

RUNNING HEAD: Distortions in Touch and Position Sense

No Correlation between Distorted Body Representations Underlying Tactile Distance  
Perception and Position Sense

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### Abstract

Both tactile distance perception and position sense are believed to require that immediate afferent signals be referenced to a stored representation of body size and shape (the *body model*). For both of these abilities, recent studies have reported that the stored body representations involved are highly distorted, at least in the case of the hand, with the hand dorsum represented as wider and squatter than it actually is. Here, we investigated whether individual differences in the magnitude of these distortions are shared between tactile distance perception and position sense, as would be predicted by the hypothesis that a single distorted body model underlies both tasks. We used established tasks to measure distortions of the represented shape of the hand dorsum. Consistent with previous results, in both cases there were clear biases to overestimate distances oriented along the medio-lateral axis of the hand compared to the proximo-distal axis. Moreover, within each task there were clear split-half correlations, demonstrating that both tasks show consistent individual differences. Critically, however, there was no correlation between the magnitudes of distortion in the two tasks. This casts doubt on the proposal that a common body model underlies both tactile distance perception and position sense.

### Introduction

Several forms of perception require that immediate sensory signals be combined with stored representations of body size and shape. This need is most acute in somatosensation, for which the primary receptor surface – the skin – is physically co-extensive with the body itself. We recently proposed a model of somatoperceptual information processing which postulated a common representation of the metric properties of the body (the *body model*) underlying perceptual abilities such as tactile distance perception and position sense (Longo, Azañón, & Haggard, 2010). In the case of touch, several recent studies have shown that illusions and similar interventions which alter the perceived size of body parts produce corresponding changes in the perceived size objects touching those parts, including effects induced by visual magnification (Taylor-Clarke, Jacobsen, & Haggard, 2004), proprioceptive illusions (de Vignemont, Ehrsson, & Haggard, 2005), cutaneous anesthesia (Berryman, Yau, & Hsiao, 2006), the rubber hand illusion (Haggard & Jundi, 2009; Bruno & Bertamini, 2010), action sounds (Tajadura-Jiménez et al., 2012; Tajadura-Jiménez, Tsakiris, Marquardt, & Bianchi-Berthouze, 2015), and tool use (Canzoneri et al., 2013; Miller, Longo, & Saygin, 2014). Together, such results support the interpretation the perception of tactile distance involves immediate tactile signals being referenced to higher-order models of the size and shape of the body.

Other studies have investigated the body representations underlying both tactile distance perception and position sense at baseline, in the absence of any manipulation of perceived bodily form. For example, Weber (1834/1996) in his classic studies on touch found that as he moved the two points of a compass across his skin, it felt like the distance between the two points increased as he moved them from a region of relatively low spatial sensitivity (e.g., the upper arm) to a region of higher sensitivity

(e.g., the palm). Subsequent studies have replicated this general pattern, showing that perceived tactile distances appear to be systematically related to the sensitivity of different skin surfaces (e.g., Goudge, 1918; Marks et al., 1982; Cholewiak, 1999; Taylor-Clarke et al., 2004; Anema, Wolswijk, Ruis, & Dijkerman, 2008; Miller, Longo, & Saygin, 2016). Similarly, large anisotropies of perceived tactile distance have been reported on the limbs, with stimuli oriented across the width of limbs being perceived as substantially farther apart than stimuli oriented along the length of the limbs (Canzoneri et al., 2013; Green, 1982; Le Cornu Knight, Longo, & Bremner, 2014; Longo, Ghosh, & Yahya, 2015; Longo & Haggard, 2011; Longo & Sadibolova, 2013; Miller, Longo, & Saygin, 2014, 2016). For example, in the study of Longo and Haggard (2011), we presented participants sequentially with two pairs of touches on each trial, one pair oriented along the proximo-distal axis of their hand and the other oriented with the medio-lateral axis. Across trials, the ratio of the distances in the medio-lateral and proximo-distal orientations was manipulated according to the method of constant stimuli. Participants were asked to make two-alternative forced-choice (2AFC) judgments of which of the two stimuli had a larger distance between the two touches. We then estimated the point-of-subjective-equality (PSE) for each participant

In the case of position sense, recent studies have provided evidence for similar distortions. Longo and Haggard (2010) developed a method to isolate and measure the stored body representation which is integrated with immediate afferent signals. In this task, participants sit with their hand underneath an occluding board and are asked to judge the perceived location of the tips and knuckles of each finger. By comparing the relative locations of judgments of each landmark, an implicit perceptual map of the hand can be constructed and compared to the actual form of the hand. Studies using this paradigm have revealed a fat, squat hand representation, with overestimation of hand

width and underestimation of finger length (e.g., Longo & Haggard, 2010, 2012a, 2012b; Longo, 2014, 2015; Lopez, Schreyer, Preuss, & Mast, 2012; Ferrè, Vagnoni, & Haggard, 2013; Mattioni & Longo, 2014; Saulton, Dodds, Bühlhoff, & de la Rosa, 2014; Saulton, Longo, Wong, Bühlhoff, & de la Rosa, 2016; Coelho, Zaninelli, & Gonzalez, in press).

