

OBSERVATION

A 2.5-D Representation of the Human Hand

Matthew R. Longo
Birkbeck, University of London

Patrick Haggard
University College London

Primary somatosensory maps in the brain represent the body as a discontinuous, fragmented set of two-dimensional (2-D) skin regions. We nevertheless experience our body as a coherent three-dimensional (3-D) volumetric object. The links between these different aspects of body representation, however, remain poorly understood. Perceiving the body's location in external space requires that immediate afferent signals from the periphery be combined with stored representations of body size and shape. At least for the back of the hand, this body representation is massively distorted, in a highly stereotyped manner. Here we test whether a common pattern of distortions applies to the entire hand as a 3-D object, or whether each 2-D skin surface has its own characteristic pattern of distortion. Participants judged the location in external space of landmark points on the dorsal and palmar surfaces of the hand. By analyzing the internal configuration of judgments, we produced implicit maps of each skin surface. Qualitatively similar distortions were observed in both cases. The distortions were correlated across participants, suggesting that the two surfaces are bound into a common underlying representation. The magnitude of distortion, however, was substantially smaller on the palmar surface, suggesting that this binding is incomplete. The implicit representation of the human hand may be a hybrid, intermediate between a 2-D representation of individual skin surfaces and a 3-D representation of the hand as a volumetric object.

Keywords: body representation, somatosensory, position sense

Information about the size and shape of one's body is critical for many forms of perception. Recent studies investigating body representations underlying position sense have revealed large distortions of body size and shape (Hach & Schütz-Bosbach, 2010; Longo & Haggard, 2010) not found for explicit judgments of body shape. This suggests that somatosensation relies on *implicit* body representations, distinct from the conscious body image. The exact nature of these representations, however, remains unclear. While we experience our body as a coherent, volumetric object, the brain also appears to maintain highly fragmented representations of individual body parts (Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009) and skin surfaces (Coslett & Lie, 2004; Mancini, Longo, Iannetti, & Haggard, 2011a). Mancini and colleagues (2011a) found systematic biases in localization of cutaneous stimuli on the hand, which were highly consistent across individuals

and stimulus types (mechanoreceptive vs. thermal), but differed dramatically between palm and dorsum. This surface-specificity suggests that these biases arise from fragmented representations of multiple 2-D skin regions, rather than from coherent 3-D body representations. Here, we investigated the spatial coherence of the implicit body representation underlying a different perceptual process: localization of one's body in external space ("position sense").

We determined whether distortions of distinct skin surfaces of a single body part (the dorsal and palmar hand surfaces) are consistent, or particular to each. If position sense derives from local sensory features of the skin and organization of somatosensory cortical maps, distinct patterns of distortion might be found, indicating fragmented, two-dimensional (2-D) representations of individual skin surfaces. In contrast, if position sense uses a three-dimensional (3-D) model of the hand as a coherent volumetric object, similar spatial distortions should be found on both surfaces, producing correlated distortions across individuals.

We used the "psychomorphometric" technique (Longo & Haggard, 2010) to compare implicit representations of the dorsal and palmar hand surfaces. Participants indicated the perceived location of landmarks on their occluded hand (see Figure 1). By having participants localize landmarks by verbal instruction, rather than somatic stimuli, we isolated body representations mediating position sense specifically, rather than processes such as localization on the skin surface. By comparing the judged locations of landmarks, we constructed implicit maps of represented hand morphology to compare with true hand morphology and across skin surfaces.

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Matthew R. Longo, Department of Psychological Sciences, Birkbeck, University of London, London, UK; Patrick Haggard, Institute of Cognitive Neuroscience, University College London, London, UK.

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Correspondence concerning this article should be addressed to Matthew R. Longo, Department of Psychological Sciences, Birkbeck, University of London, Malet Street, London WC1E 7HX, United Kingdom. E-mail: m.longo@bbk.ac.uk

