Journal of Experimental Psychology:
Human Perception and Performance
2011, Vol. 37, No. 3, 720–726

0096-1523/11/$12.00 DOI: 10.1037/a0021921

Weber's Illusion and Body Shape: Anisotropy of Tactile Size Perception on the Hand

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The perceived distance between touches on a single skin surface is larger on regions of high tactile sensitivity than those with lower acuity, an effect known as *Weber's illusion*. This illusion suggests that tactile size perception involves a representation of the perceived size of body parts preserving characteristics of the somatosensory homunculus. Here, we investigated how body *shape* is coded within this representation by comparing tactile distances presented in different orientations on the hand. Participants judged which of two tactile distances on the dorsum of their left hand felt larger. One distance was aligned with the proximodistal axis (*along* the hand), the other with the mediolateral axis (*across* the hand). Across distances were consistently perceived as larger than along ones. A second experiment showed that this effect is specific to the hairy skin of the hand dorsum and does not occur on glabrous skin of the palm. A third experiment demonstrated that this bias reflects orientation on the hand surface, rather than an eye- or torso-centered reference frame. These results mirror known orientational anisotropies of both tactile acuity and of tactile receptive fields (RFs) of cortical neurons. We suggest that the dorsum of the hand is implicitly represented as wider than it actually is and that the shape of tactile RFs may partly explain distortions of mental body representations.

Keywords: touch, anisotropy, Weber's illusion, body representation

Several sensory modalities use information about the body to form percepts of the external world. These processes include representations of the distance between the ears (Clifton et al., 1988), the spacing between the eyes (Banks, 1988), arm length (Longo & Lourenco, 2007), and eye-height (Warren & Whang, 1987). Tactile perception, likewise, is inextricably tied to representations of the body. Perceiving the metric properties (i.e., size, shape) of objects touching the skin requires referencing to a representation of the metric properties of the body part being touched (Longo, Azañón, & Haggard, 2010). For example, the size of an object that covers half the width of the hand can only be determined if one knows how big the hand is. Recent studies confirm that representations of the body underlie tactile size perception, showing that modifying the perceived size of body parts produces corresponding changes in the perceived size of objects touching the skin. Such effects have been found for changes in body perception induced by visual (Taylor-Clarke, Jacobsen, & Haggard, 2004) and proprioceptive (de Vignemont, Ehrsson, & Haggard, 2005) illusions and via cutaneous anaesthesia (Berryman, Yau, & Hsiao, 2006).

Little, however, is known about the mental models of the body that structure tactile perception. One source of information comes from Weber's (1834/1996) observation that the perceived distance between two points touching the skin increases as the points are moved from a region of low tactile sensitivity to one of higher sensitivity, an effect known as *Weber's illusion*. Though the sensitivity of a region of skin is logically independent of the size of an object touching it, Weber's illusion demonstrates that tactile acuity does, nevertheless, influence perceived size. Subsequent authors have replicated Weber's basic finding and confirmed, across a range of skin surfaces, that tactile distance perception relates systematically to tactile sensitivity and cortical magnification (i.e., the relative proportion of cortical territory coding a specific skin surface) (e.g., Green, 1982; Cholewiak, 1999). It remains to be determined whether this is a general rule of tactile perception or whether certain body parts would be exceptions. In any case, given the clear links between body representation and tactile size perception (Taylor-Clarke et al., 2004; de Vignemont et al., 2005; Berryman et al., 2006), such baseline differences in size perception across the body surface can be used to investigate the form of the body model used for touch.

In its classic form, Weber's illusion provides information regarding the relative *size* of body parts in the body model mediating touch. It has revealed a pattern of size distortions qualitatively similar to, though generally smaller than, those of the traditional somatosensory homunculus (Penfield & Boldrey, 1937). Here, we adapt the logic of this illusion to investigate the *shape* of the body in these representations. Rather than comparing the perceived size of tactile distances on two different skin surfaces, we investigated the perceived size of tactile distances in different *orientations* on a single skin surface, either the dorsum (the back of the hand) or the palm. Distortions of body shape should produce anisotropy in perceived size of tactile objects as a function of orientation. For example, if the hand (i.e., either the dorsum or the palm) is represented as being longer and more slender than it really is,

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This research was supported by Biotechnology and Biological Sciences Research Council (BBSRC) grant BB/D009529/1 to P.H.

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distances oriented proximodistally, *along* the body surface, should feel larger than those oriented mediolaterally, *across* the body surface. Conversely, if the hand is represented as being wider than it actually is, distances oriented across the hand should be perceived as larger than those oriented along the hand. Measuring tactile anisotropy, therefore, allows us to estimate the aspect ratio of the hand representation within the mental body model. Such anisotropies have, indeed, been reported on the forearm (Wong, Ho, & Ho, 1974; Green, 1982), with tactile objects being perceived as larger across than along the forearm. Such effects, however, have not been found on the hand (Green, 1982; Cholewiak, 1999), possibly because these studies tested only the glabrous skin of the palm.

