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# Implicit and Explicit Body Representations

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**Abstract.** Several forms of perception require that sensory information be referenced to representations of the size and shape of the body. This requirement is especially acute in somatosensation in which the main receptor surface (i.e., the skin) is itself coextensive with the body. This paper reviews recent research investigating the body representations underlying somatosensory information processing, including abilities such as tactile localization, tactile size perception, and position sense. These representations show remarkably large and stereotyped distortions of represented body size and shape. Intriguingly, these distortions appear to mirror distortions characteristic of somatosensory maps, though in attenuated form. In contrast, when asked to make overt judgments about perceived body form, participants are generally quite accurate. This pattern of results suggests that higher-level somatosensory processing relies on a class of implicit body representation, distinct from the conscious body image. I discuss the implications of these results for understanding the nature of body representation and the factors that influence it.

**Keywords:** body representation, body shape, body image, perception, somatosensory information processing

Our body is ubiquitous in perceptual experience, and is central to our sense of self and personal identity. As James (1890) observed, our body is not *ours*, it is *us*. Thus, how we mentally represent our body has profound implications for our sense of identity, self-esteem, and overall mental health. Indeed, disordered body representation is central to several serious and debilitating diseases, including eating disorders (Treasure, Claudino, & Zucker, 2010), body dysmorphic disorder (Phillips, Didie, Feusner, & Wilhelm, 2008), and phantom limb pain (Flor, Nikolajsen, & Staehelin Jensen, 2006).

The subjective, conscious experience of embodiment, however, is only one way in which the brain represents the body. Many forms of perception also require referencing to representations of the body, such as its size and shape. The use of binocular vision for depth perception, for example, requires that information about the spacing between the eyes be known (Banks, 1988). Similarly, the use of temporal differences in when sounds reach the two ears for auditory localization requires that the distance between the ears be known (Aslin, Pisoni, & Jusczyk, 1983; Clifton, Gwiazda, Bauer, Clarkson, & Held, 1988). Other studies have shown that other types of body representations inform perception, such as eye-height which affects the perceived passability of doorways (Warren & Whang, 1987), hand size which affects the perceived size of seen objects (Linkenauger, Ramenzoni, & Proffitt, 2010), and arm length which affects the extent of the "near space" immediately surrounding the body (Longo & Lourenco, 2007).

While information about the body is used in perceptual modalities like vision and audition, it is for the most part secondary. In somatosensation, in contrast, representations of the body are central, since the primary receptor surface – the skin – is physically coextensive with the body. While basic qualities of tactile sensations may be specified in part by distinct labeled lines for which individual nerve fibers coming from the periphery are in one-to-one correspondence with a specific sensory quality (Torebjörk, Vallbo, & Ochoa, 1987), moving beyond pure somato*sensation* to achieve rich somato*perception* requires that these immediate signals be informed by representations of body size, shape, configuration, and posture.

In this paper, I will review recent research investigating these body representations underlying somatoperception and their relation to our conscious body image. In the first part of this paper, I will review recent research investigating body representations underlying somatoperceptual information processing. A key theme of this research is the finding that these representations are systematically distorted,

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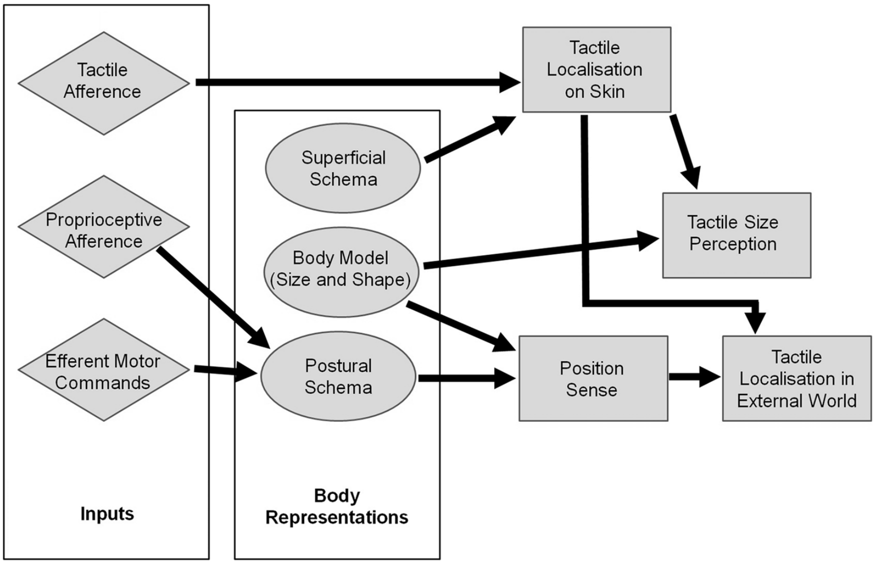