Thus, large and highly stereotyped distortions have been reported for both tactile distance perception and position sense. What is the relation between body representations underlying these two abilities? In the model of somatoperceptual information processing proposed by Longo and colleagues (2010), a common body model feeds into both of these perceptual processes. Evidence consistent with the proposal that a common body model underlies both tactile distance perception and position sense comes from findings of similar patterns of distortions for both forms of perception. For example, as discussed above, there are clear biases to overestimate the width of the hand compared to its length, both in tactile distance perception (e.g., Green, 1982; Longo & Haggard, 2011) and in position sense (e.g., Longo & Haggard, 2010). Further, distortions are substantially larger on the hairy skin of the hand dorsum than on the glabrous skin of the palm, both for tactile distance perception (Le Cornu Knight et al., 2014; Longo, Ghosh, et al., 2015; Longo & Haggard, 2011) and position sense (Longo & Haggard, 2012a).

The present study investigated whether a common body model underlies tactile distance perception and position sense by looking at whether individual differences in the magnitude of distortions are shared between these abilities. In previous research, strong correlations have been found between the magnitude of distortion on the two hands and across similar conditions for both tactile size perception (Longo, Ghosh, et al., 2015) and position sense (Longo & Haggard, 2010, 2012a; Longo, 2014; Mattioni & Longo, 2014). Thus, it is clear that reliable individual differences exist for both

perceptual abilities. Here we investigated whether these individual differences are shared across abilities by measuring both in the same people. We measured anisotropy of tactile distance perception on the dorsum of the left hand using a two-alternative forced-choice (2AFC) method similar to that we have used previously (Longo, Ghosh, et al., 2015; Longo & Haggard, 2011). Because the method described above for producing proprioceptive maps underlying position sense focuses on the fingers, we used a revised procedure we recently reported (Longo, Mancini, & Haggard, 2015) which allows mapping the hand dorsum. Specifically, instead of giving participants verbal instructions about which landmark to localize, a point on the hand is touched and participants are asked to localize the touch in external space. This allows proprioceptive maps to be constructed even for regions of skin without lexically-labeled landmarks. Indeed, we found that these maps were stretched along the medio-lateral hand axis (Longo, Mancini, et al., 2015). If a common body model underlies both tactile distance perception and position sense, we expected a correlation across participants in the magnitude of the distortions found for each task.

### Methods

#### *Participants*

Twenty-five members of the Birkbeck community (18 females; mean age: 30.5 years, SD: 8.8 years) participated after giving informed consent. All participants were right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971) ( $M$ : 82.5, range: 36.8 – 100). Five additional participants with an  $R^2$  lower than 0.50 on at least one of the two blocks of the tactile distance task were excluded from analyses. The relatively high exclusion rate is largely driven by the fact that participants needed to have good fit to their data in both of the halves of the experiment. Had the same criteria been applied

to the complete set of data from each participant, only two participants would have been excluded.

All procedures were approved by the Department of Psychological Sciences Research Ethics Committee at Birkbeck, University of London. The study was conducted in accordance with the principles of the Declaration of Helsinki.

### *Tactile Distance Task*

Procedures for the tactile distance task were similar to our previous studies using this paradigm (Longo, Ghosh, et al., 2015; Longo & Haggard, 2011; Longo & Sadibolova, 2013). Stimuli were pairs of wooden posts mounted in foamboard, separated by 2, 3, or 4 cm. The posts tapered to a blunt point (approximately 1 mm in diameter). On each trial, participants were touched twice on the dorsal surface of their left hand, once with the posts oriented across the medio-lateral hand axis (*across* orientation), and once with the posts oriented along the proximo-distal hand axis (*along* orientation). Participants made untimed two-alternative forced-choice (2AFC) judgments of which of the two distances felt physically larger. Stimuli were applied manually by an experimenter, approximately in the centre of the hand dorsum. Stimuli lasted approximately one second with an approximately one second inter-stimulus interval.

There were two blocks of 72 trials each. In each block, all nine combinations of across and along stimuli were presented eight times each, in random sequence. The order of the along and across stimuli was counterbalanced across trials. The two blocks were separated by a short break. Participants were blindfolded throughout the procedure.

The percentage of trials in which the “across” stimulus was judged as larger was analyzed as a function of the ratio of the length of the across and along stimuli, plotted logarithmically to produce a symmetrical distribution around a ratio of 1 (i.e., the point-of-actual-equality). Best-fitting cumulative Gaussian functions were fit to data from individual participants using maximum-likelihood estimation with the Palamedes toolbox (Prins & Kingdom, 2009) for MATLAB (Mathworks, Natick, MA).

For each participant, the point-of-subjective-equality (PSE) was quantified as the mean of the best-fitting Gaussian. As mentioned above, data for five participants was excluded because the  $R^2$  of the best-fitting Gaussian fit separately to Blocks 1 and 2 was below 0.50 in at least one block. For the remaining participants, there was good fit for the data with mean  $R^2$  of 0.930 overall, 0.878 for curves fit to Block 1, and 0.873 for curves fit to Block 2.

