan and colleagues (2006), for example, applied radiant heat to the forearm and asked participants to judge stimulus location by positioning a pointer above the location, without touching the skin. They found highly distorted 'perceptual maps' of the body surface, which preserved the overall somatotopic organisation of the skin, but compressed or stretched the map in idiosyncratic ways across people.

Mancini and colleagues (Mancini, Longo, Iannetti, & Haggard, 2011) measured tactile localisation biases on the hand using a task in which participants clicked a mouse cursor onto a silhouette of their hand to indicate the perceived location of each stimulus. They found highly consistent patterns of constant error across people. On the hairy skin of the

dorsal hand surface, people perceived touch as occurring farther forward on the hand than its actual location. This bias was found not only for mechanical activation of A β (innocuous touch) afferent fibres, but also following stimulation of C fibres (non-painful heat) and A δ (pinprick pain). Steenbergen and colleagues (2012) similarly found clear correspondences between localisation biases for innocuous and painful stimulation. That common biases were found regardless of the specific class of afferent fibre stimulated suggests that the biases arise from an abstract, supramodal representation of the skin, which generalises across specific sensory modalities. In contrast to the generality of biases across modalities, however, these effects are highly specific to which skin surface is stimulated: no bias to perceive touch as happening farther forward than its actual location appears on the palm. The specificity of biases to each surface, suggests that the superficial schema remains in a skin-centred, rather than a body-centred, reference frame.

The Body Model

Several forms of perception require that immediate sensory signals be combined with information about the size and shape of the body. For example, when we fixate an object visually with both eyes, the convergence angles can be used to perceive the distance of the object from the observer, but only if the distance between the eyes is known (Banks, 1988). Similarly, the difference in time between when a sound reaches the two ears can be used to perceive the direction in which the sound is coming from, but only if the distance between the ears is known (Clifton et al., 1988). The need for referencing of sensory signals to a stored representation of body size and shape is particularly acute in somatosensation, in which the primary receptor surface (the skin) is physically coextensive with the body. Longo and Haggard (2010) referred to this representation as the *body model*. The body model is similar in several respects to the body image, in that both are representations of the size and shape of

the body. Indeed, there is no obvious a priori reason why the body image itself couldn't be used as the model of size and shape for all perceptual tasks. The motivation for distinguishing between these representations is that, as described in the two examples below, the body model shows large distortions which critically do not appear to characterise the body image.

Example 1: Weber's illusion

Weber (1834/1996) was among the first researchers to systematically investigate the sense of touch. Among many curious phenomena, Weber reported a tactile size illusion which now bears his name. As he moved the two points of a compass across his skin, Weber noted that the distance between the points appeared to increase as he moved them from a region of low tactile sensitivity (like the forearm) to a region of high sensitivity (like the hand). Weber's illusion has subsequently been confirmed by numerous researchers (Cholewiak, 1999; Taylor-Clarke, Jacobsen, & Haggard, 2004). One natural interpretation of this effect is that the perceived size of touch is proportional to the relative size of the representation of each skin surface in somatosensory cortex, as memorably illustrated in the famous figure of the 'Penfield homunculus' with giant fingers and lips (Penfield & Boldrey, 1937). As the proportions of skin surfaces are 'magnified' for sensitive skin surfaces, so too would the perceived size of touch.

Critically, however, Weber's illusion is not a direct reflect of homuncular distortions. Taylor-Clarke and colleagues (2004) estimated that the magnitude of the illusion is only 10% of what would be expected based on these distortions alone. In addition, there is increasing evidence that manipulations of higher-level body representations alter the magnitude of Weber's illusion. For example, Taylor-Clarke and colleagues showed that visually magnifying the forearm and minifying the hand reduced the magnitude of Weber's illusion comparing these two surfaces. Similarly, de Vignemont, Ehrsson, and Haggard (2005) used

an effect known as the 'Pinocchio illusion' (cf. Lackner, 1988) to induce the feeling that participants' fingers had lengthened, and found a corresponding increase in the perceive size of touch applied to the finger. Bruno and Bertamini (2010) used the rubber hand illusion to alter the perceived size of the hand by using gloves of different sizes. They found that the perceived size of grasped objects increased when participants felt ownership over the big, compared with the small glove.