*Figure 1.* A simplified version of Longo and colleagues' (2010) model of somatoperceptual information processing. The key feature of the model is the combination of immediate sensory and motor signals (indicated as diamonds) and body representations (indicated as ovals) in generating high-level percepts (indicated as rectangles). In addition to the classic superficial and postural schemas, first postulated by Head and Holmes (1911), the model proposed that a Body Model providing information about the metric properties of the body (i.e., size and shape) is critical for perceptual abilities including tactile size perception and position sense.

in highly stereotyped ways across people. In contrast, people's conscious judgments about their body are generally approximately accurate, suggesting that somatoperception relies on a class of *implicit body representation*, distinct from our conscious body image. The final part of the paper discusses potential relations between these types of body representation.

## Body Representations Underlying Somatoperception

Longo, Azañón, and Haggard (2010) recently proposed a model of somatoperceptual information processing (shown, in simplified form, in Figure 1) which suggested that higher-order somatosensory percepts are constructed by combining immediate sensory signals from the peripheral nerves with stored representations of the body. In addition to the superficial and postural schemas of Head and Holmes (1911), Longo and colleagues (2010) argued that several aspects of somatoperception also required a model of the metric properties of the body (i.e., body size and shape), which they called the "body model." Specifically, they argued that the body model was required for tactile size perception and position sense. In this section, I will describe recent results investigating the nature of these body representations underlying tactile localization, tactile size perception, and position sense. In particular, I will discuss various distortions of these representations, and ways in which these appear to reflect distortions characteristic of early somatosensory maps.

In thinking about the relation between different body representations, it is important to consider the spatial scale at which they represent the body. The body itself is a volumetric, three-dimensional (3-D) object in the world, and we consciously experience it as such. In contrast, somatotopic maps of the body surface in the primary somatosensory cortex (SI) are two-dimensional (2-D). They are 2-D in the obvious sense that the cortex itself is a 2-D sheet, but also in a more profound sense. In the case of the hand, for example, separate patches of cortex represent the glabrous skin of the palmar surface of the hand, and the hairy skin of the dorsal surface of the hand (e.g., Sur, Merzenich, & Kaas, 1980). Further, cortical magnification (the relative amount of cortical tissue devoted to representing a given bit of skin) is substantially higher on the palmar than the dorsal hand surface, reflecting the palm's higher tactile sensitivity. Thus, the hand is initially represented in somatosensory cortex as two distinct, 2-D sheets, rather than a coherent 3-D object.

Do higher-order body representations represent the body as a fragmented collection of 2-D skin surfaces, or as coherent, volumetric 3-D body parts? I will discuss evidence bearing on this question for each of the representations I describe. Specifically, I will argue that distortions of representations provide a valuable tool to address this question. If part of the body is represented as a coherent, volumetric, 3-D object, then distortions should affect all sides of the body part. For example, distortions of a fully 3-D representation of the hand should appear in a consistent manner on both the palmar and dorsal surfaces of the hand. In contrast, if a body part is represented as a fragmented collection of distinct 2-D skin surfaces, then each surface may very well be distorted in different ways.

### Tactile Localization

The ability to tell where on the body a touch has occurred is among the most fundamental of sensory abilities. The location of stimulation can even be specified by single nerve fibers in the periphery (Schady, Torebjörk, & Ochoa, 1983). Head and Holmes (1911) reported several patients who could accurately report *when* they had been touched, but were unable to report *where* on their body the touch had been applied (for more recent findings, see Halligan, Hunt, Marshall, & Wade, 1995). Since these patients could still detect *that* they had been touched, it couldn't be just that the relevant location in primary somatotopic maps had been destroyed, which ought to have impaired all processing of the stimulus. Instead, the initial cortical processing of the stimulus appeared intact, with some other stage of processing being impaired. On the basis of such results, Head and Holmes proposed the concept of "schemas" mediating the interpretation of sensory signals. This higher-order representation mediating tactile localization has come in the literature to be known as the *superficial schema*.

