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Three-dimensional coherence of the conscious body image

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We experience our body as a coherent object in the three-dimensional (3-D) world. In contrast, the body is represented in somatosensory cortex as a fragmented collection of two-dimensional (2-D) maps. Recent results have suggested that some forms of higher level body representations maintain this fragmentation, for example by showing different patterns of distortion for two surfaces of a single body part, such as the palmar and dorsal hand surfaces. This study investigated the 3-D coherence of the conscious body image of the hand by comparing perceptual biases of perceived hand shape on the dorsal and palmar surfaces. Participants made forced-choice judgements of whether observed hand images were thinner or wider than their own left or right hand, and perceptual distortions of the hand image were assessed by fitting psychometric functions. The results suggested that the hand is consciously represented as a fully coherent, 3-D object. Specifically: (a) Similar overall levels of distortion were found on the palmar and dorsal hand surfaces, (b) comparable laterality effects were found on both surfaces (left hand represented as wider than right hand), and (c) the magnitude of distortions were strongly correlated across the two surfaces. Whereas other recent results have suggested that perceptual abilities such as position sense, tactile size perception, and tactile localization may rely on fragmented, 2-D representations of individual skin surfaces, the present results suggest that, in striking contrast, the conscious body image represents the body (or, at least the hand) as a coherent, 3-D object.

Keywords: Touch; Body representation; Somatosensation

Our body is unique among objects in our perceptual world. We experience our body from the outside, through vision and audition, as a physical object like any other, but we also perceive our body from within, through somatosensation and visceral sensations, as an object of direct and prereflective experience (Longo, Azañón, & Haggard, 2010). This duality in the way we experience our body raises the question of whether there are different classes of mental body representations reflecting these distinct modes. Somatotopic maps in somatosensory cortex represent the body surface as a distinct set of 2-D maps. For example, the glabrous skin of the palmar hand surface is represented with a highly ordered somatotopic representation, whereas the hairy skin of the dorsal hand surface is represented in irregular islands of cortex (Pons, Wall, Garraghty, Cusick, & Kaas, 1987; Powell & Mountcastle, 1959). In contrast, through vision we experience our body as a coherent, volumetric object in the 3-D world. For example, in his classic book on the body image, Schilder (1935/1950) described the *body image* as

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the "tri-dimensional image everybody has about himself" (p. 11). While there is little general agreement on the exact nature of the body image, most researchers have considered body image to reflect our conscious, subjective feeling of the size and shape of our body. The body image is frequently contrasting with the *body schema*, a purportedly unconscious, sensorimotor representation underlying action (e.g., Gallagher & Cole, 1995; Paillard, 1999). Little empirical research, however, has investigated the three-dimensionality of the body image. In this study, I investigate this issue by investigating the relation between perceptual distortions on the two sides of the hand (i.e., the dorsal and palmar surfaces).

As mentioned above, it seems intuitively that we experience our body as a coherent, volumetric object in the 3-D world. There is nevertheless, evidence that the brain also maintains highly fragmented representations of the body, both of individual parts (Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009) and of distinct skin surfaces (Coslett & Lie, 2004; Mancini, Longo, Iannetti, & Haggard, 2011). For example, recent results have revealed substantial perceptual distortions of body representations underlying various somatosensory processes. Critically for present purposes, these distortions appear to differentially affect different sides of individual body parts, such as the dorsal and palmar surfaces of the hand, in the case of tactile size perception (Longo & Haggard, 2011), position sense (Longo & Haggard, 2012a), and tactile localization (Mancini et al., 2011). Differential distortions on opposite sides of a single body part are inconsistent with a coherent representation of that part as a 3-D object.