In its canonical form, Weber's illusion reflects differences in the sizes of different body parts. Analogous results, however, can be shown within individual skin surfaces as a function of orientation. On most skin surfaces tested, stimuli oriented along the width of the body are perceived as bigger than the same stimuli oriented along the length of the body (e.g., Green, 1982; Longo & Haggard, 2011). For example, on the back of the hand, touches orientated across the width of the hand are perceived as approximately 40% bigger than those oriented across the length of the hand (Longo & Haggard, 2011), suggesting a representation of the hand which is squatter and fatter than actual hand shape. This bears an intriguing similarity to the geometry of receptive fields of somatosensory neurons, which generally represent an oval-shaped region of the skin with the long axis of the oval running along the long axis of the limbs (Alloway, Rosenthal, & Burton, 1989).

Example 2: Psychomorphometrics

In proprioception, several types of afferent signals from the periphery provide information about body posture, including signals from joints themselves, signals specifying skin stretch, and signals from muscle spindles indicating muscular contraction of lengthening (Proske & Gandevia, 2012). All of the signals, however, provide information only about joint *angles*, the relative flexion or extension of each joint. Critically, information about angles is insufficient to specify the absolute location of a body part in space without additional

information about the distances between joints, which is not specified by any immediate afferent signal. Thus, localising the absolute position of the body in space requires that immediate afferent signals specifying joint angles be combined with a stored representation of body size and shape.

Longo and Haggard (2010) developed a procedure to isolate and measure this representation. Participants placed their hand on a table underneath an occluding board and used a stick to indicate where they perceived the knuckle and the tip of each finger. In contrast to previous studies which have generally measured the 'error of localisation', the deviation of the participant's judgment from actual location, Longo and Haggard (2010) focused on the *internal configuration* of judgments with respect to each other, ignoring the actual location of the hand. This allowed them to construct perceptual maps of the represented structure of the hand, which could then be compared to actual hand shape.

These maps are highly distorted in stereotyped fashion across participants. In particular, there were three clear patterns of distortions: (1) an overall overestimation of the width of the hand, (2) an overall underestimation of the length of fingers, and (3) and progressive increase in the underestimation of finger length from the thumb to little finger. These distortions bear intriguing similarities to known characteristics of somatosensory maps. The overestimation of hand width mirrors the results described in the previous section showing that tactile size is perceived as bigger across the width of the hand than along its length as well as the ovular shape of somatosensory receptive fields. Similarly, the increase of underestimation of finger length across the hand mirrors the relative sensitivity and cortical magnification of each finger (Duncan & Boynton, 2007). Critically, however, when Longo and Haggard (2010) asked participants to select from an array of hand images the one most like their own, their were quite accurate, indicating that the body image maintains more veridical information about body shape than the body model.

The Body as a Semantic Domain

The first four body representations I described are aspects of somatoperception in that they underlie the formation of immediate percepts of the body itself and of the external world. The final two body representations, in contrast, are aspects of somatorepresentation in reflecting more abstract knowledge about bodies in general. Our body is an instance of many biological and physical categories (e.g., human bodies, mammals, vertebrates, solid objects, etc.) about which we know many things. Much of what we know about our body is inherited from these more general categories, such as our having a pancreas which is not something about which we have perceptual access.

Bodies, our own and those of others, are among the most frequent objects we encounter in daily life, and we have a corresponding level of knowledge about them. Kemmerer and Tranel (2008) proposed four aspects of semantic knowledge about bodies: (1) knowledge about the usual shape of body parts, (2) knowledge of the location of each part within the configuration of the whole body, (3) knowledge of the functions of each body part, and (4) knowledge about cultural associations of body parts. In addition, we have both encyclopaedic knowledge about bodies in general (e.g., human bodies generally have five fingers on each hand, all vertebrates have backbones, etc.) and more specific knowledge about our own body and those of people we know as specific instances of bodies.