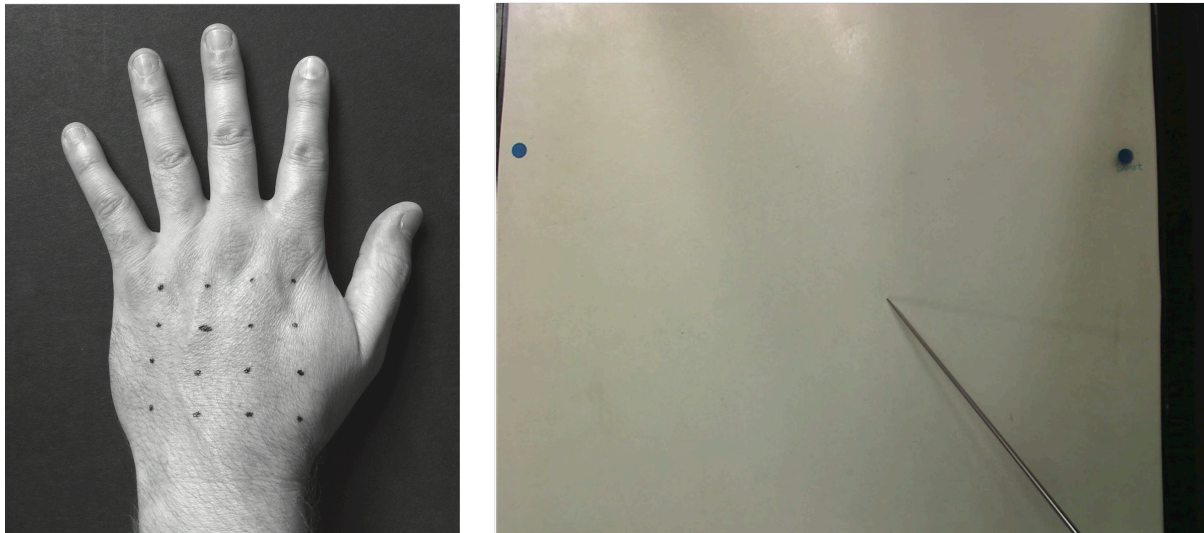
### *Proprioceptive Maps*

Procedures were similar to those in our recent paper (Longo, Mancini, et al., 2015). Participants sat with their left hand resting palm down on a table. The hand rested flat on the table, with fingers completely straight. An occluding board (40 × 40 cm) was placed over the hand, resting on four pillars (6 cm high). A camera (Logitech Webcam Pro 9000 HD) suspended on a tripod above the occluding board (27 cm high) captured photographs (1600 × 1200 pixels) controlled by a custom MATLAB script.

To identify the points of stimulation, a 4x4 grid of points was marked with a pen on the back of the participant’s hand using a plastic template (see the left panel of Figure 1). The four rows of points ran along the medio-lateral hand axis, while the four columns ran along the proximo-distal axis. On each trial, the experimenter lifted the occluding board (turning it towards the participant so that it still blocked their view of



their hand), and touched one of the points with a von Frey hair (255 milliNewtons) for approximately one second. The participant's task was to place the tip of a long baton (35 cm length, 2 mm diameter) on the occluder directly above the location where the touch had occurred. They were instructed to be precise in their judgements and avoid ballistic pointing or strategies such as tracing the outline of the hand. To ensure that they judged each landmark individually, participants moved the baton to the edge of the board before the start of each trial. When the participants indicated their response, a photograph was taken and saved for offline coding (see right panel of Figure 1).



**Figure 1:** Setup of the proprioceptive mapping task. *Left panel:* A 4x4 grid of locations was marked with pen on the back of the participant's hand. *Right panel:* On each trial, one of these locations was touched and participants used a long baton to judge the perceived location at which the touch had occurred by pointing to the corresponding location on an occluding board covering their hand. Locations of responses were captured by an overhead camera.

There were four blocks of 48 trials each. Each block included three mini-blocks of one repetition of each of the 16 stimulus locations in random order. At the beginning and the end of each block a photograph of the participant's hand was taken to measure the true locations of the applied stimuli and to check that the hand hadn't moved during the course of the block. A 10 cm ruler appeared in the photographs of the participant's hand and allowed conversion between pixel units and centimeters.

For offline data coding, the x-y pixel coordinates of each landmark were coded using a custom MATLAB script using Cogent Graphics (developed by John Romaya, Wellcome Department of Imaging Neuroscience, University College London). Mean coordinates were then calculated for each location in each experimental block. The set of mean coordinates in each block comprises two maps, one reflecting the actual shape of the stimulated locations, the other reflecting represented shape. Distances between mean pixel coordinates of pairs of locations differing in the medio-lateral and proximo-distal orientations were calculated and converted into cm. As shown in Figure 3, three types of distances were calculated in each orientation: *small* distances, between adjacent locations; *mid* distances, between locations separated by a single other location; and *large* distances, separated by two other locations. There were 12 small, 8 mid, and 4 large distances in each orientation.

