RUNNING HEAD: Bilateral Tactile Anisotropy

Bilateral Symmetry of Distortions of Tactile Size Perception

Matthew R. Longo[1], Arko Ghosh[2] and Tasneem Yahya[1]

[1]Department of Psychological Sciences, Birkbeck, University of London, UK

[2]Institute of Neuroinformatics and Neuroscience Center Zürich, University of Zürich and

ETH Zürich, Switzerland

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

The perceived distance between touches on the limbs is generally bigger for distances oriented across the width of the limb than for distances oriented along the length of the limb. The present study aimed to investigate the coherence of such distortions of tactile size perception across different skin surfaces. We investigated distortions of tactile size perception on the dorsal and palmar surfaces of both the left and right hands as well as the forehead. Participants judged which of two tactile distances felt larger. One distance was aligned with the proximodistal axis (*along* the body), the other with the mediolateral axis (*across* the body). Clear distortions were found on all five skin surfaces, with stimuli oriented across the width of the body being perceived as farther apart than those oriented along the length of the body. Consistent with previous results, distortions were smaller on the palmar than on the dorsal hand surface. Distortion on the forehead was intermediate between the dorsal and palmar surfaces. There were clear correlations between distortion on the left and right hands, for both the dorsal and palmar skin surfaces. In contrast, within each hand, there was no significant correlation between the two skin surfaces. Distortion on the forehead was not significantly correlated with that on any of the other skin surfaces. These results provide evidence for bilaterally symmetric representations underlying tactile size perception.

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Illusions of tactile size perception have been known since the classic research of Weber (1834/1996) who observed that the distance between two points of a compass touching the skin felt larger when applied to a highly sensitive region than to a less sensitive region. Numerous subsequent studies have confirmed Weber's observations, revealing a systematic relation between tactile size perception and tactile spatial acuity (e.g., Anema, Wolswijk, Ruis, & Dijkerman, 2008; Cholewiak, 1999; Taylor-Clarke, Jacobsen, & Haggard, 2004; de Vignemont, Ehrsson, & Haggard, 2005), an effect known as *Weber's illusion*. This illusion suggests that the disproportionate representation of sensitive skin surfaces in somatosensory cortex (i.e., cortical magnification) is preserved in tactile size perception, producing systematic distortions.

In its original form, Weber's illusion reflects differences in the perceived size of touch on different body parts. Similar effects, however, can also be found within individual skin surfaces as a function of the orientation of stimuli (e.g., Canzoneri et al., 2013; Green, 1982; Le Cornu Knight, Longo, & Bremner, 2014; Longo & Haggard, 2011; Longo & Sadibolova, 2013; Miller, Longo, & Saygin, 2014). Longo and Haggard (2011), for example, found that the perceived distance between two touches running across the width of the hand dorsum was about 40% bigger than the same distance running along the length of the hand. In contrast, no significant bias was observed on the glabrous skin of the palm, though there was a trend in the same direction. Le Cornu Knight and colleagues (2014) similarly found a reduction of the magnitude of anisotropy on the palmar side of the hand and forearm, though in that study a clear and significant anisotropy was nevertheless found on both sides of the hand and arm. Together, these studies have shown

a large anisotropy of tactile size perception on the hand dorsum, and a clear reduction of this effect on the palm.

What causes such anisotropy? One possibility would be a general, cross-modality anisotropy. However, the effect seems to be if anything opposite to the visual horizontal-vertical illusion in which vertical lines are perceived as longer than equivalent horizontal lines. Further, because the limbs are mobile, they do not have a fixed orientation relative to the visual (or gravitational) vertical. Moreover, even within touch, the magnitude of the anisotropy varies across skin surfaces (such as the two sides of the hand as discussed above), and even appears to be absent on some parts of the body such as the belly (Green, 1982). Nevertheless, when anisotropy of tactile distance is present it appears to reflect overestimation of width compared to length, suggesting the operation of a general organizing principle, at least within somatosensation.