Example 1: Cross-linguistic regularities

A number of anthropological studies starting in the 1970s, inspired by claims of crosslinguistic universals found in domains such as colour names (Berlin & Kay, 1969), investigated whether there were analogous universals underlying body part terms (Andersen, 1978; Brown, 1976; McClure, 1975). McClure (1975) noted that all languages she studied

had labels for 'fingers' and 'toes', though interestingly several languages, such as Romanian, lacked a specific label corresponding to the English word 'hand'. In her interviews, many Romanian speakers appeared to make no conceptual distinction between the hand and the rest of the arm. This is analogous to the way that English speakers are unlikely to conceptually distinguish the portion of the finger distal to the second knuckle from the rest of the finger, though they distinguish the finger from the hand. While some languages studied by McClure lacked a label for 'hand', if a language did have such a word, it was always a primary lexeme, not derivative from another term (e.g., 'toenail'). In contrast, Brown (1976) found that while all languages he studied appeared to have labels for 'finger' and 'toe', these were frequently secondary lexemes. Though such patterns were originally proposed to be universal features of human thought, more recent research has called their literal universality into question (e.g., Majid, 2010; Palmer & Nicodemus, 1985). Nevertheless, these regularities suggest that the structure of body part terms is widely shared across cultures.

Example 2: Selective impairment of body-part knowledge

Perhaps a more direct way to investigate the status of the body as a distinct semantic domain is to see how it is impaired following brain damage. A substantial literature in neurology and neuropsychology has reported double-dissociations between impairments of lexical-semantic knowledge related to the body and to other semantic domains. Several studies have reported selective impairment of knowledge about the body (Dennis, 1976; Laiacona, Allamano, Lorenzi, & Capitani, 2006; Suzuki, Yamadori, & Fujii, 1997). For example, Suzuki and colleagues (1997) described a patient who was unable to point to body parts when they were named verbally (e.g., 'where is your foot?'), but was successful when parts were described functionally (e.g., 'with which part do you walk?') or in relation to other objects (e.g., 'which part do you put your socks on?'). The patient described by Dennis

(1976) was similarly impaired in pointing to body parts on verbal command, but had no difficulties when asked to point to the part of her body corresponding to a part indicated on a schematic image of a body. The pattern shown by these two patients suggests that their deficit was specific to lexical information about bodies, sparing functional knowledge and cultural associations about the body.

There have also been numerous reports of the converse pattern, selective sparing of lexical-semantic knowledge about bodies (Coslett, Saffran, & Schwoebel, 2002; Kemmerer & Tranel, 2008; Shelton, Fouch, & Caramazza, 1998). Indeed, several authors have suggested that among semantic domains, the body may be unusually resilient to impairment following brain damage (Gainotti, 1984; Kemmerer & Tranel, 2008). Of 104 patients with brain lesions studied by Kemmerer and Tranel (2008), only 10 showed any difficulty in naming body parts, and only one showed an (extremely mild) impairment of comprehension of body part names. Though unable to name such familiar objects as fruits, vegetables, and tools, the patient described by Shelton and colleagues (1998) was dismissive of the idea that she might be impaired in naming body parts, "everyone knows what a hand is" (p. 342).

The Body Structural Description

The final type of body representation I will discuss, the *body structural description*, refers to knowledge about the topological organisation of bodies, that is the spatial location of each part of the body in relation to other parts. Of the body representations I have discussed, the body structural description is probably the least researched, especially in healthy participants. Several studies have shown that knowledge of body topology can be doubly dissociated from more general semantic knowledge about bodies in neurological patients (Benedet & Goodglass, 1989; Schwoebel & Coslett, 2005), suggesting that these rely on

distinct types of representation. The most dramatic evidence for the body structural description comes from the condition of autotopagnosia, which I will describe next.

Example 1: Autotopagnosia

A dramatic deficit of structural body knowledge can be seen in the condition of *autotopagnosia*. Such patients are typically unable to point to parts of their body on verbal command, nor to judge the spatial relations between body parts, yet remain relatively unimpaired in describing the functions of body parts. For example, the patient described by Sirigu and colleagues (Sirigu, Grafman, Bressler, & Sunderland, 1991) was unable to answer questions assessing knowledge of the spatial relations between body parts, such as "is the wrist next to the forearm?", but could answer questions assessing functional knowledge about body parts, such as "what are the eyes for?". Some authors have suggested that autotopagnosia, rather than reflecting a specific deficit related to representing the body, might reflect a general inability to decompose whole objects into their constituent parts (De Renzi & Scotti, 1970). While this may be true of some patients, numerous cases of body-specific topological deficits have been reported (Buxbaum & Coslett, 2001; Ogden, 1985; Semenza, 1988).

