

BIROn - Birkbeck Institutional Research Online

Longo, Matthew R. (2016) Distorted body representations in healthy cognition. *The Quarterly Journal of Experimental Psychology* 70 (3), pp. 378-388. ISSN 1747-0218.

Downloaded from: <https://eprints.bbk.ac.uk/id/eprint/13592/>

Usage Guidelines:

Please refer to usage guidelines at <https://eprints.bbk.ac.uk/policies.html> or alternatively contact lib-eprints@bbk.ac.uk.

RUNNING HEAD: Distortions of Body Representations

Distorted Body Representations in Healthy Cognition

Matthew R. Longo

Department of Psychological Sciences, Birkbeck, University of London

Address correspondence to:

Matthew R. Longo

Department of Psychological Sciences

Birkbeck, University of London

Malet Street, London WC1E 7HX

United Kingdom

m.longo@bbk.ac.uk

Abstract

Delusions and misperceptions about the body are a conspicuous feature of numerous neurological and psychiatric conditions. In stark contrast to such pathological cases, the immediacy and familiarity of our ordinary experience of our body can make it seem as if our representation of our body is highly accurate, even infallible. Recent research has begun to demonstrate, however, that large and systematic distortions of body representation are a normal part of healthy cognition. Here, I will describe this research, focusing on distortions of body representations underlying tactile distance perception and position sense. I will also discuss evidence for distortions of higher-order body representations, such as the conscious body image. Finally, I will end with a discussion of the potential relations among different body representations and their distortions.

Our body is the core of our sense of self, and central to our personal identity as an individual. We experience our body from the outside, as a physical object in the world like any other, but also from the inside, as an object of immediate experience (Bermúdez, Marcel, & Eilan, 1995). The intimate and direct connection we have with our own body can make knowledge of our body seem immune to the usual sources of perceptual error and illusion. Indeed, the very fact that we have multiple ways of knowing about our body (from inside, and from outside) could very well contribute to making the overall perception of the body highly reliable. While distortions and misperceptions of the body are a familiar result of several psychiatric and neurological conditions, it is natural to suppose that healthy adults have highly accurate – even infallible – knowledge about the physical structure of their bodies. In this paper, I will describe recent research that has begun to question this assumption, showing large and systematic distortions of body representation in healthy adults. After giving a brief summary of the varied distortions of body representation found in pathological conditions, I will describe research showing large distortions of body representations underlying somatosensory perception of tactile distance and position sense. Finally, I will discuss other results showing distortions underlying higher-level aspects of body representations and end with a discussion of the relationships among the various distortions I discuss.

Distorted body representations in disease

The various distortions and misperceptions of body representation found in disease have long attracted widespread interest, both among researchers and the wider public. In large part, this interest is due to their sheer strangeness, and the striking contrast they present to the seeming immediacy of our normal experience of our body.

Within neurology, perhaps the most widely investigated misperception is the case of phantom limbs, in which an amputated limb is perceived by the patient as continuing to exist (Melzack, 1992; Ramachandran & Hirstein, 1998). Phantoms occur in a substantial majority of cases of amputation (Melzack, 1992), and less frequently following congenital limb absence (Brugger et al., 2000). The subjectively felt presence of the missing limb can be so strong that the patient may even try to walk with a phantom leg (Melzack, 1990). Another curious condition occurs following damage to the right hemisphere, in which patients with impaired motor control over their left arm frequently deny any such problem, a delusion known as *anosognosia for hemiplegia* (Berti et al., 2005; Fotopoulou et al., 2008). In other cases, patients with motor loss may deny that the paralyzed limb is actually theirs, insisting that it belongs to, for example, a family member, a condition called *somatoparaphrenia* (Vallar & Ronchi, 2009). Sometimes, patients with damage to the right parietal lobe will simply deny that the left half of their body even exists (*asomatagnosia*; Critchley, 1953). In *autoscopical illusions* and *out-of-body experiences*, people experience a dramatic dissociation between the experienced location of the body and their first-person perspective (Brugger, Regard, & Landis, 1997; Blanke, Landis, Spinelli, & Seeck, 2004).

Strange misperceptions of the body are also found in several psychiatric conditions. Patients with eating disorders such as *anorexia nervosa*, for example, will commonly insist that they are fat, even while completely emaciated (Bruch, 1978; Treasure, Claudino, & Zucker, 2010). Such body image distortions are a strong predictor of negative prognosis (Casper, Halmi, Goldberg, Eckert, & Davis, 1979) and of relapse following recovery (Fairburn, Peveler, Jones, Hope, & Doll, 1993; Keel, Dorner, Franko, Jackson, & Herzog, 2005). Patients with *body dysmorphic disorder* are fixated on the idea that some specific part of their body is hideously ugly, though it appears normal to

everyone else (Phillips, Didie, Feusner, & Wilhelm, 2008). Finally, in the case of *body integrity identity disorder* (sometimes called *xenomelia*), individuals with apparently intact bodies insist that they would feel more complete with some specific part of their body removed (Brugger, Lenggenhager, & Giummarra, 2013; First, 2005). This represents a curious inversion of the case of phantom limbs, a sort of ‘negative’ phantom.

Such a list of conditions makes striking reading, in large part because of the difficulty in identifying with such seemingly bizarre delusions. For most of us, our ordinary experience of our body doesn’t feel anything like such cases, making them seem far removed from body representation in healthy adults. Nevertheless, an emerging body of research has begun to show that distortions of body representations are a normal part of ordinary, healthy cognitive life. It may be that these distortions reflect weak forms of the sorts of distortions seen in various diseases. Alternately, these distortions in healthy people might reflect entirely different mechanisms. In the following sections, I will discuss this research.

Distortions in tactile size perception

Distortions in perceived tactile size or distance have been known since the classic investigations of Ernst Weber in the 19th century (Weber, 1834/1996). Weber noticed that as he moved the two points of a compass across his skin, it felt as if the distance between the points changed. Specifically, perceived distance was greater on regions of relatively high tactile sensitivity (like the palm of the hand) compared to less sensitive regions (such as the forearm). Subsequent research has confirmed Weber’s observations and shown a systematic relation between the spatial sensitivity of skin surfaces and the perceived distance between two touches (e.g., Anema, Wolswijk, Ruis,

& Dijkerman, 2008; Cholewiak, 1999; Taylor-Clarke, Jacobsen, & Haggard, 2004), an effect now referred to as *Weber's Illusion*.