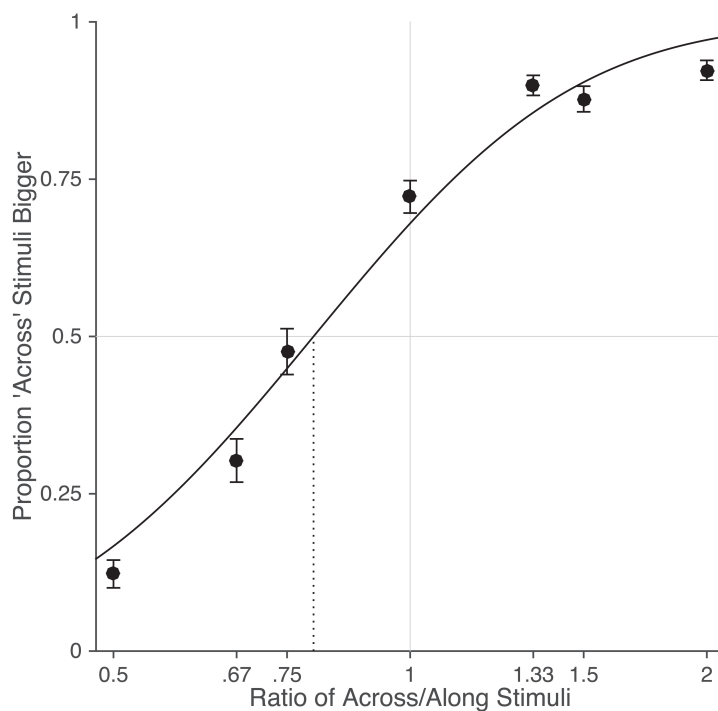
To assess overall stretch of maps, we stretched an idealized square grid reflecting the locations of the 16 points by different amounts to find the stretch that maximized the similarity with each participant's perceptual map, as well as with the actual configuration of points on their hand. Stretches were defined by the multiplication of the x-coordinate (reflecting location in the medio-lateral hand axis) by a stretch parameter. Thus, a stretch of 1 indicated a perfectly square grid, stretch of less than 1 indicated a tall thin grid, and stretch of more than 1 indicated a squat fat grid. Values between 0.33 and 3 were tested by exhaustive search with a resolution of 0.0005 units in natural logarithm space (i.e., 4,415 steps).

## Results

### *Tactile Distance Task*

Results from the tactile distance judgment task are shown in Figure 2.

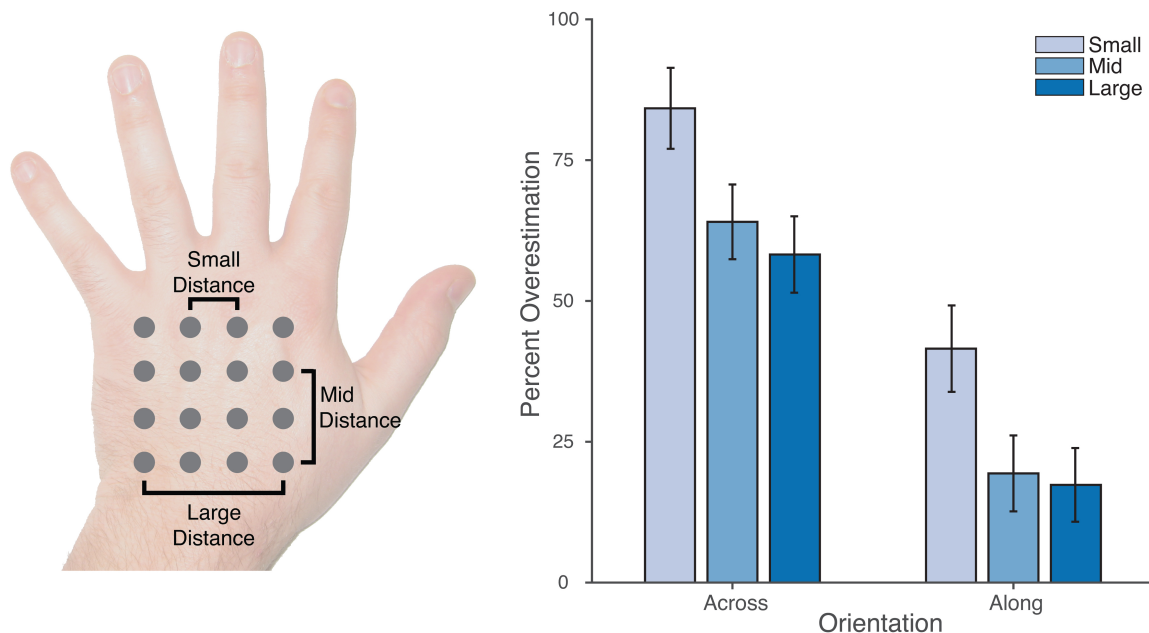
Psychometric functions were fit to the data from each participant and the point of subjective equality (PSE) was calculated as the ratio between the across and along stimuli where the curve crossed 50% (i.e., the ratio for which the participant was equally likely to judge the across or the along stimulus as bigger). There was a clear bias to perceive distances across the width of the hand as bigger than those along the length of the hand ( $M: 0.782$ ),  $t(24) = -9.79$ ,  $p < 0.0001$ ,  $d = 1.96$ . This clearly replicates the anisotropy reported previously (Canzoneri et al., 2013; Green, 1982; Le Cornu Knight et al., 2014; Longo, Ghosh, et al., 2015; Longo & Haggard, 2011; Longo & Sadibolova, 2013; Miller et al., 2014).