Does autotopagnosia reflect impaired knowledge of the topology of *one's own* body, or of bodies in general? Most patients show similar topological impairment or their own body and those of other people or mannequins (Ogden, 1985; Semenza & Goodglass, 1985), suggesting that it reflects a deficit of topological knowledge of bodies in general. However, double-dissociations between impairment for topological knowledge of one's own and of other people's bodies have been reported (Degos et al., 1997; Felician et al., 2003), suggesting that these reflect at least partly distinct representations.

Example 2: Identifying the Structural Body Knowledge with Neuroimaging

Several recent studies have investigated the body structural description using functional magnetic resonance imaging (fMRI; Corradi-Dell'Acqua, Hesse, Rumiati, & Fink, 2008; Corradi-Dell'Acqua, Tomasino, & Fink, 2009; Felician et al., 2004). For example, Felician and colleagues (2004) showed participants words referring either to parts of the participant's own body (shoulder, elbow, or knee) or to parts of the MRI scanner (back end, middle, or front end) and asked them to point to each location. As full pointing movements were not possible given the physical constraints of the MRI scanner, in which participants lie prone in a narrow tube, pointing movements were made via vertical rotations of the wrist. A region of the left superior parietal cortex was activated specifically when participants pointed to parts of their body.

In a similar study, Corradi-Dell'Acqua and colleagues (2008) showed participants images of two body parts or two building parts. After seeing each image pair, participants made one of two types of judgment. In the *identification* task, participants judged which of two presented words corresponded to one of the images seen previously. In the *spatial judgment* task, they judged which of two presented lines represented the true distance between the images. The logic of this experiment was that structural knowledge about the body should be required only for spatial judgments and not for identification, and only for body parts and not for building parts. Activations showing this pattern were found in the left posterior intraparietal sulcus. Together, these studies suggest that the left parietal cortex houses the body structural description, consistent with the clinical literature on autotopagnosia.

Conclusion

In this chapter I have given a brief introduction to six types of body representation. This list is neither meant to be definitive nor exhaustive. Indeed, there is little agreement among contemporary researchers about the exact nature or number of body representations. The aim of this chapter has therefore been to provide an illustrative overview of contemporary work. Several recent papers have provided more full reviews of this literature (e.g., Berlucchi & Aglioti, 2010; Longo & Haggard, 2012; Longo et al., 2010; Medina & Coslett, 2010).

References

- Alloway, K. D., Rosenthal, P., & Burton, H. (1989). Quantitative measurement of receptive field changes during antagonism of GABAergic transmission in primary somatosensory cortex of cats. *Experimental Brain Research*, *78*, 514–532.
- Andersen, E. S. (1978). Lexical universals of body-part terminology. In J. H. Greenberg (Ed.), Universals of human language (pp. 335-368). Stanford, CA: Stanford University Press.
- Armel, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: Evidence from skin conductance response. *Proceedings of the Royal Society of London B, 270*, 1499-1506.
- Banks, M. S. (1988). Visual recalibration and the development of contrast and optical flow perception. In A. Yonas (Ed.), *The Minnesota symposia on child psychology* (pp. 145-196). Hillsdale, NJ: Erlbaum.
- Ben-Tovim, D. I., Walker, M. K., Murray, H., & Chin, G. (1990). Body size estimates: Body image or body attitude measure? *International Journal of Eating Disorders*, 9, 57–67.
- Benedet, M. J., & Goodglass, H. (1989). Body image and comprehension of body part names. Journal of Psycholinguistic Research, 18, 485-496.
- Berlin, B., & Kay, P. (1969). *Basic color terms: Their universality and evolution*. Berkeley: University of California Press.
- Berlucchi, G., & Aglioti, S. M. (2010). The body in the brain revisited. *Experimental Brain Research, 200*, 25-35.
- Berti, A., & Frassinetti, F. (2000). When far becomes near: Remapping of space by tool use. Journal of Cognitive Neuroscience, 12, 415-420.

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. Nature, 391, 756.

Brown, C. H. (1976). General principles of human anatomical partonomy and speculations on

the growth of partonomic nomenclature. American Ethnologist, 3, 400-424.