One natural way to think about Weber's illusion is as a vestigial remnant of the well-known distortion of primary somatosensory maps, which show dramatically disproportionate representation of sensitive skin regions (i.e., cortical magnification), as famously depicted in textbook illustrations of the "Penfield homunculus" (Penfield & Boldrey, 1937), with gigantic lips, fingers, and genitals. It is obviously adaptive to have exquisite tactile sensitivity on specific skin surfaces, such as the fingertips, which allows us to perform dexterous behaviors that would be impossible were we to have homogenously mediocre sensitive across the skin surface. Weber's illusion shows that such homuncular distortions bias higher-level aspects of tactile perception, which may be a small price to pay for the benefits of specialization. Nevertheless, as Taylor-Clarke and colleagues (2004) noted, the magnitude of Weber's illusion is substantially less than would be predicted if perceived tactile distance was directly proportional to cortical magnification, suggesting the operation of some form of tactile size constancy. They estimated that the illusion was about 10% of what would be expected based on magnification. In my opinion, even this may overstate the effect. Sur, Merzenich, and Kaas (1980) found differences as big as two orders of magnitude between the magnification levels on different skin regions of owl monkeys. It is unlikely that any perceptual effect in humans would be more than 1-2% of that.

A number of studies have demonstrated tight links between tactile distance perception and higher-order aspects of body representation. For example, Taylor-Clarke and colleagues (2004) found that magnification or minification of the visual experience of body parts produced systematic alterations of perceived tactile distances subsequently applied. Similarly, de Vignemont, Ehrsson, and Haggard (2005) created an

illusion of finger elongation using a vibration-induced proprioceptive illusion, showing that this produced a corresponding lengthening of perceived tactile distance. Tajadura-Jiménez and colleagues (2012) used audio-motor cues to create the experience of one's arm being longer than its actual size. Such an illusion of elongation produced a corresponding increase in perceived tactile distances on the arm. In another study, Longo and Sadibolova (2013) found that simply looking at the stimulated hand produced a reduction in perceived tactile distances, compared to looking at a non-body object. This effect parallels other known effects of vision of the body on somatosensory processing, such as enhancing tactile spatial acuity (Cardini, Longo, & Haggard, 2011; Kennett, Taylor-Clarke, & Haggard, 2001) and reducing acute pain (Longo, Betti, Aglioti, & Haggard, 2009; Mancini, Longo, Kammers, & Haggard, 2011). Other recent research has shown that perceived tactile distance is expanded across joint boundaries, showing that the high-level segmentation of the body into discrete parts produces categorical perception effects on tactile distance (de Vignemont, Majid, Jola, & Haggard, 2009; Le Cornu Knight, Longo, & Bremner, 2014). Finally, two recent studies have shown that tool-use, which can be thought of as extending arm size, also produces systematic changes to tactile distance perception (Canzoneri et al., 2013; Miller, Longo, & Saygin, 2014).

In its classic form described to this point, Weber's illusion reflects differences in the represented size of different skin regions. An analogous logic, however, can also be applied to stimuli presented at different orientations on a single skin surface to investigate the represented *shape* of an individual skin surface. Longo and Haggard (2011), for example, asked participants to make forced-choice judgments of the perceived size of tactile distances oriented in the medio-lateral axis of the hand dorsum (i.e., *across* the hand) versus the proximo-distal axis (i.e., *along* the hand). If the hand

were represented as longer and thinner than it actually is, stimuli oriented along the length of the hand should be perceived as bigger than identical stimuli running across the width of the hand; if, in contrast, the hand were represented as squat and fat, the opposite should be true. In fact, stimuli running across the width of the hand were perceived as approximately 40% larger than those running across the length of the hand, suggesting a squat and fat bias. This bias is reduced or even eliminated on the glabrous skin of the palm (Le Cornu Knight et al., 2014; Longo & Haggard, 2011; Longo, Ghosh, & Yahya, 2015a). Moreover, while there are clear correlations across people in the magnitude of such distortion on both the dorsal and palmar surfaces of the two hands, within each hand there is no correlation between the distortions on the two surfaces (Longo et al., 2015a). Such anisotropies are not limited to the hand, but have been found on other body parts, including the forearm (Green, 1982; Le Cornu Knight et al., 2014), the leg (Green, 1982), and the face (Longo et al., 2015a), suggesting that it may reflect a basic principle of body representation, rather than something idiosyncratic to the hands, or even to limbs.

Longo and Haggard (2011) proposed a ‘pixel’ model to account for such effects. The basic idea of the pixel model is that the receptive fields (RFs) of individual neurons in a somatotopic map are treated like pixels in a two-dimensional spatial array. Distances would then be calculated by essentially counting the number of pixels separating two stimulated locations. RFs of neurons representing sensitive skin surfaces are smaller than those representing less sensitive skin surfaces (e.g., Powell & Mountcastle, 1959; Sur et al., 1980). Because the spacing between RFs is known to be a constant ratio of RF size (Sur et al., 1980), a tactile distance applied to a sensitive surface (e.g., the hand) will have more unstimulated RFs between the two stimulated points than will an identical tactile distance applied to a less sensitive skin surface (e.g.,

the forehead). This can account for Weber's illusion, since the increased number of pixels crossed by a stimulus on a sensitive skin surface will lead it to be perceived as bigger than on a less sensitive surface.