**Figure 2:** Results from the tactile distance judgment task. As in previous studies, there was a clear bias for stimuli oriented across the width of the hand dorsum to be perceived as larger than stimuli oriented along the length of the hand. The dotted vertical line indicates the point-of-subjective equality (i.e., the stimulus ratio at which participants were equally likely to judge the across or the along stimulus as bigger). Error bars are one standard error.

### *Proprioceptive Maps*

To quantify distortions in the internal configuration of the representation of the hand, we calculated the distance between judgments of pairs of locations differing in location along the medio-lateral hand axis (across the hand) or the proximo-distal axis (along the hand), as shown in the left panel of Figure 3. Distances across the hand were calculated for pairs of landmarks within each row of locations, and distances along the hand were calculated for pairs of landmarks within each column. Three sizes of distance were calculated: *small* distances, separated by a single step; *mid* distances, separated by two steps; and *large* distances, separated by two steps. There were, thus, 12 small, 8 mid, and 4 large distances in each orientation.



**Figure 3:** *Left panel:* Schematic depiction of the location of the 16 stimulus locations in the proprioceptive map task. Three types of distance were calculated in both the across and along orientations, reflecting one step between locations (*small distance*), two steps (*mid distance*), or three steps (*large distance*). *Right panel:* Overestimation of distances in the two orientations as a percentage of actual distance. While absolute overestimation was apparent in both orientations, it was substantially larger in the across than in the along orientation. Error bars are one standard error.

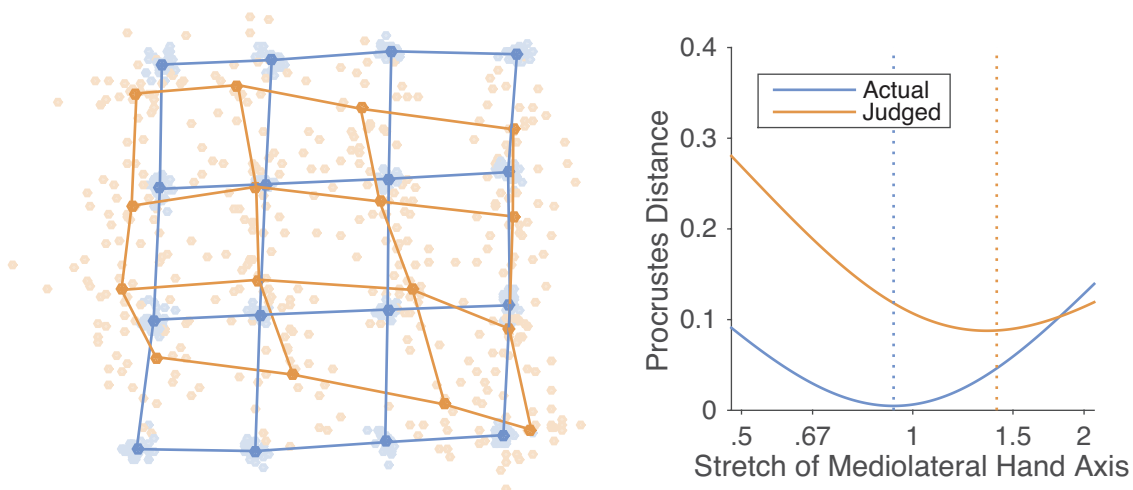
The right panel of Figure 3 shows overestimation as a percentage of actual distance for across and along distances of the three different sizes. One-sample t-tests with Holm-Bonferroni correction for multiple comparisons were used to compare the

amount of overestimation to 0. Significant overestimation was found for all distances, both across the hand: *small* ( $M = 84.2\%$ ,  $t(24) = 11.71$ ,  $p < 0.0001$ ,  $d = 2.41$ ), *mid* ( $M = 64.0\%$ ,  $t(24) = 9.65$ ,  $p < 0.0001$ ,  $d = 2.01$ ), *large* ( $M = 58.2\%$ ,  $t(24) = 8.59$ ,  $p < 0.0001$ ,  $d = 1.78$ ); and along the hand: *small* ( $M = 41.5\%$ ),  $t(24) = 5.41$ ,  $p < 0.0001$ ,  $d = 1.12$ ; *mid* ( $M = 19.4\%$ ),  $t(24) = 2.88$ ,  $p < 0.02$ ,  $d = 0.60$ ; *large* ( $M = 17.3\%$ ),  $t(24) = 2.65$ ,  $p < 0.02$ ,  $d = 0.55$ . Critically, however, the magnitude of overestimation was significantly larger in the across than in the along orientation in all cases: *small*,  $t(24) = 6.26$ ,  $p < 0.0001$ ,  $d_z = 1.31$ ; *mid*,  $t(24) = 7.40$ ,  $p < 0.0001$ ,  $d_z = 1.54$ ; *large*,  $t(24) = 7.73$ ,  $p < 0.0001$ ,  $d_z = 1.61$ .