Thus, if the body image represents the body as a coherent 3-D object, distortions of similar magnitude should be seen on both sides of the hand, which should be correlated across individuals. Studies of body image commonly employ tasks in which participants compare their own body to a template body picture (for reviews see Cash & Deagle, 1997; Smeets, Smit, Panhuysen, & Ingelby, 1997). Examples of such methods include the "distorting mirror" (Traub & Orbach, 1964), "distorted photograph" (Glucksman & Hirsch, 1969), "silhouette" (Furnham & Alibhai, 1983), and "template matching" (Gandevia & Phegan, 1999) methods. In this study, I investigated this question using a task similar to the one I used in a recent study (Longo & Haggard, 2012b), modelled on the "template matching" method of Gandevia and Phegan (1999). In their original study, Gandevia and Phegan asked participants to select from an array of finger images the one most closely matching the size of their own finger. My colleagues and I adapted this paradigm by having participants select from an array of hands the one that most closely matched the *shape* of what it felt their own hand was like (Kammers et al., 2009; Longo & Haggard, 2010). The procedure used by Longo and Haggard (2010) and in the present study differed somewhat in that only a single hand image was presented on each trial, and participants made two-alternative forced-choice (2AFC) judgements of whether the hand shown was wider or more slender than what they felt the shape of their own hand was like. Critically, in different blocks participants judged the shape of either the dorsal or the palmar hand surface, allowing separate estimation of distortion on each surface. This allowed comparison of overall magnitude of distortions, lateral asymmetries, and individual differences across the two skin surfaces.

METHOD

Participants

Fifteen individuals (nine female) between 19 and 37 years from the University of London community participated for payment. Participants were all right-handed as assessed by the Edinburgh Inventory (*M*: 80.60, range: 33.33–100). Data from one additional participant were excluded from analyses because the psychometric functions provided a poor fit to the data.

Procedure

Hand shape was quantified by the *shape index* (SI), adapted from Napier (1980), and which my colleagues and I have used to study hand shape in several recent studies (e.g., Longo & Haggard, 2010, 2012b). The shape index quantifies the overall aspect ratio of the hand. Hand width was quantified as the distance between the knuckles of the index and little fingers; hand length was quantified as the length (knuckle to tip) of the middle finger. The shape index is defined as: SI = 100 × (width/length). Large values indicate a wide hand, while small values indicate a slender hand.

Separate sets of hand images were used for male and female participants (see Figure 1). Images of different shape indices were created by stretching hand photographs so that the hand had the appropriate aspect ratio. The overall size of each image was controlled by adjusting image size so that overall image area was held constant, the images differing only in aspect ratio. Because the knuckle landmarks appear only on the dorsal surface of the hand, the shape index for the original (i.e., unstretched) image of each palm was defined as equal to the shape index of the original image of the dorsum. There were 17 hand images for each sex, with the shape index ranging from 40 to 90, logarithmically spaced. A logarithmic spacing is used since the shape index is a ratio and results in equal spacing in terms of the amount of stretch. Thus, the middle stimulus had a shape index of 60, close to the average of actual hand shapes in my previous studies (e.g., Longo & Haggard, 2010, 2012b).

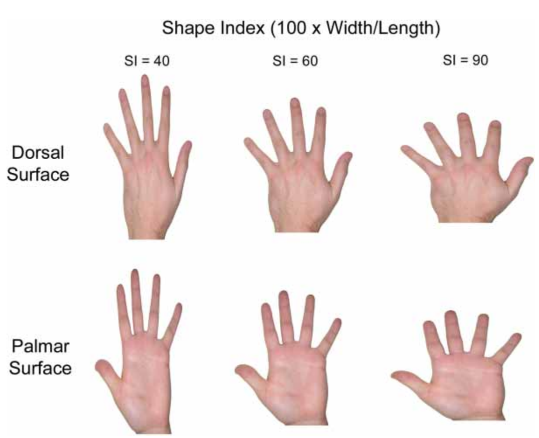

Figure 1. *Example of hand stimuli. These are male left hands for the dorsal and palmar hand surfaces with shape indices at the extreme (40, 90) and middle (60) values. Right hand stimuli were identical, but were reflected horizontally. The female hand stimuli were similar except that a woman's hand was used for the stimulus.*

Stimulus presentation and data collection were controlled by a custom MATLAB (Mathworks, Natick, MA) script using Cogent Graphics (developed by John Romaya, Laboratory of Neuroscience, Wellcome Department of Imaging Neuroscience, University College London). There were 12 blocks of trials, with each sequential set of four blocks consisting of one of each of the four conditions (i.e., left dorsum, left palm, right dorsum, right palm) in random order. Each block consisted of eight repetitions of each of the 17 hand stimuli in random sequence, making 136 trials per block. Each image remained on the screen until the participant responded. Unspeeded responses were made by pressing one of two keys marked with Velcro disks on a response pad using whichever hand they were not currently making judgements about. Participants were asked to rest their hands on their lap throughout the block so that they could not directly compare their hand to the stimuli and (except for making their responses) to keep their hands still. At the end of the study, photographs were taken of each side of both of the participant's hands, to allow calculation of the actual shape index of each hand.