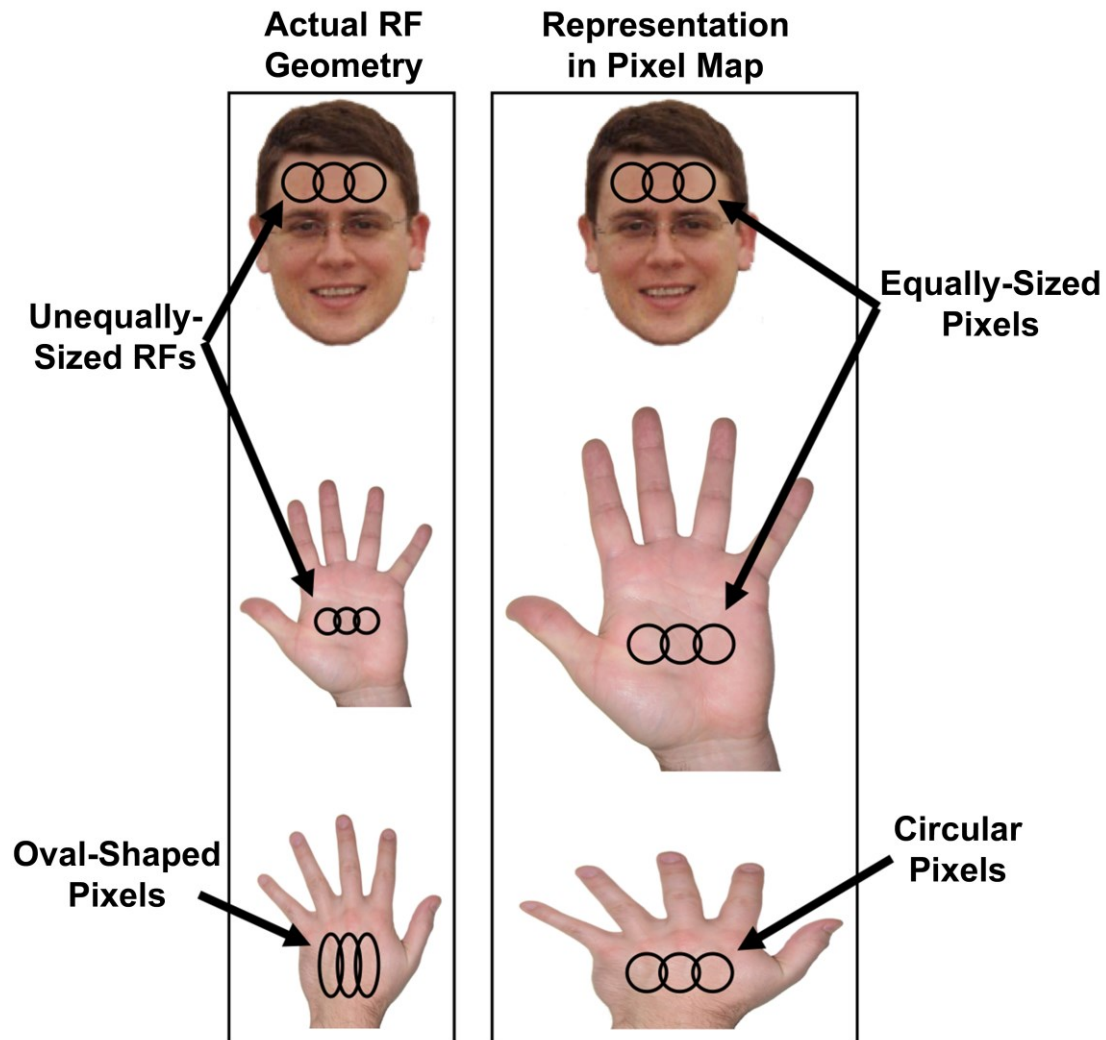


Figure 1: The 'pixel' model proposed by Longo and Haggard (2011). Distances on the body are represented in terms of the number of receptive fields (RFs) which a stimulus covers. RFs which vary in size and shape are interpreted as being equally sized and circular. Thus, is a given tactile distance is applied to two skin surfaces with differently-sized RFs (e.g., the forehead and palm), the distance applied to the surface with smaller RFs (the palm) will be perceived as bigger than that applied to the surface with larger RFs (the forehead), producing the standard form of Weber's illusion. When RFs on a single skin surface are oval-shaped (such as on the hairy skin of the hand dorsum), a tactile distance oriented with the short axis of the RFs (i.e., across the width of the hand) will be perceived as bigger than the same distance oriented with the long axis of the RFs (i.e., along the length of the hand).

Importantly, however, the pixel model can also account for the orientational version of Weber's illusion described by Longo and Haggard (2011). RFs of SI neurons

representing the hairy skin of the limbs are known to be oval-shaped, rather than circular, and with the long-axis of the RF running along the proximo-distal axis of the arm (e.g., Alloway, Rosenthal, & Burton, 1989; Brooks, Rudomin, & Slayman, 1961; Powell & Mountcastle, 1959). Because RFs are smaller in the medio-lateral axis of the limb, tactile distances applied across the width of the hand will have more unstimulated pixels than the same distance applied along the length of the hand, and should thus be perceived as bigger. On the glabrous skin of the palm, in contrast, RFs are both more circular and, when oval-shaped, do not tend to have a preferred orientation (e.g., DiCarlo & Johnson, 2002; DiCarlo, Johnson, & Hsiao, 1998). Thus, the pixel model can also account for anisotropies in tactile distance perception.

While the pixel model proposed that perceived distances in touch are calculated by essentially counting RFs, there are also reasons for believing that additional processing stages are required. First, as discussed above, the fact that Weber's illusion is dramatically smaller than would be predicted on the basis of cortical magnification alone suggests that some process of correction for differences in magnification occurs, a form of tactile size constancy. Second, the various top-down effects on tactile distance perception by illusions of body size, also discussed above, indicate that touch is referenced to a stored model of the represented metric properties of the body. Indeed, this body referencing may be how tactile size constancy is implemented. One possibility is that distances are calculated from a pixel map not in early somatosensory cortex but at higher stages of posterior parietal cortex. Tactile size constancy could be achieved by these higher-order maps having more proportional representation of different skin surfaces than more primary maps, while top-down effects of body illusions might produce plasticity in these higher-order maps without directly affecting low-level sensory maps in SI.

Distortions in position sense

Position sense is our ability to perceive the spatial locations of parts of our body, even in the absence of vision. This ability relies on several types of afferent signals, including receptors in joints signaling flexion or extension, receptors in muscle spindles specifying contraction or lengthening, and receptors in skin specifying stretch, along with efferent copies of motor commands (Proske & Gandevia, 2012). Critically, however, all of these afferent signals provide information about the *angles* of joints in terms of their relative flexion or extension, rather than their absolute location. Afferent proprioceptive signals are thus fundamentally different from global positioning system (GPS) signals, such as found in smartphones, which provide information about exact location. As a matter of simple trigonometry, information about the angles of joints is insufficient to determine their absolute spatial location. This information must be combined with information about the length of body segments between joints, information which isn't specified by any immediate afferent signal and must thus come from a stored representation of body size and shape (Longo, Azañón, & Haggard, 2010). Figure 2 shows the geometry of this situation for the case of perceiving hand location. To tell where the wrist is in relation to the shoulder, afferent information specifying the angles of the shoulder and elbow joints (θ_{shoulder} and θ_{elbow}) must be integrated with stored information specifying the lengths of the upperarm and forearm ($\text{Length}_{\text{upperarm}}$ and $\text{Length}_{\text{forearm}}$).