- Bruch, H. (1978). *The golden cage: The enigma of anorexia nervosa*. Cambridge, MA: Harvard University Press.
- Brugger, P., Kollias, S. S., Müri, R. M., Crelier, G., Hepp-Reymond, M.-C., & Regard, M.
 (2000). Beyond re-membering: Phantom sensations of congenitally absent limbs. *Proceedings of the National Academy of Sciences, USA, 97*, 6167–6172.
- Bruno, N., & Bertamini, M. (2010). Haptic perception after a change in hand size. *Neuropsychologia*, 48, 1853–1856.
- Buxbaum, L. J., & Coslett, H. B. (2001). Specialized structural descriptions for human body parts: Evidence from autotopagnosia. *Cognitive Neuropsychology*, *18*, 289–306.
- Cash, T. F., & Deagle, E. A., III (1997). The nature and extent of body-image disturbances in anorexia nervosa and bulimia nervosa: A meta-analysis. *International Journal of Eating Disorders, 22*, 107–125.
- Castiello, U., Paulignan, Y., & Jeannerod, M. (1991). Temporal dissociation of motor responses and subjective awareness: A study in normal subjects. *Brain*, 114, 2639-2655.
- Cholewiak, R. W. (1999). The perception of tactile distance: Influences of body site, space, and time. *Perception, 28,* 851-875.
- Clifton, R. K., Gwiazda, J., Bauer, J. A., Clarkson, M. G., & Held, R. M. (1988). Growth in head size during infancy: Implications for sound localization. *Developmental Psychology*, 24, 477-483.
- Cole, J. (1995). Pride and a daily marathon. Cambridge, MA: MIT Press.
- Corradi-Dell'Acqua, C., Hesse, M. D., Rumiati, R. I., & Fink, G. R. (2008). Where is a nose with respect to a foot? The left posterior parietal cortex processes spatial relationships among body parts. *Cerebral Cortex, 18*, 2879–2890.

- Corradi-Dell'Acqua, C., Tomasino, B., & Fink, G. R. (2009). What is the position of an arm relative to the body? Neural correlates of body schema and body structural description. *Journal of Neuroscience*, *29*, 4162–4171.
- Coslett, H. B., Saffran, E. M., & Schwoebel, J. (2002). Knowledge of the body: A distinct semantic domain. *Neurology*, *59*, 357–363.

Critchley, M. (1953). The parietal lobes. London: Edward Arnold & Co.

- De Renzi, E., & Scotti, G. (1970). Autotopagnosia: Fiction or reality. *Archives of Neurology*, 23, 221–227.
- de Vignemont, F., Ehrsson, H. H., & Haggard, P. (2005). Bodily illusions modulate tactile perception. *Current Biology*, *15*, 1286–1290.
- Degos, J.-D., Bachoud-Levi, A. C., Ergis, A. M., Petrissans, J. L., & Cesaro, P. (1997).
 Selective inability to point to extrapersonal targets after left posterior parietal lesions:
 An objectivization disorder? *Neurocase*, *3*, 31–39.
- Dennis, M. (1976). Dissociated naming and locating of body parts after left anterior temporal lobe resection: An experimental case study. *Brain and Language*, *3*, 147–163.
- Duncan, R. O., & Boynton, G. M. (2007). Tactile hyperacuity thresholds correlate with finger maps in primary somatosensory cortex (S1). *Cerebral Cortex*, 17, 2878-2891.
- Ehrsson, H. H., Rosén, B., Stockselius, A., Ragnö, C., Köhler, P., & Lundborg, G. (2008). Upper limb amputees can be induced to experience a rubber hand as their own. *Brain*, *131*, 3443-3452.
- Elbert, T., Pantev, C., Weinbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science*, *270*, 305–307.

Evans, J. H. (1962). On disturbance of the body image in paraplegia. Brain, 85, 687-700.

Felician, O., Ceccaldi, M., Didic, M., Thinus-Blanc, C., & Poncet, M. (2003). Pointing to body parts: A double dissociation study. *Neuropsychologia*, 41, 1307-1316.