One approach to investigating the causes of anisotropy is to investigate its symmetry across the two sides of the body. In order to work together the two hands may need to have similar levels of distortion. Indeed, across studies, similar anisotropies of tactile size perception have been found on both the left (e.g., Le Cornu Knight et al., 2014; Longo & Haggard, 2011; Longo & Sadibolova, 2013) and right (e.g., Canzoneri et al., 2013; Green, 1982; Miller et al., 2014) limbs. However, to our knowledge, no study has compared distortions on the two hands in the same participants. Several recent studies have provided evidence for lateral asymmetries in body representations (e.g., Gentilucci, Daprati, & Gangitano, 1998; Hach & Schütz-Bosbach, 2010, 2014; Linkenauger et al.,

2009), suggesting that there may be interesting differences in perceptual distortion as a function of handedness. Linkenauger and colleagues (2009), for example, found that right-handed participants overestimated the length of their right arm in comparison to their left arm, an effect which was correlated with asymmetries in grip strength between the two hands. Similarly, recent results have shown that a brief period of tool use exaggerates the baseline tactile anisotropy (Canzoneri et al., 2013; Miller et al., 2014). This effect provides evidence for causal linkages between distortions of tactile size perception and skilled motor control, making it plausible that there might be laterality effects at baseline related to handedness.

On the other hand, an increasing body of evidence suggests high levels of integration between somatosensory representations of the two sides of the body. For example, neurons with bilateral receptive fields have been reported in areas 1 and 2 of the primary somatosensory cortex (e.g., Iwamura, Iriki, & Tanaka, 1994; Iwamura et al., 2002; Lipton, Fu, Branch, & Schroeder, 2006). Similarly, studies using fMRI and MEG have reported bilateral responses to unilateral stimuli (e.g., Hlushchuk & Hari, 2006; Kanno, Nakasato, Hatanaka, & Yoshimoto, 2003; Tamè et al., 2012, 2015). At the behavioral level, there is evidence both for immediate interactions between stimuli delivered to the two hands (e.g., Braun et al., 2005; Tamè, Farnè, & Pavani, 2011) and transfer of tactile learning to homologous regions of the contralateral hand (e.g., Harrar, Spence, & Makin, 2014; Harris, Harris, & Diamond, 2001; Kaas, van de Ven, Reithler, & Goebel, 2013; Sathian & Zangaladze, 1998). Finally, a remarkable study by Calford and Tweedale (1990) showed that plastic changes to SI organization following anesthesia to one thumb

of flying foxes appeared immediately in the both the ipsilateral and contralateral hemispheres. Similarly, studies in humans have found that cutaneous anaesthesia of one hand improves tactile acuity on the contralateral hand (Björkman, Rosén, & Lundborg, 2004; Werhahn, Mortensen, Van Boven, Zeuner, & Cohen, 2002). Such results demonstrate a substantial degree of integration of organization between homologous representations of the two sides of the body in left and right SI. This suggests that tactile distortions may be symmetric across the two sides of the body. One aim of this study was therefore to investigate the bilateral coherence of distortions of tactile size perception, both in terms of the overall magnitude of distortion as well as in terms of consistent individual differences across people.

It is also important to consider the integration of skin surfaces on a single body part. A fully coherent representation of the body should reflect the body's existence as a single unified whole, rather than a fragmented collection of distinct skin surfaces. Though the body is a fully three-dimensional, volumetric object, primary maps in SI represent the body as a collection of distinct two-dimensional skin surfaces (Longo, 2015). For example, the hairy skin of the hand dorsum and the glabrous skin of the palm have separate representations within somatotopic SI maps (e.g., Sur, Merzenich, & Kaas, 1980). Perceptually, this is reflected in distinct patterns of perceptual distortion on the two sides of the hand for tasks including tactile localization (Mancini, Longo, Iannetti, & Haggard, 2011), position sense (Longo & Haggard, 2012), and (as described above) tactile size perception (Le Cornu Knight et al., 2014; Longo & Haggard, 2011). Despite these differences, there may nonetheless be strong integration between the

representations of different surfaces of a single body part. For example, while the distortions of body representations underlying position sense are smaller on the palmar than on the dorsal hand surface (Longo & Haggard, 2012), the magnitude of distortion is strongly correlated across participants. Longo and Haggard (2012) suggested that position sense might rely on a 2.5-Dimensional representation of the body, intermediate between 2-D somatotopic maps and a fully volumetric representation of the hand as a 3-D object, such as the conscious body image (Longo, in press). Thus, a second goal of this study was to investigate whether, despite differences in the overall magnitude of anisotropy, the representations of the two sides of the hand may nevertheless be integrated, resulting in consistent individual differences in the size of anisotropy.