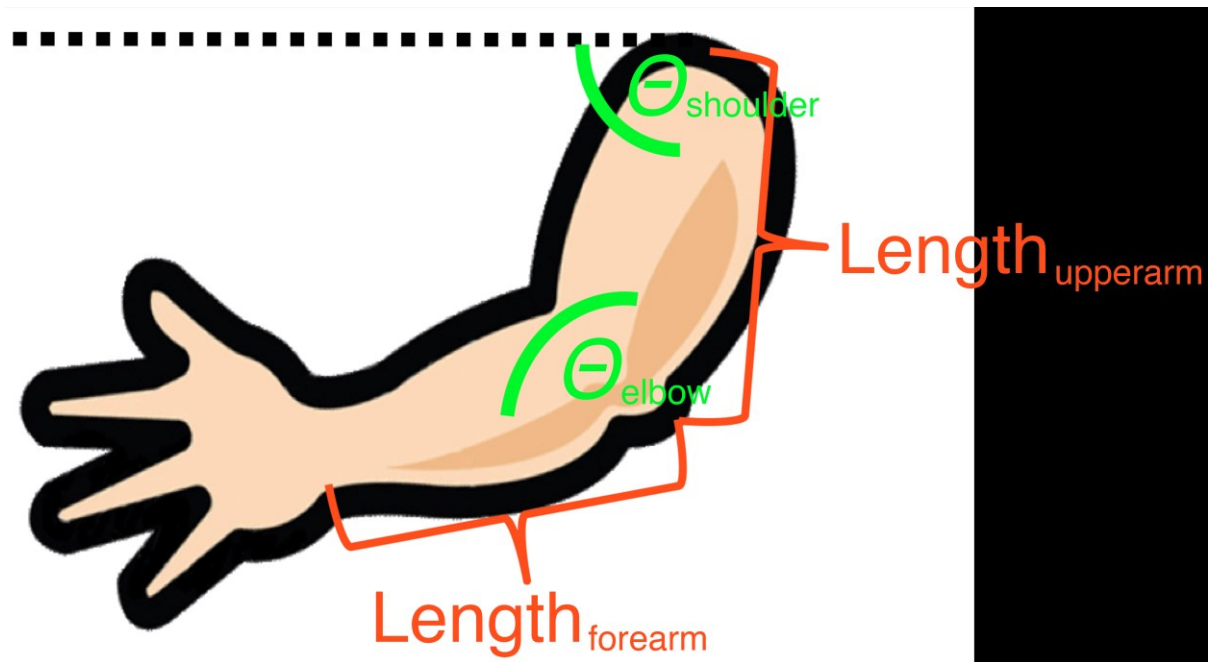


Figure 2: The need for a body model for position sense. To perceive the absolute location of the wrist relative to the shoulder, afferent signals specifying the joint angles of the shoulder (θ_{shoulder}) and of the elbow (θ_{elbow}) need to be integrated with information about the length of the segments connecting these joints, that is the forearm ($\text{Length}_{\text{forearm}}$) and the upper arm ($\text{Length}_{\text{upperarm}}$). Critically, however, such information about lengths is not specified by any immediate afferent signal, and so must come from a stored representation of body size and shape.

The general need for afferent proprioceptive information has been described by a number of authors over the past couple decades (e.g., Craske, Kenny, & Keith, 1984; Gurfinkel & Levick, 1991; Longo et al., 2010; Soechting, 1982; van Beers, Sittig, & Dernier van der Gon, 1998). It has generally been assumed, however, that accurate information about body size is readily available to the somatosensory system. Given the ubiquity of our body in our perceptual experience, this seems like a reasonable and unremarkable assumption to make. In contrast to this assumption, however, Gurfinkel and Levick (1991) reported anecdotal evidence that when participants were asked to localize two different parts of their arm, the judged locations of these parts were closer together than their actual locations. This result suggested that position might rely on a distorted representation of arm length.

Longo and Haggard (2010) developed a method for isolating and measuring this representation of body size and shape underlying position sense of the hand.

Traditionally, studies of position sense have asked participants to judge the location of a single part of the body and measured the so-called “error of localization”, the spatial deviation between the actual and judged locations of the body part. In contrast to this approach, Longo and Haggard (2010) asked participants to judge the location of multiple landmarks on the hand and analyzed the *internal configuration* of responses with respect to each other, ignoring the error of localization entirely. The advantage of this approach is that whereas constant errors of localization might arise either due to misperception of body part size or body posture, the internal configuration more directly isolates representation of body size and shape, removing biases associated with misperception of posture.



Figure 3: The ‘psychomorphometric’ paradigm of Longo and Haggard (2010). Participants rest their hand on a table (left panel). Their hand is then occluded and they use a long baton to judge the perceived location of the tip and knuckle of each finger (right panel). By comparing the relative positions of judgments, an implicit perceptual map of hand structure can be constructed and compared with actual hand size and shape.

The paradigm of Longo and Haggard (2010) is shown in Figure 3. Participants laid their hand palm-down on a table underneath an occluding board. They were then asked to localize the tip and knuckle of each finger by positioning the tip of a baton on

the occluding board directly above each landmark. By comparing the relative position of the judgments of each landmark, Longo and Haggard (2010) constructed perceptual maps of represented hand size and shape, which they then compared to participants' actual hands. Figure 4 shows the resulting hand maps. Maps from each participant were placed into best-fitting alignment using Generalized Procrustes Analysis (e.g., Bookstein, 1991), which removes differences in location, scale, and rotation, isolating information about shape. The green dots indicate average location judgments for each landmark of 18 participants after Procrustes alignment, with the green outline showing the grand-average shape across participants. The red dots indicate actual hand shape for these participants, also placed into Procrustes alignment with the perceptual maps, with the red outline indicating the grand-average shape of participants' actual hands.