- Felician, O., Romaiguère, P., Anton, J.-L., Nazarian, B., Roth, M., Poncet, M., et al. (2004). The role of the left superior parietal lobule in body part localization. *Annals of Neurology*, 55, 749-751.
- First, M. B. (2005). Desire for amputation of a limb: Paraphilia, psychosis, or a new type of identity disorder. *Psychological Medicine*, 35, 919–928.
- Gainotti, G. (2004). A metanalysis of impaired and spared naming for different categories of knowledge in patients with a visuo-verbal disconnection. *Neuropsychologia*, *42*, 299-319.
- Gallagher, S. (1986). Body image and body schema: A conceptual clarification. *Journal of Mind and Behavior*, 7, 541-554.
- Gallagher, S., & Cole, J. (1995). Body schema and body image in a deafferented subject. Journal of Mind and Behavior, 16, 369-390.
- Green, B. E. (1982). The perception of distance and location for dual tactile pressures. *Perception and Psychophysics*, *31*, 315-323.
- Head, H. (1918). Sensation and the cerebral cortex. Brain, 41, 57-253.
- Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain, 34*, 102–254.
- Holmes, N. P., Snijders, H. J., & Spence, C. (2006). Reaching with alien limbs: Visual exposure to prosthetic hands in a mirror biases proprioception without accompanying illusions of ownership. *Perception & Psychophysics*, 68, 685-701.
- Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *NeuroReport*, 7, 2325-2330.
- Kemmerer, D., & Tranel, D. (2008). Searching for the elusive neural substrates of body part terms: A neuropsychological study. *Cognitive Neuropsychology*, *25*, 601–629.
- Lackner, J. R. (1988). Some proprioceptive influences on the perceptual representation of

body shape and orientation. Brain, 111, 281-297.

- Laiacona, M., Allamano, N., Lorenzi, L., & Capitani, E. (2006). A case of impaired naming and knowledge of body parts: Are limbs a separate category? *Neurocase, 12*, 307-316.
- Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: Manipulating bodily self-consciousness. *Science*, *317*, 1096-1099.
- Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences*, USA, 107, 11727-11732.
- Longo, M. R., & Haggard, P. (2011). Weber's illusion and body shape: Anisotropy of tactile size perception on the hand. *Journal of Experimental Psychology: Human Perception* and Performance, 37, 720-726.
- Longo, M. R., & Haggard, P. (2012). What is it like to have a body? *Current Directions in Psychological Science*, 21, 140-145.
- Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia*, *44*, 977-981.
- Longo, M. R., Schüür, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition*, *107*, 978-998.
- Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: Body representation beyond primary somatosensory cortex. *Neuropsychologia*, *48*, 655-668.
- Majid, A. (2010). Words for parts of the body. In B. C. Malt & P. Wolff (Eds.), Words and the mind: How words capture human experience (pp. 58-71). New York: Oxford University Press.
- Mancini, F., Longo, M. R., Iannetti, G. D., & Haggard, P. (2011). A supramodal representation of the body surface. *Neuropsychologia*, *49*, 1194-1201.

Maravita, A., & Iriki, A. (2004). Tools for the body (schema). Trends in Cognitive Sciences,

8, 79-86.

- McClure, E. F. (1975). Ethno-anatomy: The structure of the domain. *Anthropological Linguistics*, *17*, 78-88.
- Medina, J., & Coslett, H. B. (2010). From maps to form to space: Touch and the body schema. *Neuropsychologia*, *48*, 645-654.
- Melzack, R. (1990). Phantom limbs and the concept of a neuromatrix. *Trends in Neuroscience, 13*, 88–92.
- Moseley, G. L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., & Spence, C.
 (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proceedings of the National Academy of Sciences, USA, 105*, 13169-13173.
- Ogden, J. A. (1985). Autotopagnosia: Occurrence in a patient without nominal aphasia and with an intact ability to point to parts of animals and objects. *Brain, 108,* 1009-1022.
- Paillard, J. (1999). Body schema and body image A double dissociation in deafferented patients. In G. N. Gantchev, S. Mori, & J. Massion (Eds.), *Motor control: Today and tomorrow* (pp. 197-214). Sofia, Bulgaria: Academic Publishing House.
- Paillard, J., Michel, F., & Stelmach, G. (1983). Localization without content: A tactile analogue of 'blind sight'. *Archives of Neurology*, 40, 548-551.
- Palmer, G. B., & Nicodemus, L. (1985). Coeur d'Alene exceptions to proposed universals of anatomical nomenclature. *American Ethnologist*, 12, 341-359.
- Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain, 60,* 389–443
- Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: Perceptual illusion of body swapping. *PLOS ONE*, *3*, e3832.
- Phillips, K. A., Didie, E. R., Feusner, J., & Wilhelm, S. (2008). Body dysmorphic disorder:

Treating an underrecognized disorder. *American Journal of Psychiatry*, *165*, 1111–1118.