Most of the studies described above have focused on the hands and arms. It is important, however, to understand to what extent conclusions drawn from the hands generalize to the rest of the body. Green (1982) found a clear anisotropy of tactile size perception on the thigh, though smaller in magnitude than on the hand dorsum. This suggests that anisotropy may be a general characteristic of the representation of the limbs. In contrast, Green reported no significant anisotropy on the belly, suggesting that it is not a universal characteristic of the representation of the entire body. Thus, a third goal of the present study was to investigate anisotropy of tactile size perception on a non-hand body part, specifically the face. We considered the face as of particular interest for three reasons. First, Hänzi & Ghosh (2014) recently reported an anisotropy of tactile acuity on the forehead analogous to that previously reported for the limbs (e.g., Cody, Garside, Lloyd, & Poliakoff, 2008; Gibson & Craig, 2005), making it highly plausible that there will also

be an anisotropy in tactile size perception. Second, the representations of the hand and face are adjacent in somatotopic SI maps (e.g., Penfield & Boldrey, 1937). Finally, plastic changes in SI are known to transfer between hand and face (e.g., Gandevia & Phegan, 1999; Hänzi et al., 2014a, 2014b; Ramachandran, Rogers-Ramachandran, & Stewart, 1992).

Method

Participants

Thirty-seven individuals (25 females) between 17 and 55 years of age (*M*: 30.1 years) participated after giving informed consent. All but five were right-handed as assessed by the Edinburgh Inventory (*M*: 66.2; range: -100 – 100; Oldfield, 1971). Procedures were approved by the local ethics committee.

Materials

Tactile stimuli were wooden posts which tapered to a point, but were not sharp. Pairs of posts were mounted in foamboard, separated by 20, 30, or 40 mm, as in our previous studies (Le Cornu Knight et al., 2014; Longo & Haggard, 2011; Longo & Sadibolova, 2013; Miller et al., 2014).

Procedure

The experiment was divided into 10 blocks of 40 trials each. Each block involved stimulation of one of the five skin surfaces (forehead, left dorsum, left palm, right

dorsum, right palm). The first five blocks included one block of each skin surface in random sequence, as did the final five blocks.

On each trial, participants were touched twice, once with the posts oriented across the width of the hand/forehead, and once with the posts oriented along the length of the hand/forehead. Touch was applied approximately in the centre of each skin surface. Participants made unspeeded two-alternative forced-choice judgments of whether the distance between the posts felt bigger the first time they were touched or the second time, and responded verbally.

There were five pairs of stimuli, according to the distance in the across and the along orientations (across/along): 2/4 cm, 2/3 cm, 3/3 cm, 3/2 cm, 4/2 cm. Each pair was presented 8 times in each block, making 40 trials in total. The order of the along and across stimuli was counterbalanced across trials within each block and the order of trials within each block was randomized. Stimuli were delivered manually by an experimenter. The duration of each stimulus was approximately one second with an inter-stimulus interval between the two touches of approximately one second. Participants were blindfolded throughout the procedure.

Analysis

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). Cumulative Gaussian functions were fit to each participant's data on each skin surface with least-squares regression using R 3.0.2 software.

Two participants had R^2 values for the psychometric functions below 0.5 in at least one condition and were therefore excluded from analyses. Across skin surfaces, R^2 values indicated good fit to the remaining participants' data (*M*: 0.961, *SD*: 0.070).

The point-of-subjective-equality (PSE) was calculated for each curve as the ratio of across to along stimuli at which the psychometric function crossed 50%. The magnitude of distortion was compared across skin surfaces using ANOVA. In addition, we investigated correlations between the different skin surfaces. The question here is whether there are consistent individual differences in the magnitude of distortions across the skin. In particular, if there is a single, coherent representation of the hand underlying distortions on the palm and dorsum, then participants who show a relatively large distortion on the dorsum of a given hand should also show a relatively large distortion on the palm of that hand. Analogously, if the representation of the hand is strongly bilaterally symmetric, then there should be a correlation between the left and right hands for a given skin surface.

Results

Figure 1 shows the grand average results with best-fitting psychometric function, across the five skin surfaces and Figure 2 shows mean PSEs across the five skin surfaces. If there is no perceptual anisotropy, PSEs should on average equal 1 (i.e., the along and

across stimuli should be perceived as equal in size when they are in fact equal size).