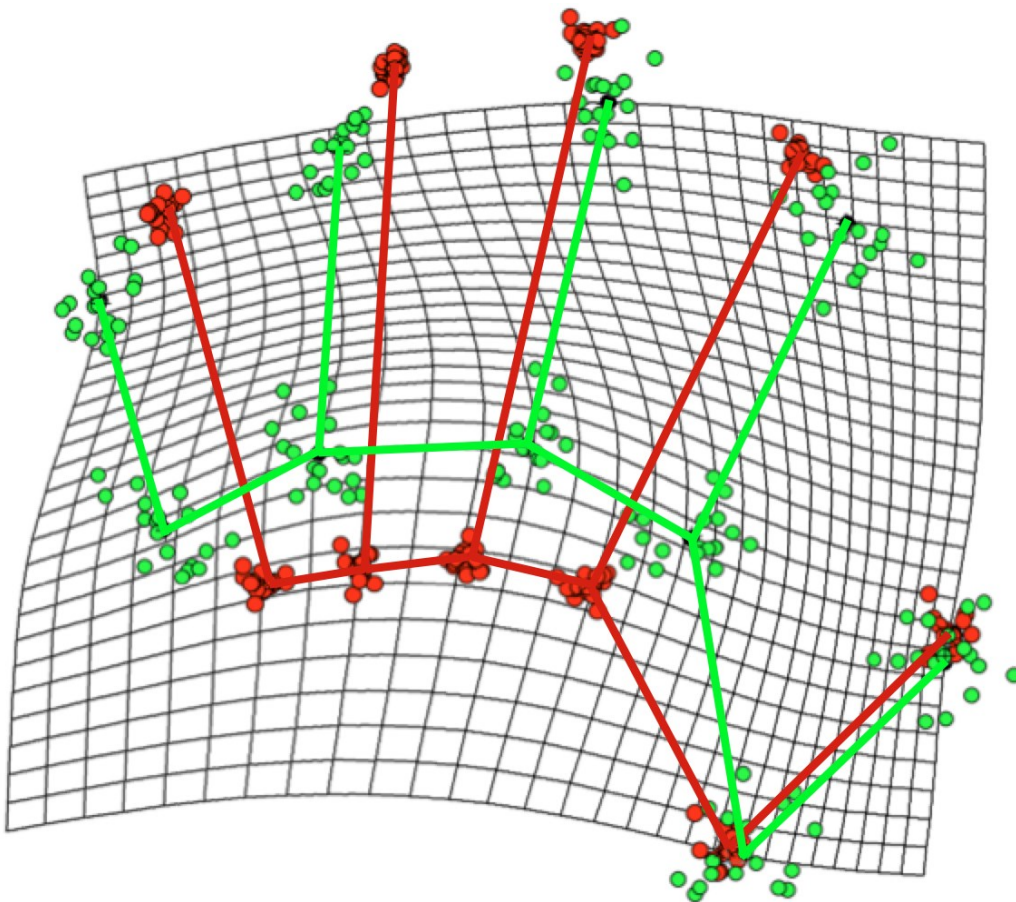


Figure 4: Results from Longo and Haggard's (2010) study. Implicit perceptual hand maps from 18 participants (green) are shown in best-fitting Procrustes alignment with actual hand shape

(red). The green and red lines connect the tip and knuckle of each finger and the knuckles of adjacent fingers to give an overall sense of grand-average hand shape. The warped grid shows how a rectangular grid superimposed on actual hand shape would have to be stretched to transform actual hand shape to the shape of the implicit hand map.

As is clearly apparent in Figure 4, perceptual maps of hand structure were systematically, and massively, distorted (Longo & Haggard, 2010). Three specific distortions were apparent: (1) an overestimation of hand width (approximately 75-80%), as measured by the distance between the knuckles of the index and little fingers; (2) overall underestimation of finger length (~30-40%), as measured by the distance between the knuckle and tip of each finger; and (3) a radial-ulnar gradient, with underestimation of finger length increasing progressively from the thumb to the little finger. Subsequent studies using this paradigm have replicated this basic pattern of results and extended them in several ways (e.g., Ferrè, Vagnoni, & Haggard, 2013; Longo, 2014, 2015b; Longo & Haggard, 2012a, 2012b; Longo, Long, & Haggard, 2012; Longo, Mancini, & Haggard, 2015b; Mattioni & Longo, 2014; Saulton, Dodds, Bühlhoff, & de la Rosa, 2015). For example, Longo and Haggard (2012a) found that these distortions were smaller in magnitude when participants judged locations on the palmar surface of the hand. Other studies showed that similar distortions are apparent when participants localize a touch using the same apparatus, showing that the effects are not an artifact of the use of verbal labels given to landmarks (Longo et al., 2015b; Mattioni & Longo, 2014).

What underlies these distortions? Intriguingly, there appear to be similarities between the distortions apparent in hand maps, and known distortions of primary somatosensory maps in the cortex. For example, the overestimation of hand width relative to length mirrors the effects described in the previous section regarding tactile distance perception and RF geometry. In all three cases, there is a clear anisotropy on

the back of the hand, with a reduced anisotropy on the palmar side of the hand.

Similarly, the radial-gradient in underestimation across the hand mirrors gradients in both tactile sensitivity (Duncan & Boynton, 2007; Vega-Bermudez & Johnson, 2001) and cortical magnification (Duncan & Boynton), which are both highest on the thumb and decrease progressively across the hand. Thus, Longo and Haggard (2010) suggested that the representation of the body's metric properties underlying position sense, what they termed the *body model*, might preserve distortions characteristic of somatotopic maps in somatosensory cortex, though in attenuated form.

Distortions in higher-level body representations

Longo and Haggard (2010) distinguished the distorted body model they described from the conscious body image on the basis of the different amounts of distortion observed across tasks. They measured the body image by adapting Gandevia and Phegan's (1999) *template matching* task. They showed participants an array of hand images that had been stretched in various ways, asking them to select the hand image most similar in shape to what it felt like the shape of their own hand image was. In contrast to the large distortions observed in the hand localization task, participants' selections in the template matching task were quite accurate. Subsequent studies using similar tasks have also found quite accurate judgments of hand shape (Longo, 2015c; Longo & Haggard, 2012b). Given that the distortions apparent in the localization task appeared to be selective for position sense, without influencing explicit judgments of hand shape, Longo and Haggard (2010) argued that the body model underlying position sense was distinct from the conscious body image.

Subsequent studies, however, have revealed distortions analogous to those found in the hand mapping task in different types of body image tasks. Longo and

Haggard (2012b) used a 'line length' task to measure perceived hand size in which participants were shown lines of different lengths on a monitor and asked to judge whether each line was longer or shorter than some part of their hand, such as one of their fingers or the width of the hand. In contrast to the accurate judgments in the template matching task, in the line length task there was clear underestimation of finger length, which increased from the thumb to the little finger (Longo & Haggard, 2012b). This pattern is remarkably similar to that found in the hand localization task, though smaller in magnitude. This effect, thus, calls into question the sharp distinction between the body model and body image made by Longo and Haggard (2010).

A series of studies by Sally Linkenauger and her colleagues has, similarly, demonstrated distortions in explicit judgments of body size and shape. For example, Linkenauger and colleagues (2009) asked participants to adjust the length of a tape measure to match the perceived length of their arms, finding a lateral asymmetry such that right-handed people judged their right arm as longer than their left. They suggested that this effect might reflect differences in the representation of the dominant and non-dominant limbs in sensorimotor cortex. Linkenauger and colleagues (2015) asked participants to make judgments about the length of different parts of the body in terms of some other body part (e.g., "How many hand lengths would it take to match your height?"). Large misestimations were apparent in such judgments, but were not seen when participants performed the same task using a non-body object as a metric (e.g., "How many of these sticks would it take to match your height?").