Longo and colleagues (2010) argued that the well-known plasticity of somatosensory cortex following both physical changes to the body (Merzenich et al., 1984; Pons et al., 1991) and learning (Elbert, Pantev, Weinbruch, Rockstroh, & Taub, 1995; Pascual-Leone & Torres, 1993) implied that there could be no hard-wired representation between locations in somatotopic maps and locations on the body. They suggested that tactile localization required an additional linking function connecting these locations, which could be thought of as constituting the superficial schema. A fascinating example of this is a study by Rapp, Hendel, and Medina (2002), reporting two patients with lesions to the left hemisphere who show highly structured, but massively distorted, patterns of localization. On each trial, the patient was touched somewhere on the hand with eyes closed, then opened their eyes and pointing with their other hand to the perceived location of stimulation, which was recorded on a drawing of a hand outline. The perceived locations of touch were systematically shifted in these patients. Critically, the errors these patients made preserved the overall somatotopic arrangement of skin locations with respect to each other, suggesting that the overall somatotopic arrangement of skin locations with respect to each other was preserved. Each point, however, was systematically misplaced. This pattern is strongly suggestive of preserved somatotopic maps, with an impaired linking function between locations in these maps and locations on the body, that is, an impaired superficial schema.

A series of studies by Trojan and colleagues have revealed intriguing distortions of perceptual maps of the body surface (Trojan et al., 2006, 2009). In these studies, radiant heat was applied to specific locations on the forearm using a $CO_2$ laser, and participants indicated the perceived location of touch by positioning a pointer connected to a 3-D motion-tracking system above their arm, without touching the skin. While all participants showed a clearly somatotopic pattern of responses, there were striking patterns of mislocalization, with some participants having compressed, and others stretched, perceptual maps across the longitudinal axis of the forearm (Trojan et al., 2006). A recent study used this paradigm to have participants judge the position of electric shocks applied to the forearm showed strong re-test reliability, suggesting that though the distortions of perceptual maps were idiosyncratic across individuals, they were nevertheless highly stable within each individual (Steenbergen, Buitenweg, Trojan, & Veltink, 2013).

A recent study by Mancini, Longo, Iannetti, and Haggard (2011) investigated the superficial schema in healthy participants by measuring tactile localization on the hand using a very simple paradigm in which participants were touched and then judged where on their hand they had been touched by clicking a mouse cursor on the corresponding location on a silhouette of their hand. In contrast to the studies of Trojan and colleagues on the forearm who found idiosyncratic distortions across individuals, Mancini and colleagues found highly consistent patterns of constant errors. On the dorsal hand surface, there were large distal biases in localization (i.e., touch was perceived farther forward on the hand than it had actually been). These biases were highly consistent across different types of stimulation. For example, nearly identical distal biases were found following stimulation of mechanoreceptive and thermal afferent fibers. This generality suggests that these biases emerge from a supramodal representation of hand, abstracting across categories of stimuli. A recent study by Steenbergen, Buitenweg, Trojan, Klaassen, and Veltink (2012), measuring localization on the forearm, found similar (though less striking) correspondence between sensory modalities.

In striking contrast to the large distal biases they observed on the hand dorsum, Mancini and colleagues (2011) found no such biases on the palmar hand surface. Thus, in contrast to the generality found across different types of stimulation, the biases were highly specific to individual skin surfaces. This surface specificity suggests that the superficial schema relies on fragmented representations of individual skin regions as 2-D surfaces, rather than the body as a coherent, volumetric 3-D object.

## Tactile Size Perception

The metric properties of objects, their size and shape, can be perceived through passive touch in multiple ways. When we hold an object between our thumb and index finger, we can perceive its size through proprioception, which requires referencing to body representations for reasons described in the next section. We can also perceive the size of objects touching a single skin surface. Suppose, for example, that you are touched at two points on opposite sides of the back of your hand. While each of the afferent volleys produced by those touches may be sufficient to localize each stimulus (cf. Schady et al., 1983), there is nothing intrinsic to either of the signals or their combination that specifies *how far apart* they are. The problem of perceiving the distance between two objects on either side of your hand effectively reduces to the problem of knowing how big your hand is.

What sort of representation of body size and shape is used for tactile size perception? More than a century and a half ago, Weber (1834/1996) found that as he moved two tactile points across his skin, the distance he perceived between the two points changed. Specifically, it felt like the points were father apart when they were on a region of relatively high tactile sensitivity (e.g., the palm of the hand), compared to when they were on a region of lower tactile sensitivity (e.g., the forearm), an effect now referred to as

*Weber's illusion*. Subsequent research has confirmed and extended Weber's finding, showing systematic relations between tactile sensitivity and tactile size perception (e.g., Anema, Wolswijk, Ruis, & Dijkerman, 2008; Cholewiak, 1999; Goudge, 1918; Taylor-Clarke, Jacobsen, & Haggard, 2004). Thus, body representations mediating tactile size perception may preserve distortions characteristic of primary somatosensory maps (e.g., the "Penfield homunculus," Penfield & Boldrey, 1937).