Consistent with previous results, there was a clear anisotropy on the dorsal surfaces of the left hand ($M = 0.740$), $t(34) = -8.42$, $p < 0.0001$, $d = 1.42$, and on the right hand ($M = 0.735$), $t(34) = -10.70$, $p < 0.0001$, $d = 1.81$. There were also significant anisotropies on the palm of both the left hand ($M = 0.883$), $t(34) = -6.11$, $p < 0.0001$, $d = 1.03$, and the right hand ($M = 0.889$), $t(34) = -6.80$, $p < 0.0001$, $d = 1.15$. The magnitude of anisotropy was clearly larger on the dorsum than on the palm for both the left hand, $t(34) = 3.96$, $p < 0.0005$, $d_z = 0.669$, and the right hand, $t(34) = 5.87$, $p < 0.0001$, $d_z = 0.993$, as reported in previous studies (Green, 1982; Le Cornu Knight et al., 2014; Longo & Haggard, 2011). There were no significant differences between anisotropies on the left and right hands, either on the dorsum, $t(34) = 0.17$, n.s., or palm, $t(34) = -0.31$, n.s.
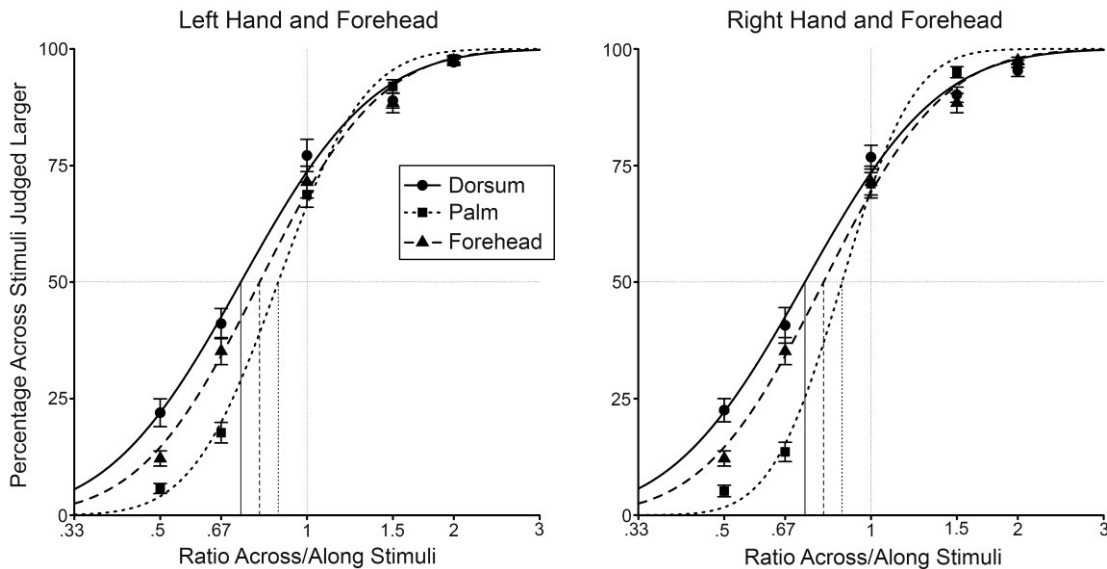
Figure 1: Psychophysical functions on each skin surface. The left panel shows data from the left hand and the right panel shows data from the right hand. Data from the forehead is presented on both graphs. The curves are cumulative Gaussian functions fit with least-squares regression. Error bars are one standard error. The vertical lines represent the point of subjective equality (i.e., where the curve crosses 50%).
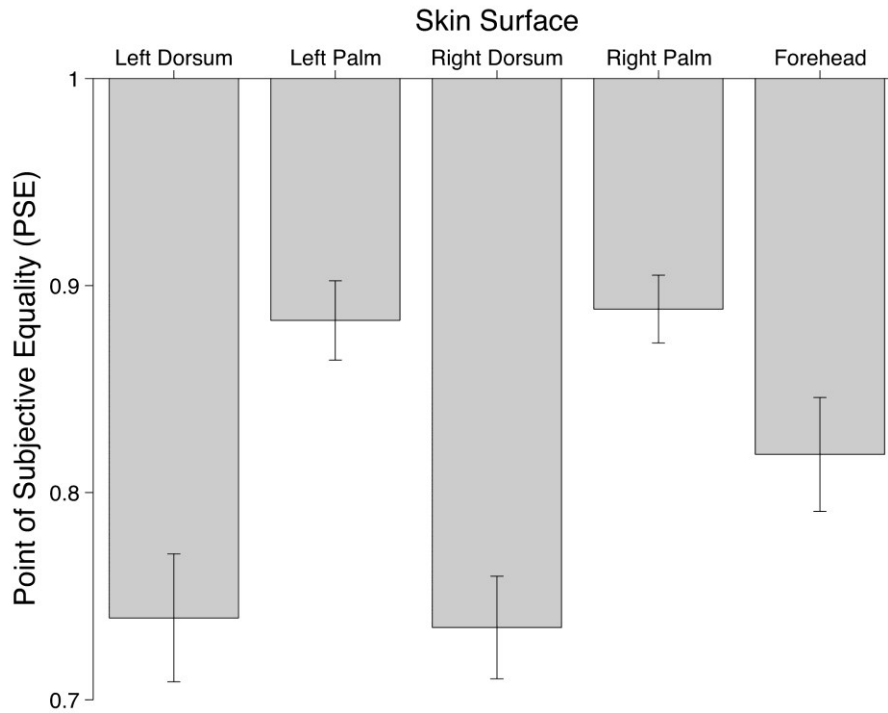
Figure 2: Mean PSEs (i.e., the ratio of across to along stimuli for which the two stimuli are perceived as equal) across the five skin surfaces. Error bars are one standard error.