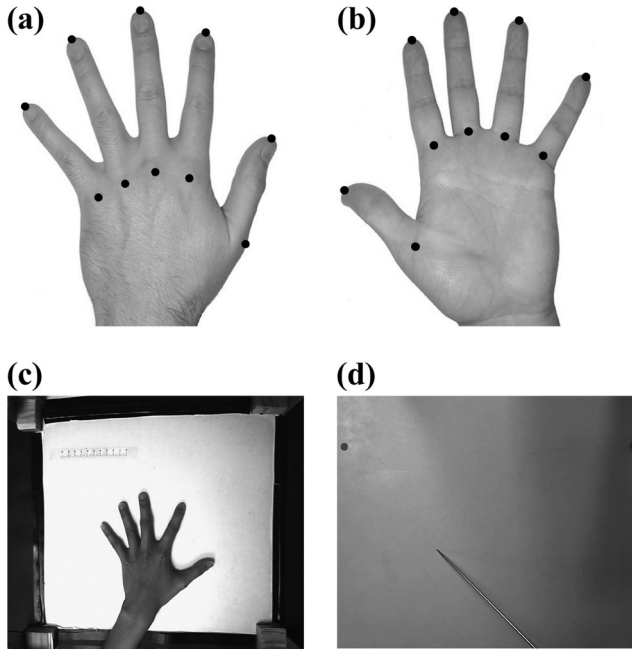


Figure 1. (a–b) Landmarks used in this experiment. On the dorsal surface of the back of the hand (a), the knuckle and tip (i.e., the most distal point) of each finger were judged. On the palmar surface of the hand (b), the center of the skin crease at the base of each finger where it meets the palm and the tip of each finger were judged. (c–d) Experimental set-up and apparatus. Participants placed their hand either dorsum or palm up on a surface (c), which was then occluded with a board. They judged where in space each landmark on their hand was by placing the tip of a long baton on the board directly above the perceived location of each landmark (d), and responses were recorded with a camera.

Method

Participants

Twelve individuals (nine female) between 19 and 30 years old participated. All but three were right-handed by the Edinburgh Inventory, $M: 43.04$, range: -78.95 – 100 .

Procedure

Participants sat with their left hand on a table, either the palm or dorsum facing up. Participants rested their hand flat, fingers completely straight. A board (40×40 cm) was placed over the hand, resting on four pillars (6 cm high). A camera suspended above the board captured still images ($1,280 \times 960$ pixels).

Participants used a baton (35 cm length; 2 mm diameter) to indicate the perceived location of landmarks on the palm or dorsum of their occluded left hand. For the dorsum, the landmarks were the center of the knuckle at the base of each finger and each fingertip. For the palm, the landmarks were the center of the skin crease at the base of each finger where it meets the palm, and each fingertip. On each trial, participants were verbally instructed which landmark to judge. Participants were instructed to take their time, be precise, avoid ballistic pointing, and avoid strategies such as tracing the outline of the hand.

Before each trial, participants moved the tip of the baton to a blue dot at the edge of the board.

There were four blocks of 20 trials, dorsum and palm blocks alternating in counterbalanced ABBA sequence. Each block comprised two miniblocks of 10 trials, each landmark in random order. Immediately before and after blocks, a picture was taken without the occluder, showing the hand.

Analysis

Analysis methods have been described in full elsewhere (Longo & Haggard, 2010). Pixel coordinates of landmarks were coded and averaged, resulting in one map for each block. Distances were calculated between the tip of each finger and its base and between the bases of finger pairs.

Additionally, we compared actual and represented hand shape using generalized Procrustes analysis (GPA). GPA aligns sets of homologous landmarks, removing differences in location, rotation, and scale, isolating differences in shape (Bookstein, 1991). Before GPA, fingers were rotated to a common set of angles to remove postural differences. GPA was conducted using CoordGen (Integrated Morphometrics Program, H. David Sheets, Canisius College, <http://www.canisius.edu/~sheets/morphsoft.html>). Finally, thin-plate splines, depicting represented hand shape as a deformation of actual hand shape, were computed using tpsSpln (F. James Rohlf, SUNY Stony Brook, <http://life.bio.sunysb.edu/morph/index.html>).

Results

We previously found several characteristic distortions of the implicit representation of the dorsum (Longo & Haggard, 2010): (1) overestimation of hand width (~ 60 – 80%), (2) underestimation of finger length ($\sim 20\%$), and (3) a radial-ular gradient of magnification, finger length underestimation increasing from thumb to little finger. All three results were replicated here (see Figure 2). As a measure of hand width, we used the distance between the bases of the index and little fingers. There was clear overestimation of the width of the dorsal surface ($M: 79.2\%$ overestimation), $t(11) = 6.54$, $p < .0001$. Clear overestimation was also observed on the palmar surface ($M: 49.0\%$ overestimation), $t(11) = 5.72$, $p < .0001$, but significantly less than on the dorsum, $t(11) = 4.39$, $p < .005$. The magnitude of overestimation on the two surfaces was strongly correlated, $r(11) = .834$, $p < .0005$.