Several studies have found that interventions which alter perceived body size produce corresponding changes in tactile size perception. For example, Taylor-Clarke and colleagues (2004) used a video image to provide participants with the visual appearance of their forearm magnified and hand minified. After this experience, the relative perceived size of touch on the forearm – compared to the hand – was increased. de Vignemont, Ehrsson, and Haggard (2005) used a combination of an illusion of body posture and self touch to alter perceived finger length. By applying vibration to the tendons of the biceps or triceps muscles, they generated illusions of forearm extension or flexion, respectively (the "vibrotactile illusion"; cf. Goodwin, McCloskey, & Matthews, 1972). By having participants hold the index finger of their contralateral hand during these postural illusions, they produced the illusion that the finger was becoming shorter or longer (the "Pinocchio illusion"; cf. Lackner, 1988, see below). The illusion of finger lengthening (though, interestingly, not the illusion of finger shortening) produced a corresponding change in the perceived size of tactile stimuli applied to the finger. Similarly, Bruno and Bertamini (2010) showed that using the rubber hand illusion to create the illusion of increased hand size produced corresponding increases on the haptic perception of object size. Analogously, Tajadura-Jiménez et al. (2012) manipulated apparent arm length by playing sounds from speakers at varying distances time-locked to participants' knocks on the floor. The illusion of arm lengthening increased the perceived size of touch on the acting arm, compared to the contralateral arm.

In its classical form, Weber's illusion suggests that the perceived size of sensitive skin surfaces is overestimated compared to less sensitive surfaces. Longo and Haggard (2011) applied the same logic to investigate the representation of body *shape* by comparing the size of tactile stimuli applied to the body in different orientations. The logic of this approach was that if the hand is represented as longer and more slender than it actually is, then the distance between touches applied in the proximo-distal orientation (running *along* the hand) should be overestimated relative to touches applied in the medio-lateral orientation (running *across* the hand). Conversely, if the hand is represented as wider and squatter than it actually is, the opposite pattern should be found, with touches oriented across the hand perceived as bigger than those along the hand. In fact, Longo and Haggard (2011) found that stimuli running across the hand dorsum are perceived as approximately 40% larger than those running along the hand, suggesting that touch is being informed by a fat, squat model of the hand. Intriguingly, this bias mirrors other known properties of the somatosensory system, including increased tactile acuity in the across orientation on the limbs (Cody, Garside, Lloyd, & Poliakoff, 2008; Weber, 1834/1996), and the fact that tactile receptive fields of both spinal (Brown, Fuchs, & Tapper, 1975) and cortical (Alloway, Rosenthal, & Burton, 1989) neurons are generally oval-shaped (rather than circular), with their long axis running along the length of the limbs.

Thus, the bias in tactile size perception found on the hairy skin of the hand dorsum mirrors the geometry of tactile receptive fields in somatosensory cortex. But what about the glabrous skin of the palm of the hand? Does tactile size perception rely on a 2-D or a 3-D representation of the body? In contrast to the large anisotropy found on the hairy skin of the hand dorsum, Longo and Haggard (2011) did not find any apparent bias on the glabrous skin of the palm. This difference is consistent with results showing that receptive fields on the palmar hand surface are generally more circular than on the dorsal surface and, when oval-shaped, the long axis of the oval is distributed more uniformly (DiCarlo & Johnson, 2002; Vega-Bermudez & Johnson, 1999). Thus, the representations of the dorsal and palmar sides of the hand appear to be stretched in different ways, a basic violation of 3-D geometry. Thus suggests that tactile size perception, like tactile localization, may rely on a set of fragmented, 2-D representations of individual skin surfaces.

## Position Sense

Position sense refers to the ability to perceive where the different parts of our body are located in space, even when we can't see them. Though position sense usually remains in the background of our mental life, it is critically important for all our everyday behaviors. The importance of position sense is strikingly evident when it is lost in patients such as I.W., who suffered a near total loss of the sensory fibers below the neck at age 19, leaving him completed deafferented and without position sense (Cole, 1995). Though the fibers carrying motor information to his body were unimpaired, I.W. was only able to teach himself to walk again through an intense program of practice using constant and vigilant visual guidance, leading the neurologist who worked with him to refer to I.W.'s life as a "daily marathon" (Cole, 1995).