Cumulative Gaussian functions were fitted to each participant's data in each condition using least squares regression with R 2.8.0 software. The point of subjective equality (PSE; i.e., the hand shape for which the participant was equally likely to judge it wider or more slender than their own hand) was calculated as the shape index at which the psychometric function crossed 50%. The precision of responses was calculated as the interquartile range (IQR), the difference in shape indices between where the psychometric function crossed 75% and 25%. The IQR assesses the slope of the psychometric function and is directly proportional to the standard deviation of the cumulative Gaussian.

RESULTS

Figure 2 shows the data from each condition along with best fitting curves, while Figure 3 shows mean shape indices for participants' actual hands and for the PSEs in each condition. While there was a

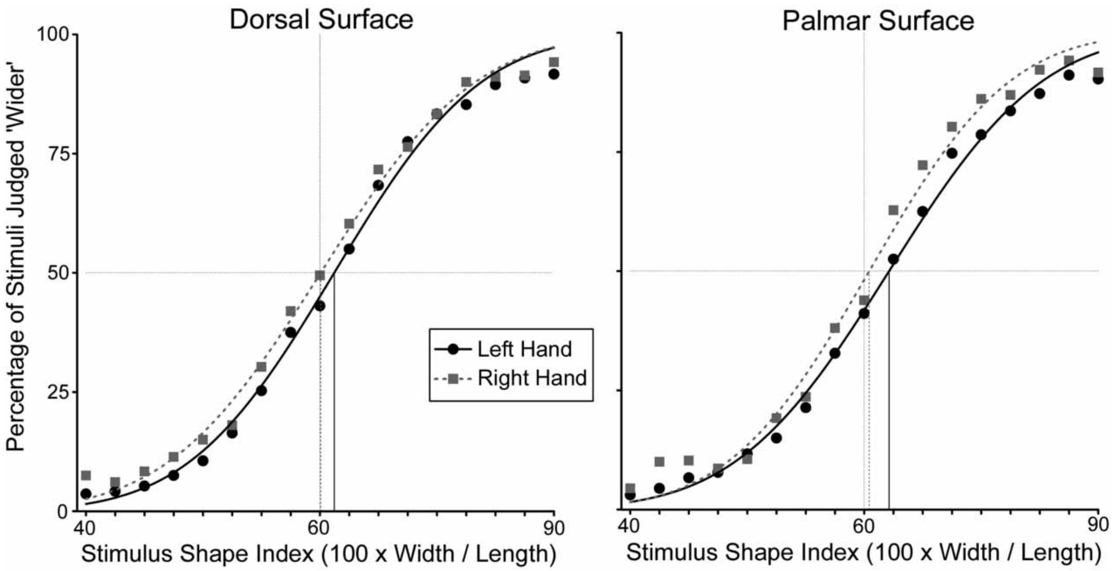

Figure 2. *Psychometric functions showing percentage of stimuli judged as "wider" than the participant's own hand as a function of stimulus shape index.*

slight tendency to overestimate hand width, there was no overall difference between judged and actual shape indices, $t(14) = 1.50$, *ns*, consistent with previous findings that the hand image is approximately veridical (Longo & Haggard, 2010, 2012b). A repeated measures analysis of variance (ANOVA) with factors *laterality* (right, left) and *hand side* (dorsal, ventral) was conducted on the difference between judged and actual shape indices. There was a significant main effect of laterality, $F(1, 14) = 13.70, p < .005$, with the left hand represented as wider than the right. Follow-up *t* tests revealed significant biases to represent the left hand as wider on both the dorsal, $t(14) = 2.42$, $p < .05$, and the palmar, $t(14) = 3.03$, $p < .01$, surfaces. In contrast, there was no significant effect of hand side, $F(1, 14) = 0.05$, *ns*, nor an interaction of the two factors, $F(1, 14) = 0.74$, *ns*. Thus, while there was a clear laterality effect, within each of the two hands, the two sides of the hand showed highly consistent biases. An analogous ANOVA on IQR scores did not reveal any significant differences between conditions on the precision of responses.