Underestimation of finger length was observed for the dorsal ($M: 11.9\%$ underestimation), $t(11) = -2.58$, $p < .05$, but not palmar ($M: 1.8\%$ overestimation), $t(11) = .36$, *ns*, surface. There was a significant difference between surfaces, $t(11) = 4.00$, $p < .005$. Again, under- or overestimation for the two sides was strongly correlated, $r(11) = .751$, $p < .005$.

We found previously that underestimation of finger length on the dorsum increased from thumb to little finger. We quantified this radial-ular gradient with least-squares regression, using digit number (1 = thumb to 5 = little finger) to predict underestimation. A clear radial-ular gradient was observed on the dorsum, mean $\beta = 4.6\%/digit$, $t(11) = 3.37$, $p < .01$. On the palm, gradients were not significantly different from 0, mean $\beta = -2.5\%/digit$, $t(11) = -1.83$, $p = .095$, but were reduced from the dorsum, $t(11) = 4.58$, $p < .001$.

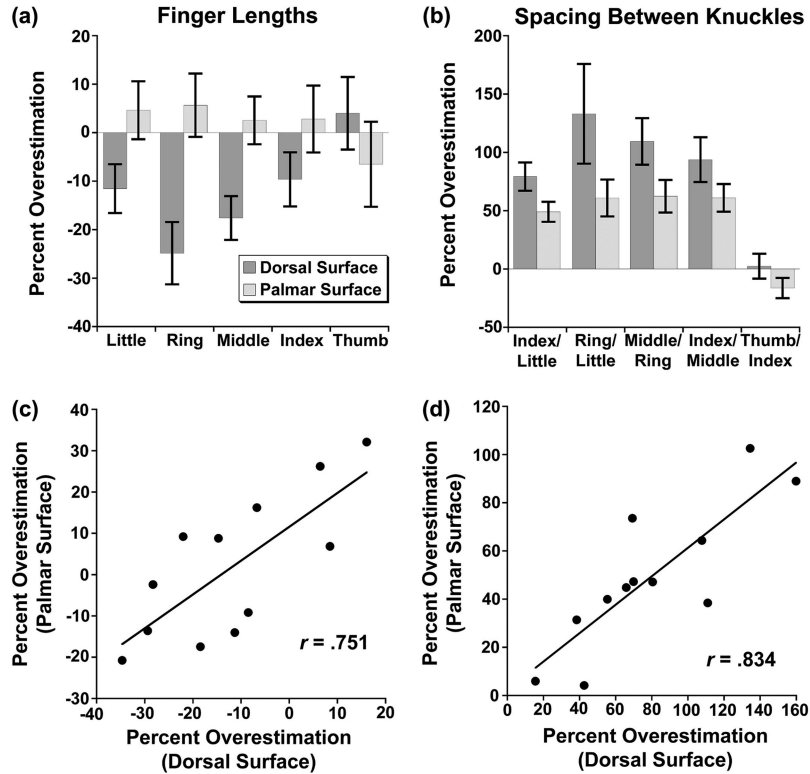


Figure 2. (a) Percent overestimation [that is, $100 \times (\text{judged length} - \text{actual length})/\text{actual length}$] of finger lengths. Clear underestimation of finger length was observed on the dorsal, but not on the palmar, surface of the hand. (b) Percent overestimation of spacing between pairs of knuckles. Clear overestimation was observed on both sides of the hand but was significantly reduced on the palmar compared with the dorsal surface. (c-d) Scatterplots showing relation between overestimation of finger length (c) and hand width (d) on the two skin surfaces. Clear relations were observed for both measures.

GPA maps are shown in Figure 3. To normalize size, GPA normalizes the *centroid size* (the square root of the sum of squared distances of each point from their center of mass). Centroid size thus quantifies overall map size, independent of shape. Overestimation of size was observed both for the dorsal ($M: 11.8\%$, $t(11) = 2.33$, $p < .05$, and palmar ($M: 17.4\%$, $t(11) = 4.05$, $p < .002$, hand surfaces. Overestimation was significantly larger on the palmar surface, $t(11) = 2.32$, $p < .05$, but strongly correlated across participants, $r(11) = .877$, $p < .0001$.