A 2x2 analysis of variance (ANOVA) was used to investigate PSEs on the hands, including factors 'laterality' (left hand, right hand) and 'surface' (dorsal, palmar). There was a highly significant main effect of surface, $F(1, 34) = 32.760$, $p < 0.0001$, $\eta_p^2 = 0.491$, with anisotropy being clearly larger on the dorsal than the palmar skin surface. However, there was no significant effect of laterality, $F(1, 34) = 0.001$, *n.s.*, nor an interaction between the two factors, $F(1, 34) = 0.079$, *n.s.*

There was also a clear anisotropy in the same direction on the forehead ($M = 0.818$), $t(34) = -6.60$, $p < 0.0001$, $d = 1.11$. The magnitude of the anisotropy on the face was intermediate between that on the dorsal and palmar hand surfaces. Anisotropy on the face

was not significantly correlated with that on any of the other four skin surfaces (all *p*'s > 0.4).
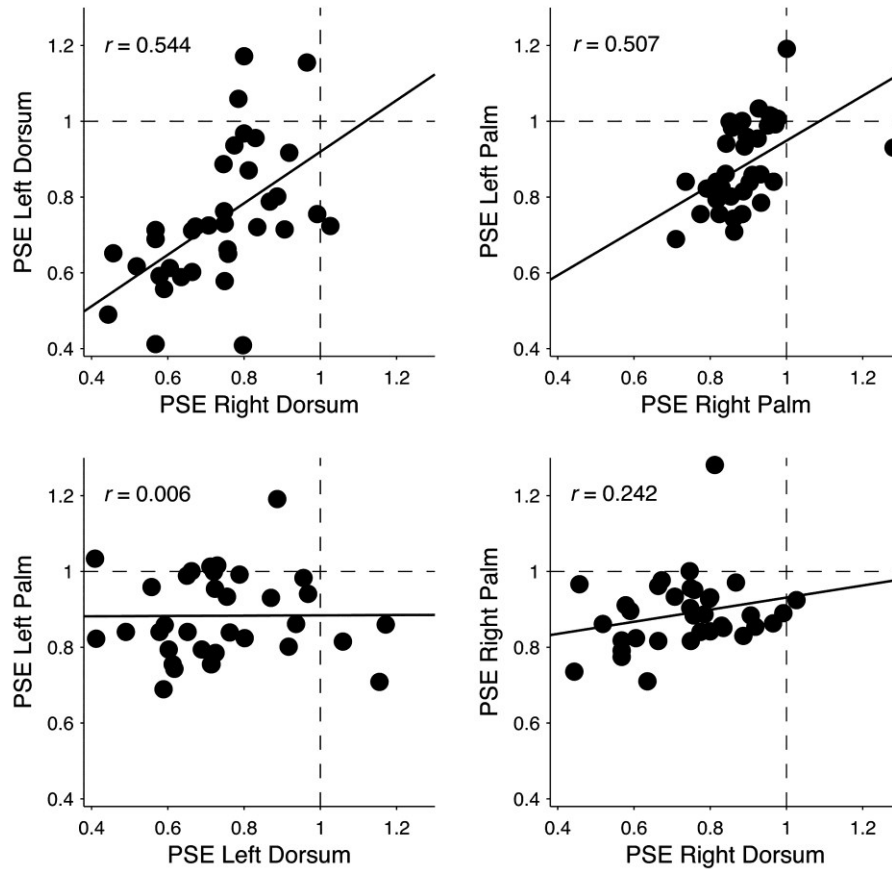
Figure 3: The top row shows scatterplots of PSEs for the left and right dorsums (top left) and the left and right palms (top right). Clear correlations between the two hands were found for both surfaces. The bottom row shows scatterplots of PSEs for the two surfaces of the left hand (bottom left) and the right hand (bottom right). The solid lines are least-squares regression lines; the dashed lines indicate a PSE of 1 (i.e., no anisotropy).