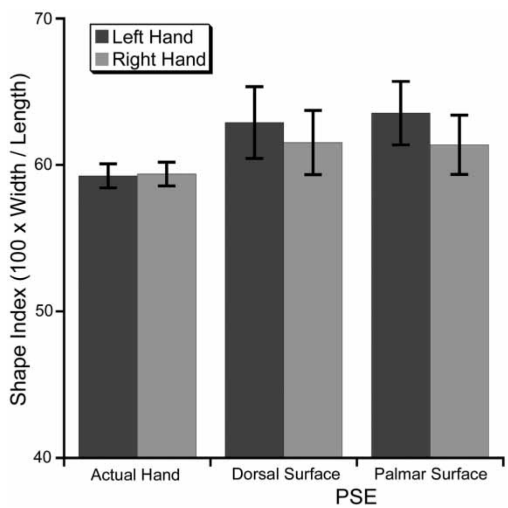

Figure 3. *Mean shape indices for participants' actual hands and for points of subjective equality (PSEs) in each of the four conditions. Error bars are one standard error.*

Figure 4 shows scatterplots showing the relation between distortion (i.e., judged – actual shape index). Distortions on the two skin surfaces were very strongly correlated, both on the left hand, $r(13) = .879$, $p < .0001$, and on the right hand, $r(13) = .806$, $p < .0005$. Thus, not only are

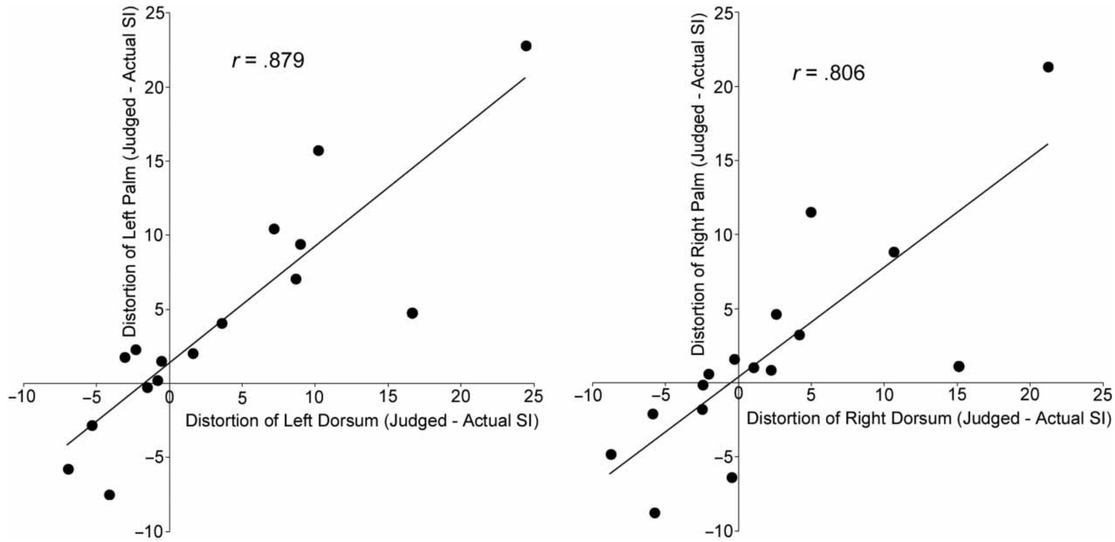

Figure 4. *Scatterplots showing relation between distortion of the dorsal and palmar hand surfaces for the left hand (left panel) and the right hand (right panel). SI = shape index.*

distortions of the two sides of similar overall magnitude, but there are clear shared individual differences on the two surfaces, consistent with a fully 3-D body image.