A 2x3 repeated-measures analysis of variance (ANOVA) was conducted with orientation (across vs. along) and size (small, medium, large) as factors. There was a clear main effect of orientation,  $F(1, 24) = 63.71$ ,  $p < 0.0001$ ,  $\eta_p^2 = 0.73$ , with distances across the width of the hand overestimated relative to those along the length of the hand. There was also a main effect of size,  $F(1.21, 29.09) = 34.77$ ,  $p < 0.0001$ ,  $\eta_p^2 = 0.59$ , with overestimation decreasing monotonically with size. There was no interaction,  $F(1.62, 38.80) = 0.439$ , *n.s.*,  $\eta_p^2 = 0.02$ .

The analyses reported so far calculate separate measures of overestimation for each dimension. To calculate a single measure of distortion of maps as a whole, we conducted an additional analysis using a method called *Procrustes alignment* (Bookstein, 1991; Rholf & Slice, 1990). Procrustes alignment superimposes configurations of homologous landmarks by translating, scaling, and rotating them so as to minimize the distance between pairs of landmarks. We used this in two ways. First, we used Generalized Procrustes Analysis (Gower, 1975) to mutually superimpose maps from all participants to construct grand-averages of both perceptual maps and actual hand shape. These maps are shown in the left panel of Figure 4 and allow a visualization of the overall pattern of distortions.

Second, we used the Procrustes distance, the sum-of-squares of the residual distances between pairs of homologous landmarks, as a measure of the dissimilarity between two maps. This allowed us to estimate the overall stretch of perceptual maps in the medio-lateral axis by finding the stretch applied to an idealized rectangular grid that minimized the dissimilarity with each map. We multiplied the x-coordinates of a 4x4 rectangular grid by a stretch parameter to generate grids of varying levels of stretch. When the stretch parameter was equal to 1, the grid was perfectly square. When it was greater than 1, the grid was stretched in the medio-lateral axis. When it was less than 1, the grid was stretched in the proximo-distal axis. For each participant, we determined the value of the stretch parameter that minimized the dissimilarity in shape (i.e., that minimized the Procrustes distance) between the stretched grid and the participant's perceptual map. The right panel of Figure 4 shows the mean values of the Procrustes distance for values of the stretch parameter. The best-fitting stretch parameters were significantly greater than 1 ( $M: 1.40$ ),  $t(24) = 6.96$ ,  $p < 0.0001$ ,  $d = 1.39$ .

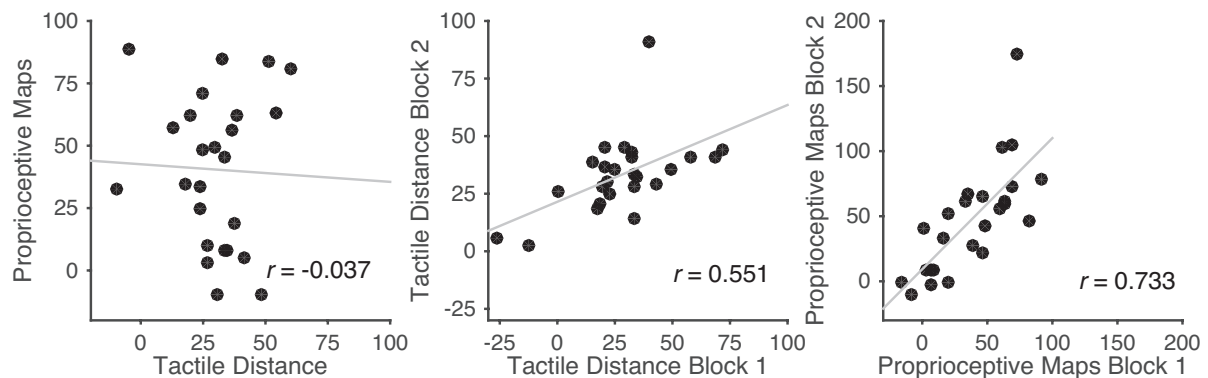


**Figure 4:** *Left panel:* Generalized Procrustes alignment of the actual configuration of points on the hand (blue dots and lines) and perceptual maps (orange dots and lines). The light dots are data from individual participants, while the dark dots represent the average shape. *Right panel:* mean Procrustes distance between actual and perceptual maps and idealized grids stretched by different amounts. A stretch of 1 indicates a square grid; stretches greater than 1 indicate stretch in the medio-lateral axis, while stretches less than 1 indicate stretch in the proximo-distal axis.