Several types of afferent signal from the periphery contribute to position sense, including receptors from joints signalling flexion or extension, from the skin signalling stretch, and from muscle spindles signalling contraction or lengthening (Proske & Gandevia, 2012). Together with efferent copies of motor comments, these signals provide a specification of the postural configuration of the body (Burgess, Wei, Clark, & Simon, 1982). Critically, all of these signals specify joint *angles*, that is, the relative flexion or extension of each joint. There is no afferent signal, or combination of signals, that function like a global positioning system (GPS) signal, providing information about the absolute location of body parts in external space. As a matter of trigonometry, information about joint angles is insufficient to determine the absolute position in external

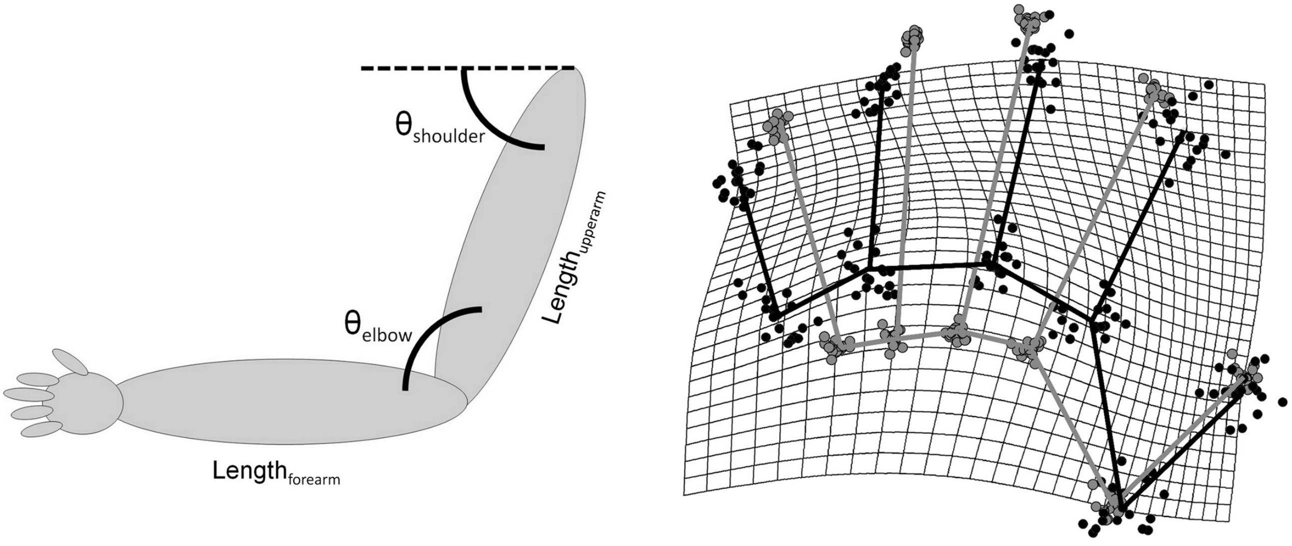

*Figure 2.* Left panel: A schematic depiction of the need for stored body representations in position sense in the case of the arm. Proprioceptive afferent signals specify joint angles, such as those at the shoulder ($\theta_{\text{shoulder}}$) and elbow ($\theta_{\text{elbow}}$). However, determining the absolute spatial position of the hand with respect to the shoulder also requires information about the length of the upper ($\text{Length}_{\text{upperarm}}$) and forearm ($\text{Length}_{\text{forearm}}$), which critically is not specified by immediate sensory signals from the body. Right panel: Results from Longo and Haggard's (2010) study, showing implicit perceptual maps of judged locations (in black) put into Procrustes alignment with actual hand shape (in gray) for 18 participants. The black and gray lines connect the knuckle and tip of each finger, as well as adjacent knuckles, to give an overall sense of hand shape. The grid shows how a rectangular grid superimposed on actual hand shape would have to be stretched to transform actual hand shape into represented hand shape. The implicit hand maps clearly overestimate hand width, and underestimate finger length.

space of part of the body. As shown in Figure 2, perceiving the absolute spatial position of the body requires that information about joint angles, which is specified by immediate proprioceptive afferent signals, be combined with information about the length of body segments, which is not specified by any immediate sensory signal.