Discussion

These results replicate the characteristic distortions of hand representation we recently reported (Longo & Haggard, 2010). These distortions are substantially reduced, though qualitatively similar, on the palmar compared with the dorsal hand surface. We experience our body as a coherent volumetric whole, subject to the same physical and geometric laws as other rigid bodies. That different *magnitudes* of distortion found on the two sides of a single body part, however, suggest that the body model used for position sense is not a fully unified representation of the hand as a coherent, 3-D object. At the same time, however, the strong correlation between the distortions on the two skin surfaces suggests that the body model does not contain entirely independent

2-D representations of the two skin surfaces either. While our recent findings suggest that localization of somatic stimuli on the skin relies on a fragmented representation of individual skin surfaces (Mancini et al., 2011a), the present findings suggest that the implicit representation underlying external spatial localization of the hand is intermediate between a fragmented, 2-D representation of individual skin surfaces and an integrated, 3-D representation of the hand as a volumetric object. We suggest that this representation can be conceived as a 2.5-D body model, a somatosensory analogy to Marr's (1982; Marr & Nishihara, 1978) classic description of the '2[1/2]D sketch' in vision.

How might such a "hybrid" representation emerge? The analogy with vision is potentially instructive. Marr (1982) postulated the 2[1/2]-D sketch as a representation intermediate between 2-D retinal images and 3-D representations of objects, describing local surfaces and their orientations, but not integrating them into a fully 3-D representation. The body model revealed here may be similarly intermediate between a purely local representation of individual skin surfaces and a fully volumetric 3-D body. Indeed, there are bidirectional influences between somatosensory maps and the conscious body image. For example, cutaneous anesthesia leads the anesthetized body part to feel larger than it really is (Gandevia & Phegan, 1999). Conversely, manipulating the body image, for