### Correlations between Tasks

The left panel of Figure 5 shows a scatterplot of distortions in the two tasks, in both cases quantified as the percentage overestimation of the medio-lateral hand axis relative to the proximo-distal axis. There was no apparent relationship whatsoever, with a highly non-significant correlation,  $r(23) = -0.037$ ,  $p = 0.861$ .

To ensure that this lack of correlation does not reflect an absence of meaningful individual differences in these measures or a lack of statistical power, we investigated the split-half correlations between the two blocks of each task. A scatterplot showing the relation between performance on the two blocks of the tactile distance judgment task is shown in the centre panel of Figure 5, and a corresponding scatterplot for the proprioceptive localisation task in the right panel of Figure 5. As is clear in the Figure, clear split-half correlations were apparent in both the tactile distance,  $r(23) = 0.551$ ,  $p < 0.005$ , and proprioceptive localisation,  $r(23) = 0.733$ ,  $p < 0.0001$ , tasks.



**Figure 5:** Scatterplots showing the relation between the two tasks (left panel), and between the first and second halves of each of the two tasks individually (centre and right panels). Units are percent overestimation of the medio-lateral relative to the proximo-distal hand axis. There was no correlation between the magnitude of the distortion in the two tasks. Critically, however, within each task, clear split-half correlations were apparent.

### Discussion

These results replicated the distortions that have previously been reported on the hand dorsum for both tactile distance perception (e.g., Green, 1982; Longo & Haggard, 2011) and position sense (Longo & Haggard, 2010, 2012a). Moreover, also consistent with previous results, there were clear individual differences in the magnitude of these distortions, as measured by split-half correlations. Critically, however, there was no evidence that individual differences were shared between tactile distance perception and position sense, with no apparent correlation between distortions in the two cases. These results cast doubt on the suggestion that both abilities rely on a common representation of the body's metric properties (i.e., body model), as we suggested previously (Longo et al., 2010), in which case common individual differences should be apparent in both cases.

What causes individual differences in these tasks? To this point, we have assumed that the split-half correlations we find reflect differences between people in the extent to which the representation of the hand's metric properties (i.e., the body model) is distorted. It is certainly possible, however, that these correlations might instead reflect differences between people in the way they approach the task or the amount of effort they exert. Given that the tasks we used are superficially very different, person-to-person differences in how the tasks are approached might affect the tasks in different ways. Thus, it is possible that the overall similar distortions in the two tasks seen at the level of the overall mean reflect the influence of a common body model on both tasks, but that the split-half correlations reflect idiosyncratic differences in how participants approach each task. The present results cannot exclude this interpretation. However, in a recent study (Longo, Ghosh, et al., 2015) we found that while there were clear correlations in the magnitude of distortions of tactile distance perception across the two hands, there were no correlations between distortions on the palm and dorsum



of each hand. Given that the task was exactly the same for both skin surfaces, the lack of correlation between the palm and dorsum is difficult to interpret in terms of how participants approached the task.

What do the present results tell us about the relation between distortions in tactile distance perception and position sense? In both cases, the nature of the distortions appears to parallel lower-level aspects of somatosensory organization. For example, the overestimation of hand width relative to length mirrors findings of greater tactile spatial acuity in the medio-lateral than in the proximo-distal axis of the limbs (e.g., Weber, 1834/1996; Cody, Garside, Lloyd, & Poliakoff, 2008) and the fact that receptive fields of neurons in the spinal cord and cortex representing the limbs tend to be oval-shaped, with the long axis running along the proximo-distal limb axis (e.g., Powell & Mountcastle, 1959; Brooks, Rudomin, & Slayman, 1961; Brown, Fuchs, & Tapper, 1975; Alloway, Rosenthal, & Burton, 1989). Distortions in both tactile distance perception and position sense, however, are much smaller than would be predicted on the basis of receptive field size alone (Taylor-Clarke et al., 2004; Longo, in press), suggesting that low-level distortions are at least partly corrected before affecting tactile distance perception and position sense. Thus, one possibility is that body representations underlying tactile distance perception and position sense are completely distinct, but both are shaped by lower-level somatosensory maps, and inherit their distortions. This could account for the fact that both perceptual abilities show qualitatively similar patterns of distortion, which are nevertheless not correlated across people. Another possibility is that both tactile distance perception and position sense rely on a common body model, but that the specific demands of each type of judgment alter responses, resulting in different patterns of individual difference in the two cases. The present results do not exclude either of these possibilities.

The procedure for mapping implicit body representations developed by Longo and Haggard (2010) relies on the body part being mapped having numerous distinct landmarks with verbally-specifiable names. This worked in the case of the hands, which have many such lexically-coded landmarks, at least on the fingers. Together with a recent study (Longo, Mancini, et al., 2015), the present results show that this paradigm can be extended to regions of the body which do not have such landmarks. In both of these studies, perceptual maps analogous to those obtained by Longo and Haggard (2010) were obtained for the hand dorsum, which (unlike the fingers) lacks many distinct landmarks. Critically, these maps showed overestimation of hand width relative to length, analogous to the underestimation of finger length and overestimation of hand width described by Longo and Haggard (2010). This demonstrates that the distortions seen in previous studies cannot be an artifact of the use of verbal categories for cueing responses. That implicit perceptual maps can be obtained in the absence of distinct landmarks also allows the possibility of mapping regions of the body beyond the hands.