While many authors have identified the need for stored metric information about the size and shape of the body for position sense (e.g., Craske, Kenny, & Keith, 1984; Gurfinkel & Levick, 1991; Longo et al., 2010; Soechting, 1982; van Beers, Sittig, & Denier van der Gon, 1998), it has usually been assumed that such information is readily available to the somatosensory system. This seems like quite a reasonable assumption to make, for several reasons. Though the size and shape of our body changes substantially over developmental time, on the everyday time scale the body remains largely constant. The body, moreover, is ubiquitous in perceptual experience and metric information about the body is available through vision or self-touch. Further, inaccurate body representations would seem to pose major barriers to skilled, dextrous action. Despite all this, Gurfinkel and Levick (1991) provided an intriguing anecdotal report that when participants were asked to judge the location of two parts of their arm, the judgments were closer together than the two points actually were, suggesting the position sense may in fact rely on a distorted body representation.

Longo and Haggard (2010) developed a novel procedure to isolate and measure the representation of body size and shape underlying position sense of the hand. The participant's hand was placed palm-down on a table and covered with an occluding board. They were then asked to judge the location of the knuckles and tips of their fingers by placing the tip of a long baton on the board, directly above each location. Each judgment was photographed by an overhead camera. Previous studies of proprioceptive localization have focused on the "error of localization," the spatial displacement of judged location from actual location, measuring bias as the constant error of localization, and precision as the variable error. In contrast, Longo and Haggard (2010) focused on the *internal configuration* of judgments to each of the landmarks with respect to each other, completely ignoring where judgments were in relation to the participant's actual hand. This allowed them to construct perceptual maps of represented hand form, which they then compared to the actual form of each participant's hand.

The resulting hand maps from Longo and Haggard's (2010) first experiment are shown in the right panel of Figure 2. Remarkably, these maps were massively distorted in a highly consistent and stereotyped way across participants. In particular, there were three clear patterns of distortions: (1) overestimation of hand width, quantified as the distance between pairs of knuckles; (2) overall underestimation of finger length, quantified as the distance between the knuckle and tip of each finger; and (3) a radio-ulnar gradient, with underestimation of finger length increasing systematically from the thumb to the little finger. Intriguingly, these biases appear to mirror known characteristics of primary somatosensory cortical maps. For example, the overestimation of hand width compared to length mirrors anisotropies in RF geometry and tactile size perception described in the previous section. Similarly, the radial-ulnar gradient of finger size mirrors differences in tactile sensitivity and cortical magnification of the five fingers (Duncan & Boynton, 2007; Vega-Bermudez & Johnson, 2001).

In a subsequent study, Longo and Haggard (2012a) investigated the level of spatial abstraction at which these implicit maps are organized, using the same logic discussed above for tactile localization and tactile size perception. If the hand is represented as two distinct 2-D skin surfaces, there may be different distortions on each. If, in contrast, the two sides of the hand are integrated into a fully 3-D representation of the hand as volumetric object in the world, then consistent distortions should appear on both sides of the hand, and should be correlated across people. Longo and Haggard (2012a) found that distortions on the dorsal and palmar hand surfaces were qualitatively similar, and strongly correlated across participants, suggesting that the representations of the two skin surfaces are bound into a common representation, suggesting something more abstract than a purely 2-D representation. However, the distortions were of different *magnitude* on the two surfaces, being substantially reduced on the palmar surface. This is a clear violation of the geometry of 3-D space, suggesting something less abstract than a fully 3-D volumetric representation. Thus, Longo and Haggard (2012a) suggested that position sense may rely on something intermediate between a 2-D representation of distinct skin surfaces and a fully 3-D representation of the hand as a volumetric object, which they called a *2.5-D representation*, in analogy to Marr's (1982) "2.5-D sketch" in vision.

## Relations Between Implicit and Explicit Body Representations

In the first part of this paper, I have described several large and highly stereotyped distortions of body representation underlying perceptual processing. Intuitively, this seems quite surprising, since for most of us it seems like we have quite an accurate sense of what our body is like. Surely, if there's anything we "know like the back of our hand" it would be the actual back of our hand. Do the distortions I have described also characterize our conscious experience of our body, our *body image*? To address this question, Longo and Haggard (2010) adapted the "template matching" procedure of Gandevia and Phegan (1999) to measure participant's conscious experience of their hand. The same participants who produced the distorted hand maps in Figure 2 were shown arrays of hand images which had been stretched in various ways, resulting in a range of hand shapes, from very long and slender to very squat and wide. In contrast to their highly distorted hand maps in the localization task, participants on average selected hands quite similar to their actual hand shape. Thus, the explicit image of the hand is approximately veridical, even as somatoperception relies on a set of implicit, and highly distorted, representations.