Christina Fuentes and her colleagues (Fuentes, Longo, & Haggard, 2013; Fuentes, Pazzaglia, et al., 2013; Fuentes, Runa, et al., 2013) took a different approach to measuring explicit representations of body structure. They adapted a task originally developed for use with neurological patients (Daurat-Hmeljiak, Stambak, & Berges,

1978), in which participants are shown an image of a head meant to represent their own hand and asked to judge where other parts of their body would be. Whereas the original study had focused on gross, qualitative mislocalizations as a measure of disruption of the body image following brain damage, Fuentes and colleagues (Fuentes, Longo, & Haggard, 2013) investigated the precise metric relationship between judged locations using methods similar to those used by Longo and Haggard (2010) to investigate perceptual hand maps in position sense. Both in the case of the body as a whole (Fuentes, Longo, & Haggard, 2013) and the face specifically (Fuentes, Runa, et al., 2013), these maps showed large overestimation of body width compared to height.

Finally, two recent studies have suggested the people may also show distortions even for conceptual understanding of the locations of different body parts. Longo (2015d) asked participants to indicate the location of their knuckles (i.e., the metacarpophalangeal joint) by placing the tip of a baton on their palm at the location directly opposite the location of the knuckle. Remarkably, participants showed a distal bias, judging their knuckles as too far forward in the hand, for all fingers except the thumbs. This effect was also clearly apparent when participants responded while blindfolded, relying only on tactile cues, suggesting that it does not reflect an effect of visual capture by, for example, the crease at the base of the fingers on the palmar hand surface. Moreover, the same effect was found when participants judged the locations of the experimenter's knuckles, suggesting that it does not reflect something about people's representations of their own hands specifically, but rather something about their conceptual understanding of hands in general. Margolis and Longo (2015) found a similar distal bias when participants were asked to locate their knuckles on a silhouette image of their hand.

How are different distortions related?

I have described several types of distortion of body representations in healthy adults. This naturally begs the question of what the relation is between these different distortions. I will describe three types of proposal that have been recently made about the potential relations between distorted body representations. Longo and colleagues (2010) argued that both tactile distance perception and position sense required that immediate afferent signals be referenced to a stored representation of body size and shape, suggesting that both abilities might rely on a single representation they called the 'body model'. The findings that similar distortions (e.g., overestimation of hand width vs. length, larger on the dorsal than the palmar hand surface) are found for both tactile distance perception (Longo & Haggard, 2011; Longo et al., in press) and position sense (Longo & Haggard, 2010, 2012a) is consistent with this proposal for a common body model underlying both. Nevertheless, the overall emphasis of the model of somatoperceptual information processing proposed by Longo and colleagues (2010) was on categorical distinctions between different types of body representation. For example, the body model was presented as completely distinct from other body representations such as the 'postural schema', related to real-time tracking of limb posture, and the 'superficial schema' involved in tactile localization on the skin surface. For example, Mancini and colleagues (Mancini, Longo, Iannetti, & Haggard, 2011) found large and stereotyped biases in tactile localization on the skin, which had no apparent relation to those found for tactile distance perception or position sense. Similarly, Longo and Haggard (2010) argued that the body model was distinct from the conscious body image based on the presence of distortions for the former but not the latter. Thus, where qualitatively distinct patterns of distortion are found, different representations may be involved.

As described above, however, subsequent research has found that some types of body image task do appear to show distortions analogous to those found in position sense (Longo & Haggard, 2012b). This result challenges the proposal that the body model and body image are entirely separate representations, suggesting instead that they may be affected by common influences, though perhaps to different degrees. Further, there are clear bi-directional influences between high-level visual representations of the body and low-level somatosensory representations. For example, altering somatosensory afferent signals through anesthesia alters the conscious body image (Gandevia & Phegan, 1999; Türker, Yeo, & Gandevia, 2005), while vision of the body modulates low-level aspects of somatosensory (e.g., Kennett et al., 2001; Longo, Pernigo, & Haggard, 2011) and even autonomic (e.g., Sadibolova & Longo, 2014) processing. Longo (2015a) proposed a hierarchical model of body representations, which suggests that implicit body representations (such as the body model) and explicit ones (such as the body image) lie at opposite ends of a continuum. This continuum can be thought of in terms of the spatial scale at which the body is represented. At one extreme of the continuum like primary somatotopic maps of the body surface, such as those in SI; at the other extreme is our conscious experience of our body as a coherent volumetric object in the world. On this interpretation, body representations along the continuum will be characterized by different weightings of (distorted) somatosensory representations and (largely veridical) visual representation. This can, thus, account for the finding of qualitatively similar distortions for the body model and body image (e.g., Longo & Haggard, 2012b), which nevertheless differ in magnitude.

A third possibility was recently proposed by Linkenauger et al. (2015). On their interpretation, visual representations of the body show distortions directly *opposite* to those of somatosensory representations. By showing such *inverse distortion*, the

combination of visual and somatosensory could be used to correct for the distortions that result in Weber's illusion. As discussed above, the magnitude of Weber's illusion is dramatically smaller than would be predicted based on differences in cortical magnification across skin surfaces alone. Inverse distortion could thus account for the process of tactile size constancy producing this reduction. At present, the exact relations between different body representations and their distortions remains unclear. I have described three potential models of these relations. Understanding this issue is an important goal for future research.

Conclusions

This paper has discussed research demonstrating that distorted body representations are not limited to disease, but a ubiquitous part of healthy human cognition. In ordinary English, to know something "like the back of one's hand" is to emphasize the intimacy and accuracy of one's knowledge. The results I have described show that we don't know the back of our hand like the back of our hand. Understanding the causes and implications of such distorted body representations is an important goal for future research.

Our experience and mental representation of our body goes right to the core of some of the most central issues in experimental psychology, including our sense of self and our personal identity as an individual. William James (1890) noted that our body is not really *ours*, but is *us*. Recent work in philosophy and neuroscience has emphasized the importance of the body as the core of 'minimal phenomenal selfhood' (Blanke & Metzinger, 2009). The putative role of the body as the bedrock of our sense of individuality and selfhood makes the distortions I have described seem both more profoundly strange and puzzling. Recent research using paradigms like the rubber hand

illusion (e.g., Botvinick & Cohen, 1998; Longo et al., 2008) and full-body illusions (e.g., Lenggenhager, Tadi, Metzinger, & Blanke, 2007; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2009) has revealed that abnormal bodily experiences can profoundly influence our sense of self. An important goal for future research is to understand how our ordinary experience of our body – distortions and all – shapes selfhood and personal identity.