- Piryankova, I. V., Wong, H. Y., Linkenauger, S. A., Stinson, C., Longo, M. R., Bülthoff, H. H., & Mohler, B. J. (2014). Owning an overweight or underweight body:
 Distinguishing the physical, experienced and virtual body. *PLOS ONE*, *9*, e103428.
- Poeck, K., & Orgass, B. (1971). The concept of the body schema: A critical review and some experimental results. *Cortex*, *7*, 254-277.
- Proske, U., & Gandevia, S. C. (2012). The proprioceptive senses: Their roles in signaling body shape, body position and movement, and muscle force. *Physiological Reviews*, 92, 1651-1697.
- Ramachandran, V. S., & Hirstein, W. (1998). The perception of phantom limbs: The D. O. Hebb Lecture. *Brain, 121*, 1603–1630.
- Rapp, B., Hendel, S. K., & Medina, J. (2002). Remodeling of somatosensory hand representations following cerebral lesions in humans. *NeuroReport*, 13, 207–211.
- Riddoch, G. (1941). Phantom limbs and body shape. Brain, 64, 197-222.
- Rossetti, Y., Rode, G., & Boisson, D. (1995). Implicit processing of somaesthetic information: A dissociation between where and how? *NeuroReport, 6*, 506-510.
- Schilder, P. (1950). *The image and appearance of the human body*. New York: International Universities Press. (Original work published 1935.)
- Schwoebel, J., & Coslett, H. B. (2005). Evidence for multiple, distinct representations of the human body. *Journal of Cognitive Neuroscience*, *17*, 543–553.
- Semenza, C. (1988). Impairment in localization of body parts following brain damage. *Cortex, 24*, 443–449.
- Semenza, C., & Goodglass, H. (1985). Localisation of body parts in brain-injured subjects. *Neuropsychologia*, 23, 161–175.

- Shelton, J. R., Fouch, E., & Caramazza, A. (1998). The selective sparing of body part knowledge: A case study. *Neurocase*, 4, 339–351.
- Sirigu, A., Grafman, J., Bressler, K., & Sunderland, T. (1991). Multiple representations contribute to body knowledge processing. *Brain*, 114, 629–642.
- Slater, M., Perez-Marcos, D., Ehrsson, H. H., & Sanchez-Vives, M. V. (2009). Inducing illusory ownership of a virtual body. *Frontiers in Neuroscience*, *3*, 214-220.
- Slater, M., Spanlang, B., Sanchez-Vives, M. V., & Blanke, O. (2010). First person experience of body transfer in virtual reality. *PLOS ONE*, *5*, e10564.
- Steenbergen, P., Buitenweg, J. R., Trojan, J., Klaassen, B., & Veltink, P. H. (2012). Subjectlevel differences in reported locations of cutaneous tactile and nociceptive stimuli. *Frontiers in Human Neuroscience*, 6, 325.
- Suzuki, K., Yamadori, A., & Fujii, T. (1997). Category-specific comprehension deficit restricted to body parts. *Neurocase*, *3*, 193–200.
- Taylor-Clarke, M., Jacobsen, P., & Haggard, P. (2004). Keeping the world a constant size: Object constancy in human touch. *Nature Neuroscience*, *7*, 219–220.
- Treasure, J., Caludino, A. M., & Zucker, N. (2010). Eating disorders. Lancet, 375, 583-593.
- Trojan, J., Kleinböhl, D., Stolle, A. M., Andersen, O. K., Hölzl, R., & Arendt-Nielsen, L.
 (2006). Psychophysical 'perceptual maps' of heat and pain sensations by direct localization of CO2 laser stimuli on the skin. *Brain Research*, *1120*, 106-113.
- Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: Visuotactile integration and self attribution. *Journal of Experimental Psychology: Human Perception and Performance, 31*, 80-91.
- Türker, K. S., Yeo, P. L., & Gandevia, S. C. (2005). Perceptual distortion of face deletion by local anaesthesia of the human lips and teeth. *Experimental Brain Research*, 165, 37-43.

- Vallar, G., & Ronchi, R. (2009). Somatoparaphrenia: A body delusion. A review of the neuropsychological literature. *Experimental Brain Research*, *192*, 533-551.
- Weber, E. H. (1996). *De subtilitate tactus* (H. E. Ross, Trans.). In H. E. Ross & D. J. Murray (Eds.), *E. H. Weber on the tactile senses, 2nd ed* (pp. 21–128). London: Academic Press. (Original work published 1834)

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