## Implicit Body Representations and the Cognitive Unconscious

The dissociation between implicit and explicit body representations fits within a larger trend in psychology and the cognitive sciences over the past few decades emphasizing that much of cognitive processing remains inaccessible to conscious awareness as part of the so-called "cognitive unconscious" (Kihlstrom, 1987). While we are clearly able to introspect on much of our psychological life, we are also unaware of much of the cognitive machinery underlying our thoughts, beliefs, and actions (e.g., Nisbett & Wilson, 1977; Tranel & Damasio, 1985; Tulving & Schacter, 1990).

In the domain of perception, there are numerous clinical reports of preserved ability to use perceptual information which appears entirely inaccessible to conscious awareness, including blindsight (Weiskrantz, 1986), visual object agnosia (Milner & Goodale, 2006), and numb-sense (Paillard, Michel, & Stelmach, 1983). The research reviewed above is similar in showing dissociations between the cognitive machinery of perception and conscious awareness, but also strikingly different in showing that these implicit processes are highly inaccurate, in contrast to more veridical explicit representations. This parallels findings of implicit processes producing highly biased results in multiple domains, including reasoning and decision making (Tversky & Kahneman, 1981; Kahneman, 2011) and attitudes (Greenwald & Banaji, 1995; Nosek, Hawkins, & Frazier, 2011), even while more deliberate reflection may produce more rational decisions and more egalitarian attitudes.

## A Hierarchy of Body Representations

What, then, is the relationship between our explicit, conscious body image, and implicit body representations? One possibility is that they reflect entirely distinct representations emerging from different sensory modalities, the body image arising through vision and distorted implicit representations through somatosensation. However, there is strong evidence for bidirectional interactions between the visual body image and somatosensory processing. For example, cutting off inputs from the peripheral nerves with cutaneous anesthesia produces the subjective experience that that body part has gotten larger, both on the hand (Gandevia & Phegan, 1999) and the mouth (Türker, Yeo, & Gandevia, 2005). This experience may be familiar to anyone unfortunate enough to have had dental anesthesia, in which the gums and teeth begin to feel enormous. Conversely, visual illusions producing the experience of the body being larger than it actually is produce corresponding changes in the perceived size of touch, as described above (Bruno & Bertamini, 2010; Taylor-Clarke et al., 2004). Thus, somatosensory and visual body representations do not appear to be entirely independent.

Another possibility, which I will defend here, is that implicit and explicit body representations lie at opposite ends of a continuum of body representations. This continuum can be thought of in terms of the different spatial scales at which the body is represented, which I discussed in the first part of the paper. At one end are primary somatosensory maps, representing the body surface as a mosaic of individual receptive fields, each constituting a single ''pixel.'' At the other end is our conscious experience of our body as a volumetric object in the world. In between these extremes may be 2-D maps of individual skin surfaces (such as I have argued may underlie tactile localization and tactile size perception), and 2.5-D representations (such as I have argued underlies position sense).

Intriguingly, there is some evidence that different measures of the conscious body image may index different points along this continuum. For example, Longo and Haggard (2012b) compared three different measures of hand representation: (1) the localization task measuring implicit body representations underlying position sense, (2) the template matching task described above, and (3) a ''line length'' task in which participants judged whether a line presented on the monitor was shorter or longer than different parts of their hands. As in their previous study described above, Longo and Haggard (2012b) found that the hand representation revealed by the localization task was massively distorted, while that revealed through template matching was approximately veridical. The line length task, however, appeared intermediate between the two. Participants in the line length task showed distortions of perceived hand size and shape qualitatively similar to those found in the localization task, but smaller in magnitude. The template matching task, as a purely visual recognition task, may be a purer measure of the ''visual'' end of this continuum of body representations, while the line length task may involve a larger contribution of the ''somatosensory'' side of body representation.

On this view, body representations emerge from the operation and mutual interactions of complementary bottom-up and top-down processes. First, from the bottom-up, somatosensation represents the body surface as a mosaic of discrete receptive fields, which become progressively agglomerated into larger and larger units of organization, a process I call *fusion*. Second, from the top-down, vision starts out depicting the body as an undifferentiated whole, which is progressively broken into smaller parts, a process I call *segmentation*. Thus, body representation operates from the bottom-up as a process of fusion of primitive elements into larger complexes, as well as from the top-down as a process of segmentation of an initially undifferentiated whole into more basic parts.