Figure 3 shows scatterplots between the different skin surfaces of the hands. There was a significant correlation across participants in the magnitude of anisotropy on both the dorsal surfaces of the two hands, $r(33) = 0.544$, $p < 0.001$, and on the palmar surface, $r(33) = 0.507$, $p < 0.002$. In striking contrast, there were no similar correlations between

the two skin surfaces within each hand, either on the left hand, $r(33) = 0.006$, *n.s.*, or the right hand, $r(33) = 0.242$, *n.s.*

Finally, although there were no overall lateral differences in the magnitude of anisotropy, we investigated whether the differences in anisotropy on the two hands was correlated across individuals with handedness. There was no significant correlation between Edinburgh handedness inventory scores and the difference in PSEs between the right and left dorsums, $r(33) = -0.082$, or palms, $r(33) = -0.159$, *n.s.*

Discussion

Significant anisotropies were found on all five skin surfaces investigated. In each case, pairs of tactile stimuli oriented across the width of the body were perceived as farther apart than those oriented along the length of the body. Nevertheless, clear differences between surfaces were apparent, both in terms of the absolute size of anisotropy as well as in the presence of consistent individual differences across people. The largest anisotropies were found on the dorsal surfaces of the two hands, while considerably smaller anisotropies were found on the palms, replicating previous findings (e.g., Green, 1982; Le Cornu Knight et al., 2014; Longo & Haggard, 2011). The magnitude of anisotropy on the forehead was intermediate between that on the dorsum and palm. There were clear correlations between anisotropy on the left and right hands, for both the dorsal and palmar skin surfaces. In contrast, within each hand, there was no significant correlation between the two skin surfaces. Anisotropy on the forehead was not significantly correlated with that on any of the other skin surfaces.

Clear symmetry was found for distortions on the left and right hands. This was apparent both in terms of the absolute magnitude of anisotropy found on the two hands, as well as correlations across individuals. This result is consistent with a range of neurophysiological (e.g., Iwamura et al., 1994, 2002), neuroimaging (e.g., Kanno et al., 2003; Tamè et al., 2012), and behavioural (e.g., Harris et al., 2001; Sathian & Zangaladze, 1998) results showing integration between the somatosensory representations of the two sides of the body. This bilateral symmetry is in striking contrast to the differences between the palmar and dorsal surfaces of each hand, which have anisotropies of different magnitude and which are uncorrelated across individuals. This pattern suggests that bilateral integration of somatosensory signals occurs prior to integration of individual 2-D skin surfaces to form a coherent representation of the body as a 3-D object.

The bias to perceive tactile distances as larger when oriented across the width of the hand bears a similarity to recently reported distortions underlying position sense in which the hand is represented as wider and more squat than it actually is (Longo & Haggard, 2010). A recent study found that these distortions were significantly reduced on the palmar compared to the dorsal side of the hand (Longo & Haggard, 2012), again mirroring the pattern seen for tactile size perception in the present study. Nevertheless, Longo and Haggard (2012) found that even though distortions of the palmar side of the hand were smaller than on the dorsal side, the magnitude of these distortions was strongly correlated across people. This contrasts with the present results in which no correlation between

distortions on the two sides of each hand were apparent. This pattern suggests that while qualitatively similar forms of distortion affect body representations underlying tactile size perception and position sense, the former may rely on a more fragmented representation than the latter. That is, the strongly-linked individual differences across the two sides of the hand for position sense (Longo & Haggard, 2012) suggest that the hand is represented, at least partially, as a coherent, integral whole. In contrast, the absence of such shared individual differences in the case of tactile size perception in the present study suggests, in contrast, that tactile size perception relies on a representation of the hand in which the palm and dorsum are more distinct.