Considering each skin surface separately, there were also strong correlations between the left and the right hands, both on the dorsal, $r(13) = .964$, $p < .0001$, and on the palmar, $r(13) = .931$, $p < .0001$, surfaces. Thus, while there was an overall bias for the left hand to be represented as wider than the right hand, these shared individual differences nevertheless suggest a high level of bilateral integration of the body image, consistent with previous results (Fuentes, Longo, & Haggard, 2013). The magnitude of the laterality effect (i.e., the difference between shape indices for the left and right hands) was not correlated with handedness as measured with the Edinburgh Inventory on either the palmar, $r(13) = -.163$, *ns*, or the dorsal surface, $r(13) = .027$, *ns*.

Longo and Haggard (2010) found a significant correlation between shape indices of participants' actual hand shape and of hand images selected from an array of stretched hand images. This result suggests that template matching measures a self-specific representation of the participant's own hand, rather than a generic visual representation of the shape of hands in general. In the present data, collapsing across the palmar and dorsal surfaces, there were modest though non-significant positive correlations between actual and judged hand shape indices, both for the left, $r(13) = .338$, *ns*, and the right, $r(13) = .303$, *ns*, hands. There was, however, one clear outlier, who although they had the second most slender hands among all participants, judged their hands as substantially wider than any other participant. With this participant removed, there were significant correlations on both the left, $r(12) = .638$, $p < .02$, and the right, $r(12) = .643$, $p < .02$, hands.

DISCUSSION

The present study provides three pieces of evidence that the body image represents the hand as a coherent 3-D object: (a) There are similar overall levels of spatial distortion on the palmar and dorsal hand surfaces; (b) comparable laterality effects (i.e., left hand represented as wider than right hand) were found on both skin surfaces; and (c) for both hands, there were strong correlations across participants between distortion on the two sides of the hand. These results provide support for the interpretation, which some authors have taken as if it were by definition (e.g., Schilder, 1950), that the conscious body image represents the body as a coherent, 3-D, volumetric object, at least in the specific case of the hand.

A hierarchy of body representations

Recent results have suggested that perceptual abilities such as position sense (Longo & Haggard, 2012a), tactile size perception (Longo & Haggard, 2011), and tactile localization (Mancini et al., 2011) rely on fragmented representations of individual skin surfaces. Although the body is a volumetric, 3-D object, somatotopic maps of the body in somatosensory cortex represent the body as a set of distinct, 2-D maps (Pons et al., 1987; Powell & Mountcastle, 1959). Thus, a critical question to ask about any body representation is whether it represents the body as a collection of fragmented 2-D surfaces, or as an integrated 3-D whole. Intriguingly, recent research has suggested that the answer to this question differs across different types of body representations, suggesting that they form a hierarchy, differing in terms of the spatial reference frame by which they represent the body (Longo, in press).

First, consider tactile localization. Mancini et al. (2011) measured biases in localization using a simple task in which participants were touched on their hand and were then asked to position a mouse cursor above the perceived location of touch on a photograph of their hand. On the hairy skin of the hand dorsum, large distal biases were found (i.e., participants perceived stimuli as being located farther forward on the hand than they actually were). In contrast, no such distal biases were observed on the glabrous skin of the palm. These results suggest that localization is defined in a reference frame specific to each skin surface as a 2-D sheet, rather than to the hand as a 3-D whole. Next, consider the implicit representation underlying position sense, described by Longo and Haggard (2010, 2012a, 2012b). These representations show a qualitatively similar (and strongly correlated) pattern of biases on the palm and dorsum, indicating that position sense does not rely on fully distinct representations of each surface (Longo & Haggard, 2012a). However, the magnitude of distortions is different on the two surfaces, indicating that it does not rely on a representation of the hand as a fully volumetric, 3-D object either. Thus, in analogy to Marr's (1982) "2.5-D sketch", Longo and Haggard suggested that position sense relies on a 2.5-D representation, intermediate between 2-D representations of distinct skin surfaces and 3-D representations of entire body parts.