## Implications for Clinical Disorders of Body Representation

While most of the studies I have described have been conducted with healthy individuals, this research also has potential implications for understanding clinical disorders involving disrupted body representation. While this connection remains speculative, in this final part of the paper I will discuss some ways in which the distinction between implicit and explicit body representations may relate to conditions such as eating disorders.

It has been widely accepted since the classic work of Bruch (1978) that anorexia nervosa involves a distorted body image. Indeed, such distortions are strong predictors of poor prognosis for recovery (Casper, Halmi, Goldberg, Eckert, & Davis, 1979) and of relapse following remission of symptoms (Fairburn, Peveler, Jones, Hope, & Doll, 1993; Keel, Dorer, Franko, Jackson, & Herzog, 2005). Could the distortions of the conscious body image seen in such cases reflect normal distortions of somatosensory body representations which have risen into conscious awareness, implicit representations which have become explicit? While the majority of the results I have described have investigated representation of the hand, it is nevertheless intriguing that the distortions of implicit representations are for the hand to be wider and squatter than it actually is, mirroring the body image distortions of individuals with eating disorders who experience their body as fat.

Two sets of considerations may seem to make this hypothesis unlikely. First, while meta-analyses of studies of eating disorders have found clear evidence for distortions of perceived body size (e.g., Cash & Deagle, 1997; Smeets, Smit, Panhuysen, & Ingelby, 1997), these same studies have found even stronger effects for bodily attitudes, suggesting that perceptual aspects of body image may be secondary to disrupted attitudes. Indeed, some authors have suggested that body-size estimates themselves may actually reflect attitudes, rather than perception (Ben-Tovim, Walker, Murray, & Chin, 1990). Second, eating disorders and distorted body image are widely linked to the visual depiction of bodies in the Western mass-media (Becker & Hamburg, 1996; Derenne & Beresin, 2006), making top-down effects of vision seem more critical than bottom-up effects of somatosensation.

Recently, however, several lines of evidence have suggested that somatosensation, and potentially implicit body representations, may have a greater role in eating disorders than previously believed. Intriguingly, recent results have revealed that individuals with anorexia show evidence for overestimation of body size in implicit action-based tasks (Guardia et al., 2010, 2012; Keizer et al., 2013). Critically, these studies are less susceptible than overt size estimates to the critique of implicitly reflecting attitudes toward the body, rather than distorted body representation per se (cf. Ben-Tovim et al., 1990). Further, and more directly related to somatosensation, recent results have found that individuals with anorexia show impaired tactile processing, overestimating the size of tactile stimuli (Keizer et al., 2011; Keizer, Smeets, Dijkerman, van Elburg, & Postma, 2012). Intriguingly, this bias, though apparent on the arm as well, was strongest on the abdomen, and predicted the severity of body dissatisfaction.

Studies using neuroimaging have also produced intriguing findings suggesting that individuals with eating disorders may actually be *less* reliant on visual perception of bodies than healthy individuals. For example, Uher et al. (2005) found reduced activations to visually-presented images of bodies in patients with eating disorders in several visual brain areas. Similarly, Suchan et al. (2010) found reduced gray-matter density within the extrastriate body area (EBA), a brain area specialized for the visual perception of bodies (Downing, Jiang, Shuman, & Kanwisher, 2001), in women with anorexia. In a subsequent study, these authors reported reduced functional connectivity between the EBA and another region of the ventral visual cortex specialized for body perception, the fusiform body area (FBA) (Suchan et al., 2013). Consistent with those results, Favaro and colleagues (2012), analyzing resting-state functional connectivity of fMRI data in individuals with anorexia and healthy controls, found that the patients showed reduced connectivity within the ventral visual network. Remarkably, these authors also found that anorexia was linked to *increased* connectivity within somatosensory cortex.

Thus, in contrast to the long-standing idea that body image distortions may arise from visual exposure to extreme bodies (Becker & Hamburg, 1996; Derenne & Beresin, 2006), these results suggest that in some ways individuals with eating disorders may be paradoxically *less* sensitive to visually-depicted bodies. Together, these results are consistent with the hypothesis that individuals with eating disorders may be relatively more reliant on somatosensory body representations, and less on visual ones. This raises the possibility that the distortions of implicit body representations underlying several aspects of somatosensation which I have described here may play a role in producing distortions of the explicit body image.

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