Several recent studies have found evidence for lateral asymmetries in body representations related to handedness (e.g., Gentilucci et al., 1998; Hach & Schütz-Bosbach, 2010; Linkenauger et al., 2009). In the studies of Hach and Schütz-Bosbach (2010) and Linkenauger and colleagues (2009), right-handed participants judged the right side of their body as bigger than the left side. No such lateral asymmetry was apparent in anisotropy of tactile size perception in the present study, with nearly identical effects on the two hands. This pattern mirrors that reported by Longo and Haggard (2010, Exp 3) for body representations underlying position sense in which largely mirror symmetric distortions were found on the two hands. It is not entirely clear why some studies find handedness-related asymmetries and others do not. One possibility is that the tasks used in the present study and that of Longo and Haggard (2010) may be more implicit than those used by the other studies. This interpretation seems reasonable in relation to the study of Linkenauger and colleagues, in which participants instructed an experimenter to

adjust a tape measure to match the perceived length of their arms. It is less convincing in relation to the study of Hach and Schütz-Bosbach, which was quite similar to that of Longo and Haggard (2010) in having participants localize landmarks on their body in external space. Another possibility is that laterality effects may be more apparent at larger spatial scales. While the present study and that of Longo and Haggard (2010) focused specifically on the hand, studies showing lateralized effects have focused on the entire arm (Linkenauger et al., 2009) or the torso (Hach & Schütz-Bosbach, 2010).

To our knowledge, this study is the first to show anisotropy of tactile size perception on the face. This result is consistent with the recent finding of Hänzi and Ghosh (2014) of an anisotropy of two-point discrimination thresholds on the forehead, with higher sensitivity across the width of the face. This correspondence between anisotropies of tactile acuity and size perception provides further support to the interpretation of Weber's illusion as a systematic relation between spatial sensitivity and size perception in touch. For tactile size perception, 'fat' biases have been found on the hand (this study, Green, 1982; Le Cornu Knight et al., 2014; Longo & Haggard, 2011; Longo & Sadibolova, 2013; Miller et al., 2014), forearm (Canzoneri et al., 2013; Green, 1982; Le Cornu Knight et al., 2014; Miller et al., 2014), thigh (Green, 1982), and forehead (this study). The only body part investigated for which anisotropy has not been found is, intriguingly, the belly (Green, 1982). Analogous distortions have also been found on tasks in which representations of body size and shape are inferred from the pattern of proprioceptive localization judgments, both for the hand (Longo & Haggard, 2010, 2012) and torso (Hach & Schütz-Bosbach, 2010). Fuentes and colleagues have also found similar biases using a 'body

image task' in which participants judge the relative location of body landmarks by clicking the corresponding place on a monitor, both for the body as a whole (Fuentes, Longo, & Haggard, 2013a; Fuentes et al., 2013b) and the face specifically (Fuentes et al., 2013c). The finding of qualitatively similar distortions on widely disparate skin surfaces and across tasks raises the possibility that a general bias to represent the body as squatter and fatter than it is may reflect a basic principle of body representation.

Could the reported anisotropies reflect use-dependent plasticity? The data seem inconsistent with this, since two surfaces of single hand will presumably be more strongly correlated than surfaces on opposite hands. However, the sensory statistics experienced by the dorsal surfaces of the two hands will be similar (e.g., in terms of environmental exposure, temperature, etc.) in virtue of their mirrored positions, as will those experienced by the palmar surfaces. The fact that anisotropies across several body parts all go in the same direction is difficult to interpret in terms of use-dependent plasticity and seems to suggest instead the operation of a hard-wired (pre-set) organizational plan. However, the fact that anisotropies are of different magnitudes on different skin surfaces, and the fact that they're not all correlated with each other, suggests that this pre-set plan is modulated by other factors, potentially other pre-set plans or experience.

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Acknowledgments