References

- Alloway, K. D., Rosenthal, P., & Burton, H. (1989). Quantitative measurements of receptive field changes during antagonism of GABAergic transmission in primary somatosensory cortex of cats. *Experimental Brain Research*, 78, 514-532.
- Anema, H. A., Wolswijk, V. W., Ruis, C., & Dijkerman, H. C. (2008). Grasping Weber's illusion: The effect of receptor density differences on grasping and matching. *Cognitive Neuropsychology*, 25, 951-967.
- Bermúdez, J. L., Marcel, A., & Eilan, N. (1995). *The body and the self*. Cambridge, MA: MIT Press.
- Berti, A., Bottini, G., Gandola, M., Pia, L., Smania, N., Stracciari, A., Castiglioni, I., Vallar, G., & Paulesu, E. (2005). Shared cortical anatomy for motor awareness and motor control. *Science*, 309, 488-491.
- Blanke, O., Landis, T., Spinelli, L., & Seeck, M. (2004). Out-of-body experience and autoscapy of neurological origin. *Brain*, 127, 243-258.
- Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences*, 13, 7-13.
- Bookstein, F. L. (1991). *Morphometric tools for landmark data: Geometry and biology*. Cambridge: Cambridge University Press.
- Botvinick, M., & Cohen, J. (1998). Rubber hand "feel" touch that eyes seen. *Nature*, 391, 756.
- Brooks, V. B., Rudomin, P., & Slayman, C. L. (1961). Peripheral receptive fields of neurons in the cat's cerebral cortex. *Journal of Neurophysiology*, 24, 302-325.
- Bruch, H. (1978). *The golden cage: The enigma of anorexia nervosa*. Cambridge, MA: Harvard University Press.
- Brugger, P., Kollias, S. S., Muri, 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.
- Brugger, P., Lenggenhager, B., & Giummarra, M. J. (2013). Xenomelia: A social neuroscience view of altered bodily self-consciousness. *Frontiers in Psychology*, 4, 204.
- Brugger, P., Regard, M., & Landis, T. (1997). Illusory reduplication of one's own body: Phenomenology and classification of autoscopic phenomena. *Cognitive Neuropsychiatry*, 2, 19-38.
- Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., & Serino, A. (2013). Tool-use reshapes the boundaries of body and peripersonal space representations. *Experimental Brain Research*, 228, 25-42.
- Cardini, F., Longo, M. R., & Haggard, P. (2011). Vision of the body modulates somatosensory intracortical inhibition. *Cerebral Cortex*, 21, 2014-2022.
- Casper, R. C., Halmi, K. A., Goldberg, S. C., Eckert, E. D., & Davis, J. M. (1979). Disturbances in body image estimation as related to other characteristics and outcome in anorexia nervosa. *British Journal of Psychiatry*, 134, 60-66.
- Cholewiak, R. W. (1999). The perception of tactile distance: Influences of body site, space, and time. *Perception*, 28, 851-875.
- Craske, B., Kenny, F. T., & Keith, D. (1984). Modifying an underlying component of perceived arm length: Adaptation of tactile location induced by spatial discordance. *Journal of Experimental Psychology: Human Perception and Performance*, 10, 307-317.
- Critchley, M. (1953). *The parietal lobes*. London: Edward Arnold & Co.
- Daurat-Hmeljiak, C., Stambak, M., & Berges, J. (1978). *Il test dello schema corporeo. Una*

prova di conoscenza e costruzione dell'immagine del corpo [The body schema test: An examination of the knowledge and construction of the body image]. Florence, Italy: Organizzazioni Speciali.

de Vignemont, F., Ehrsson, H. H., & Haggard, P. (2005). Bodily illusions modulate tactile perception. *Current Biology*, 15, 1286-1290.

de Vignemont, F., Majid, A., Jola, C., & Haggard, P. (2009). Segmenting the body into parts: Evidence from biases in tactile perception. *Quarterly Journal of Experimental Psychology*, 62, 500-512.

DiCarlo, J. J., & Johnson, K. O. (2002). Receptive field structure in cortical area 3b of the alert monkey. *Behavioural Brain Research*, 135, 167-178.

DiCarlo, J. J., Johnson, K. O., & Hsiao, S. S. (1998). Structure of receptive fields in area 3b of primary somatosensory cortex in the alert monkey. *Journal of Neuroscience*, 18, 2626-2645

Duncan, R. O., & Boynton, G. M. (2007). Tactile hyperacuity thresholds correlate with finger maps in primary somatosensory cortex (S1). *Cerebral Cortex*, 17, 2878-2891.

Fairburn, C. G., Peveler, R. C., Jones, R., Hope, R. A., & Doll, H. A. (1993). Predictors of 12-month outcome in bulimia nervosa and the influence of attitudes to shape and weight. *Journal of Consulting and Clinical Psychology*, 61, 696-698.

Ferrè, E., Vagnoni, E., & Haggard, P. (2013). Vestibular contributions to bodily awareness. *Neuropsychologia*, 51, 1445-1452.

First, M. B. (2005). Desire for amputation of a limb: Paraphilia, psychosis, or a new type of identity disorder. *Psychological Medicine*, 35, 919-928.

Fotopoulou, A., Tsakiris, M., Haggard, P., Vagopoulou, A., Rudd, A., & Kopelman, M.

- (2008). The role of motor intention in motor awareness: An experimental study on anosognosia for hemiplegia. *Brain*, 131, 3432-3442.
- Fuentes, C. T., Longo, M. R., & Haggard, P. (2013). Body image distortions in healthy adults. *Acta Psychologica*, 144, 344-351.
- Fuentes, C. T., Pazzaglia, M., Longo, M. R., Scivoletto, G., & Haggard, P. (2013). Body image distortions following spinal cord injury. *Journal of Neurology, Neurosurgery, and Psychiatry*, 84, 201-207.
- Fuentes, C. T., Runa, C., Blanco, X. A., Orvalho, V., & Haggard, P. (2013). Does my face FIT? A face image task reveals structure and distortions of facial feature representation. *PLOS ONE*, 8, e76805.
- Gandevia, S. C., & Phegan, C. M. (1999). Perceptual distortions of the human body image produced by local anesthesia, pain and cutaneous stimulation. *Journal of Physiology*, 514, 609-616.
- Green, B. E. (1982). The perception of distance and location for dual tactile pressures. *Perception and Psychophysics*, 31, 315-323.
- Gurfinkel, V. S., & Levick, Y. S. (1991). Perceptual and automatic aspects of the postural body scheme. In J. Paillard (Ed.), *Brain and space* (pp. 147-162). Oxford, UK: Oxford University Press.
- James, W. (1890). *The principles of psychology*. New York: Dover.
- Keel, P. K., Dorer, D. J., Franko, D. L., Jackson, S. C., & Herzog, D. B. (2005). Postremission predictors of relapse in women with eating disorders. *American Journal of Psychiatry*, 162, 2263-2268.
- Kennett, S., Taylor-Clarke, M., & Haggard, P. (2001). Noninformative vision improves the spatial resolution of touch in humans. *Current Biology*, 11, 1188-1191.
- Le Cornu Knight, F., Longo, M. R., & Bremner, A. J. (2014). Categorical perception of