## 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
- Berryman, L. J., & Yau, J. M., & Hsaio, S. S. (2006). Representation of object size in the somatosensory system. *Journal of Neurophysiology*, *96*, 27-39.
- Bookstein, F. L. (1991). *Morphometric tools for landmark data: Geometry and biology*. Cambridge: Cambridge University Press.
- 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
- Brown, P. B., Fuchs, J. L., & Tapper, D. N. (1975). Parametric studies of dorsal horn neurons responding to tactile stimulation. *Journal of Neurophysiology*, *38*, 19–25.
- Bruno, N., & Bertamini, M. (2010). Haptic perception after a change in hand size. *Neuropsychologia*, *48*, 1853-1856.
- 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.
- Cholewiak, R. W. (1999). The perception of tactile distance: Influences of body site, space, and time. *Perception*, *28*, 851-875.
- Cody, F. W., Garside, R. A., Lloyd, D., & Poliakoff, E. (2008). Tactile spatial acuity varies with site and axis in the human upper limb. *Neuroscience Letters*, *433*, 103-108.
- Coelho, L. A., Zaninelli, G., & Gonzalez, C. L. (in press). A kinematic examination of hand

perception. *Psychological Research*.

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

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

Goudge, M. E. (1918). A qualitative and quantitative study of Weber's illusion. *American Journal of Psychology*, *29*, 81-119.

Gower, J. C. (1975). Generalized procrustes analysis. *Psychometrika*, *40*, 33–51.

Green, B. G. (1982). The perception of distance and location for dual tactile pressures. *Perception and Psychophysics*, *31*, 315–323.

Haggard, P., & Jundi, S. (2009). Rubber hand illusions and size-weight illusions: Self-representation modulates representation of external objects. *Perception*, *38*, 1796-1803.

Le Cornu Knight, F., Longo, M. R., & Bremner, A. J. (2014). Categorical perception of tactile distance. *Cognition*, *131*, 254–262.

Longo, M. R. (2014). The effects of immediate vision on implicit hand maps. *Experimental Brain Research*, *232*, 1241–1247.

Longo, M. R. (2015). Posture modulates implicit hand maps. *Consciousness and Cognition*, *36*, 96–102.

Longo, M. R. (in press). Distorted body representations in healthy cognition. *Quarterly Journal of Experimental Psychology*.

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., Ghosh, A., & Yahya, T. (2015). Bilateral symmetry of distortions of tactile

- size perception. *Perception*, *44*, 1251–1262.
- 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., Mancini, F., & Haggard, P. (2015). Implicit body representations and tactile spatial remapping. *Acta Psychologica*, *160*, 77–87.
- Longo, M. R., & Sadibolova, R. (2013). Seeing the body distorts tactile size perception. *Cognition*, *126*, 475–481.
- Lopez, C., Schreyer, H.-M., Preuss, N., & Mast, F. W. (2012). Vestibular stimulation modifies the body schema. *Neuropsychologia*, *50*, 1830–1837.
- Marks, L. E., Girvin, J. P., Quest, D. O., Antunes, J. L., Ning, P., O'Keefe, M. D., et al (1982). Electrocutaneous stimulation II. The estimation of distance between two points. *Perception and Psychophysics*, *32*, 529–536.
- Mattioni, S., & Longo, M. R. (2014). The effects of verbal cueing on implicit hand maps. *Acta Psychologica*, *153*, 60–65.
- 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.

- Miller, L. E., Longo, M. R., & Saygin, A. P. (2016). Mental body representations retain homuncular shape distortions: Evidence from Weber's illusion. *Consciousness and Cognition, 40*, 17-25.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*, 97–113.
- 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.
- Prins, N., & Kingdom, F. A. A. (2009). Palamedes: Matlab routines for analyzing psychophysical data. <http://www.palamedestoolbox.org>.
- Rholf, F. J., & Slice, D. E. (1990). Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology, 39*, 40–59.
- Saulton, A., Dodds, T. J., Bühlhoff, H. H., & de la Rosa, S. (2014). Objects exhibit body model like shape distortions. *Experimental Brain Research, 233*, 1471–1479.
- Saulton, A., Longo, M. R., Wong, H. Y., Bühlhoff, H. H., & de la Rosa, S. (2016). The role of visual similarity and memory in body model distortions. *Acta Psychologica, 164*, 103–111.
- 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.
- Tajadura-Jiménez, A., Tsakiris, M., Marquardt, T., & Bianchi-Berthouze, N. (2015). Action sounds update the mental representation of arm dimension: Contributions of kinaesthesia and agency. *Frontiers in Psychology, 6*, 689.
- Taylor-Clarke, M., Jacobsen, P., & Haggard, P. (2004). Keeping the world a constant size:

Object contancy in human touch. *Nature Neuroscience*, 7, 219-220.

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, 2<sup>nd</sup> Ed.* (pp. 21-128). Hove, UK: Erlbaum.

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