The current results suggest, in striking contrast, that the conscious body image represents the body as fully coherent, 3-D object. Thus, not only does the body image differ from more somatosensory body representations in being less distorted, it also appears to be more internally coherent. Together, these results suggest that body representations differ in terms of their spatial scale and reference frame, ranging from 2-D sheets of receptive fields and individual skin surfaces, characteristic of primary somatosensory maps, to 3-D, volumetric wholes, characteristic of our visual experience of our body.

There is also evidence of interactions between these levels. For example, manipulations of low-level somatosensory inputs, for example through cutaneous anaesthesia, affect high-level body representations such as the conscious body image, producing body-part specific increases in perceived size (Gandevia & Phegan, 1999). Such findings demonstrate that bottom-up afferent signals shape high-level body representations. Conversely, manipulations affecting vision of the body also influence low-level somatosensory processes, such as tactile size perception, with visual expansion producing corresponding increases in the perceived size of tactile stimuli (Taylor-Clarke, Jacobsen, & Haggard, 2004). Those results suggest that top-down influences from vision modulate early somatosensory processing.

The hand is a particularly convenient body part for investigating these issues, because it is relatively flat, easy to stimulate, and more obviously made up of two distinct sides than many other body parts. It is possible that these characteristics, which for the hand are easy to study, also make it unrepresentative of the body as a whole. Thus, it will be an important goal of future research to investigate the extent to which this hierarchical organization reflects a general principle of body representation and the extent to which it is specific to the case of the hand.

Lateral asymmetries

To my knowledge, the present results are the first to report lateral asymmetries in the perceived shape of individual body parts. Two previous studies have investigated whether the two cerebral hemispheres maintain distinct representations of the entire body (Mohr, Porter, & Benton, 2007; Smeets & Kosslyn, 2001). Smeets and Kosslyn (2001), using a visual distortion method similar to that in the present study but with images of the participant's whole body, reported that women with anorexia nervosa judged their body as fatter when presented in the right visual field (projecting to the left hemisphere) than when presented in the left visual field (projecting to the right hemisphere). Mohr and colleagues (2007), using a nonclinical sample of women and men, found a general bias to perceive one's body as fatter when stimuli were presented in the right visual field, but a bias only for women in the left visual field.

While such results are interesting in suggesting hemispheric differences in body image distortions, the present findings are qualitatively different in showing different distortions of the different sides of the body. These results suggest that the two hemispheres may have at least partly distinct representations of the contralateral side of the body. That is, each hemisphere may maintain a distinct hemi-image of the contralateral side of the body, as opposed to a single hand image, which is reflected to produce images of either hand. This interpretation is consistent with neurological conditions that feature body image alterations specific to the contralesional side of the body, such as asomatognosia, in which patients report that the contralesional side of their body has disappeared (Critchley, 1953), and somatoparaphrenia, in which patients claim that their contralesional arm belongs to someone else (Vallar & Ronchi, 2009). Similarly, Nico et al. (2010) found that while healthy controls and patients with left parietal lobe damage made generally accurate estimates of their body boundaries, right parietal lobe patients, like people with anorexia, overestimated the extent of the left side of their body.

While the present results suggest some level of independent representation of the two hands, there are also reasons to think there are strong connections between these representations. For example, in the present study there were very strong correlations across participants between the distortions of the two hands. Similarly, in a recent study investigating implicit representations of the entire body, Fuentes et al. (2013) found strong bilateral symmetry, suggesting a high level of integration of the body image across the two sides of the body.

CONCLUSION

The present study demonstrates that our conscious body image maintains highly coherent representations of the dorsal and palmar surfaces of the hand. This coherence is in striking contrast to recent results showing distinct representations of the two sides of the hand in body representations underlying perceptual abilities such as tactile localization (Mancini et al., 2011), tactile size perception (Longo & Haggard, 2011), and position sense (Longo & Haggard, 2012a). This pattern provides further support for the claim that the conscious body image is distinct from the implicit body representations underlying tasks such as position sense (Longo & Haggard, 2010). Understanding the exact relation between these types of body representation remains an important goal for future research.

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