- tactile distance. *Cognition*, 131, 254-262.
- Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: Manipulating bodily self-consciousness. *Science*, 317, 1096–1099.
- Linkenauger, S. A., Witt, J. K., Bakdash, J. Z., Stefanucci, J. K., & Proffitt, D. R. (2009). Asymmetrical body perception: A possible role for neural body representations. *Psychological Science*, 20, 1373-1380.
- Linkenauger, S. A., Wong, H. Y., Guess, M., Stefanucci, J. K., McCulloch, K. C., Bühlhoff, H. H., Mohler, B. J., & Proffitt, D. R. (2015). The perceptual homunculus: The perception of the relative proportions of the human body. *Journal of Experimental Psychology: General*, 144, 103-113.
- Longo, M. R. (2014). The effects of immediate vision on implicit hand maps. *Experimental Brain Research*, 232, 1241-1247.
- Longo, M. R. (2015a). Implicit and explicit body representations. *European Psychologist*, 20, 6-15.
- Longo, M. R. (2015b). Posture modulates implicit hand maps. *Consciousness and Cognition*, 36, 96-102.
- Longo, M. R. (2015c). Three-dimensional coherence of the conscious body image. *Quarterly Journal of Experimental Psychology*, 68, 1116-1123.
- Longo, M. R. (2015d). Intuitive anatomy: Distorted conceptual knowledge of hand structure. *Cognition*, 142, 230-235.
- Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences of the United States of America*, 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. (2012a). A 2.5-D representation of the human hand. *Journal of Experimental Psychology: Human Perception and Performance*, 38, 9-13.
- Longo, M. R., & Haggard, P. (2012b). Implicit body representations and the conscious body image. *Acta Psychologica*, 141, 164-168.
- Longo, M. R., & Sadibolova, R. (2013). Seeing the body distorts tactile size perception. *Cognition*, 126, 475-481.
- Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: Body representation beyond primary somatosensory cortex. *Neuropsychologia*, 48, 655-668.
- Longo, M. R., Betti, V., Aglioti, S. M., & Haggard, P. (2009). Visually induced analgesia: Seeing the body reduces pain. *Journal of Neuroscience*, 29, 12125-12130.
- Longo, M. R., Ghosh, A., & Yahya, T. (2015a). Bilateral symmetry of distortions of tactile size perception. *Perception*, 44, 1251-1262.
- Longo, M. R., Long, C., & Haggard, P. (2012). Mapping the invisible hand: A body model of a phantom limb. *Psychological Science*, 23, 740-742.
- Longo, M. R., Mancini, F., & Haggard, P. (2015b). Implicit body representations and tactile spatial remapping. *Acta Psychologica*, 160, 77-87.
- Longo, M. R., Pernigo, S., & Haggard, P. (2011). Vision of the body modulates processing in primary somatosensory cortex. *Neuroscience Letters*, 489, 159-163.
- Longo, M. R., Schüür, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition*, 107, 978-998.
- Mancini, F., Longo, M. R., Iannetti, G. D., & Haggard, P. (2011). A supramodal representation of the body surface. *Neuropsychologia*, 49, 1194-1201.

- Mancini, F., Longo, M. R., Kammers, M. P. M., & Haggard, P. (2011). Visual distortion of body size modulates pain perception. *Psychological Science*, 22, 325-330.
- Margolis, A. N., & Longo, M. R. (2015). Visual detail about the body modulates tactile localisation biases. *Experimental Brain Research*, 233, 351-358.
- Mattioni, S., & Longo, M. R. (2014). The effects of verbal cueing on implicit hand maps. *Acta Psychologica*, 153, 60-65.
- Melzack, R. (1990). Phantom limbs and the concept of a neuromatrix. *Trends in Neuroscience*, 13, 88-92.
- Melzack, R. (1992). Phantom limbs. *Scientific American*, 266(4), 120-126.
- Miller, L. E., Longo, M. R., & Saygin, A. P. (2014). Tool morphology constrains the effects of tool use on body representations. *Journal of Experimental Psychology: Human Perception and Performance*, 40, 2143-2153.
- 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.
- 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.
- Powell, T. P. S., & Mountcastle, V. B. (1959). Some aspects of the functional organization of the cortex of the postcentral gyrus of the monkey: A correlation of findings obtained in a single unit analysis with cytoarchitecture. *Bulletin of the Johns Hopkins Hospital*, 105, 133-162.
- 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.
- Sadibolova, R., & Longo, M. R. (2014). Seeing the body produces limb-specific modulation of skin temperature. *Biology Letters*, 10, 20140157.
- Saulton, A., Dodds, T. J., Bühlhoff, H. H., & de la Rosa, S. (2015). Objects exhibit body model like shape distortions. *Experimental Brain Research*, 233, 1471-1479.
- 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.
- Soechting, J. F. (1982). Does position sense at the elbow reflect a sense of elbow joint angle of one of limb orientation? *Brain Research*, 248, 392-395.
- Sur, M., Merzenich, M. M., & Kaas, J. H. (1980). Magnification, receptive-field area, and “hypercolumn” size in areas 3b and 1 of somatosensory cortex in owl monkeys. *Journal of Neurophysiology*, 44, 295-311.
- Tajadura-Jiménez, A., Väljamäe, A., Toshima, I., Kimura, T., Tsakiris, M., & Kitagawa, N. (2012). Action sounds recalibrate perceived tactile distance. *Current Biology*, 22, R516-R517.
- 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., Claudino, A. M., & Zucker, N. (2010). Eating disorders. *Lancet*, 375, 583-593.
- 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.
- van Beers, R. J., Sittig, A. C., & Denier van der Gon, J. J. (1998). The precision of proprioceptive position sense. *Experimental Brain Research*, 122, 367-377.

Vega-Bermudez, F., & Johnson, K. O. (2001). Differences in spatial acuity between digits.

Neurology, 56, 1389-1391.

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.* Hove, UK: Erlbaum. (Original

work published in 1834).

Acknowledgments

MRL was supported by European Research Council grant ERC-2013-StG-336050 under the FP7.