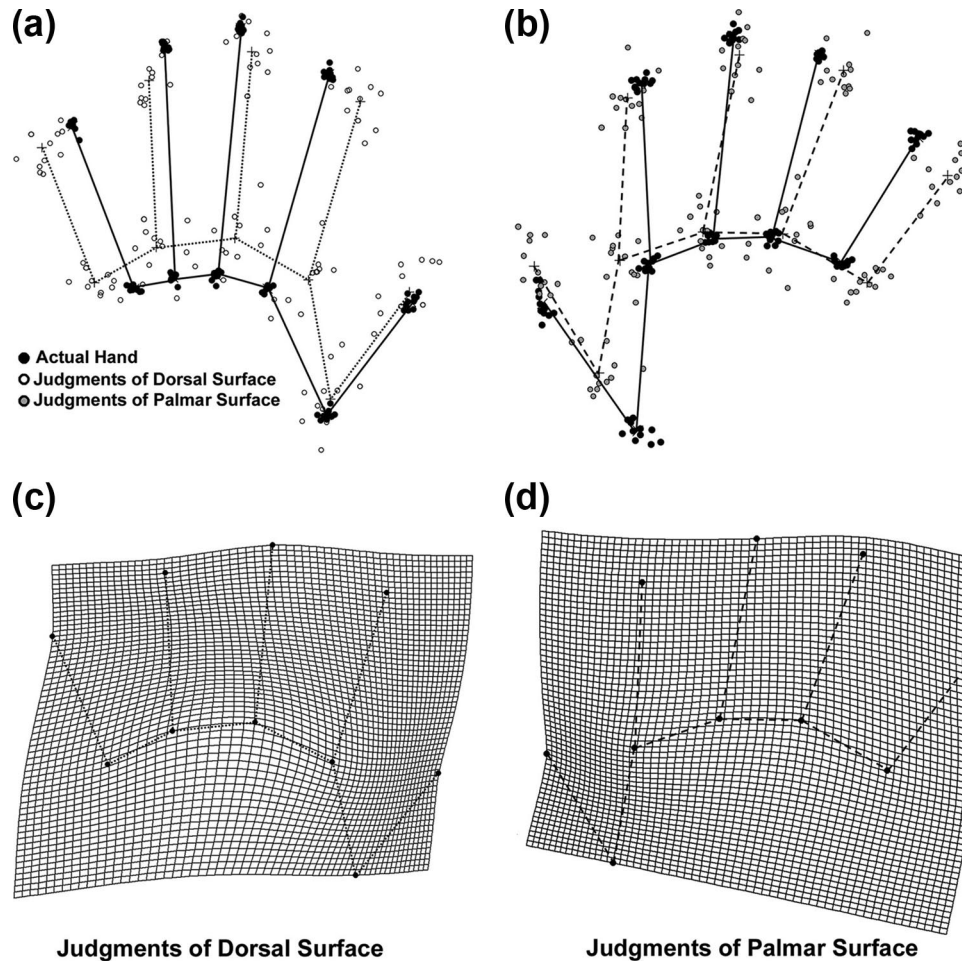


Figure 3. (a–b) Generalized Procrustes analysis (GPA) alignment of maps of actual and represented hand shape on the dorsal (a) and palmar (b) hand surfaces. (c–d) Thin-plate splines depicting represented hand shape as a deformation of actual hand shape on the dorsal (c) and palmar (d) hand surfaces.

example by visual distortion, modulates basic somatosensation (Kennett, Taylor-Clarke, & Haggard, 2001; Mancini, Longo, Kammers, & Haggard, 2011b). Such findings suggest that interaction between 2-D and 3-D representations is a general feature of somatosensory hierarchies (cf. Longo, Azañón, & Haggard, 2010) and may underlie the hybrid representation of the body itself. We recently found that the posterior parietal cortex is involved in remapping touch from a skin-centered to an external reference frame (Azañón, Longo, Soto-Faraco, & Haggard, 2010). The present results suggest there may be an analogous “remapping” problem in constructing a representation of the 3-D structure of the body itself from underlying 2-D representations of individual skin surfaces. It is unclear from the present data, however, whether the 2.5-D representation is stored by the brain in some intermediate format or is built up in real-time from 2-D and 3-D representations, whether it is an “online” or an “offline” representation (cf. Caruthers, 2008).

We previously suggested that differences in cortical magnification, receptive field size, and innervation density were related to distortions in implicit body representation (Longo & Haggard, 2010, 2011). However, at the larger spatial scale of palm versus

dorsum, receptor innervation appears not to predict represented size. Although the palm has higher sensitivity and cortical magnification than the dorsum (Pons, Wall, Garraghty, Cusick, & Kaas, 1987), the palm was not represented as *larger*, but rather was represented *more accurately*. That is, overestimation of hand width was reduced on the palm, and underestimation of finger length was replaced by a near-accurate representation. Thus, while high cortical magnification may in some cases produce perceptual distortions, such as the “Weber illusion” (Taylor-Clarke, Jacobsen, & Haggard, 2004; Weber, 1834/1996), it may also enhance accuracy for other perceptual abilities, such as position sense. Higher accuracy on the palm may also relate to the more orderly, somatotopic representation of glabrous skin, compared with hairy skin which is represented irregularly in islands of cortex intermixed with the map of the glabrous skin (Powell & Mountcastle, 1959; Pons et al., 1987).

Interestingly, the perceived distance between tactile stimuli also appears to depend on a body representation featuring overestimation of the dorsum (Longo & Haggard, 2011): stimuli oriented medio-laterally (*across* the hand) are perceived as approximately 40% larger than identical stimuli oriented proximo-distally (*along*

the hand). This common distortion suggests that position sense and tactile size perception may use a common implicit body representation. Indeed, overestimation of hand width in both cases mirrors anisotropies both in tactile acuity (Cody, Garside, Lloyd, & Poliakoff, 2008) and receptive field geometry (Alloway, Rosenthal, & Burton, 1989). Intriguingly, no such distortion in tactile size perception was found on the glabrous skin of the palm. Thus, both for tactile size perception (Longo & Haggard, 2011) and position sense (this study), the implicit representation of the palm is less distorted than the dorsum. If the brain used a single, coherent model of the hand as a volumetric object, one might expect the more accurate representation of the palm to be transferred, or extruded, to the dorsum. Our results show that this transfer is partial, at best. The brain's ability to maintain a single, coherent model of the body, capable of integrating diverse somatosensory inputs, may be highly limited.

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