How and why might the represented shape of the hand differ from its true shape? Anisotropies in *primary* tactile perception have been known at least since Weber's (1834/1996) observation that two-point discrimination thresholds are lower for stimuli oriented mediolaterally than those oriented proximodistally. More recent studies have found similar results for several locations on the hand and forearm (Gibson & Craig, 2005; Cody, Gaarside, Lloyd, & Poliakoff, 2008) and leg (Fuchs & Brown, 1984). Furthermore, numerous studies have found that RFs representing hairy skin at many levels of the nervous system are generally oval-shaped, with the long axis running proximodistally (e.g., Powell & Mountcastle, 1959; Brooks, Rudomin, & Slayman, 1961; Brown, Fuchs, & Tapper, 1975; Alloway, Rosenthal, & Burton, 1989). Although some RFs on the glabrous skin of the palm and fingers show a degree of elongation (Johansson & Vallbo, 1980), RFs here are generally smaller and less elongated than those on the hairy skin (Powell & Mountcastle, 1959), and any elongation is uniformly distributed in all orientations (DiCarlo, Johnson, & Hsiao, 1998; Vega-Bermudez & Johnson, 1999; DiCarlo & Johnson, 2002).

In this study, we investigated the mental representation of the hand underlying tactile size perception. On each trial, two pairs of touches defining different tactile distances were applied sequentially to the hand, one pair oriented proximodistally (*along* the hand), the other oriented mediolaterally (*across* the hand). Participants made two-alternative forced choice (2AFC) judgments of which distance felt larger. The method of constant stimuli was used to estimate biases in the perception of size as a function of orientation. In Experiment 1, we investigated biases on the hairy skin of the dorsum of the left hand. Given known anisotropies in RF geometry on hairy skin, we predicted a corresponding anisotropy of tactile size perception, with stimuli running across the hand perceived as larger than identical stimuli running along the hand. In Experiment 2, we compared such biases on the dorsum to the glabrous skin of the palm. Given that RF geometry on glabrous skin is less anisotropic than on hairy skin, we hypothesized a corresponding reduction of anisotropy for tactile size perception. In Experiment 3, we varied the orientation of the hand to the body to make sure that biases were due to stimulus orientation on the hand, rather than biases in egocentric spatial representation.

Experiment 1: Tactile Size Perception Along Versus Across the Hand Dorsum

Method

Participants. Twenty volunteers (16 female) between 18 and 33 years of age participated. Participants were generally right-handed, as assessed by the Edinburgh Inventory (Oldfield, 1971, $M = 58.7$, range $= -81.0$ to 100), and reported no known abnormalities of tactile perception and normal or corrected-to-normal vision. They gave written informed consent and were paid for their participation. Procedures were approved by the local ethics committee.

Materials. Stimuli were pairs of pointed metal rods (diameter 1.5 mm), mounted in foamboard and separated by 2, 3, or 4 cm. The tip of each rod tapered to a point but was not sharp.

Procedure. On each trial, participants were touched twice on the dorsum of their left hand, once with the posts oriented along the proximodistal axis of the hand (along stimulus), and once oriented along the mediolateral axis (across stimulus). Touch was applied approximately in the center of the dorsum. Participants made untimed two-alternative forced choice judgments of whether the two points felt farther apart in the along or the across orientation and responded verbally. There were five pairs of stimuli, according to the size of the along and across stimuli (across/along): 2/4 cm, 2/3 cm, 3/3 cm, 3/2 cm, and 4/2 cm. Each pair was applied 14 times, for a total of 70 trials. The order of along and across stimuli was counterbalanced within each stimulus pair, and order of trials was randomized. Stimuli were administered manually by an experimenter. The duration of each touch was approximately one second, with an interstimulus interval of approximately one second. Participants were blindfolded throughout the procedure and were not allowed to see the stimuli before testing commenced.

Analysis. The proportion of trials in which the 'across' stimulus was judged as larger was analyzed as a function of the ratio of the length of the along and across stimuli, plotted logarithmically to produce a symmetrical distribution about the point-of-actual-equality (i.e., ratio equals 1). Cumulative Gaussian functions were fit to each participant's data with least-squares regression using R 2.8.0. Points of subjective equality (PSEs) were determined as the point at which the psychometric function crossed 50%. We also computed interquartile ranges (IQR) as a measure of the slope of the psychometric function (i.e., the distance between where the psychometric function crossed 25% and 75%).

Results and Discussion

R-squared values for the psychometric functions of individual participants ranged from .726 to 1 ($M = .943$, $SD = .076$), indicating good fit to the data. The mean IQR was .250 (range = .081–.861).

Our main experimental question concerned the PSEs. If there is no distortion of hand shape, PSEs should, on average, equal 1, indicating that stimulus orientation does not bias perceived size. If the hand is represented as being longer and more slender than it is, stimuli running across the hand would have to be larger than those running along the hand for the two to feel equivalent, and PSEs greater than 1 would be expected. Conversely, if the hand is represented as wider and more squat than it really is, stimuli running along the hand would have to be larger than those running across the hand for the two to feel equivalent, and PSEs less than 1 would be expected.

The mean PSE was .758 (see Figure 1), significantly less than 1, $t(19) = -11.19$, $p < .0001$, indicating a bias to represent the hand as wider than it really is. That is, tactile stimuli running mediolaterally are systematically perceived as larger than stimuli running

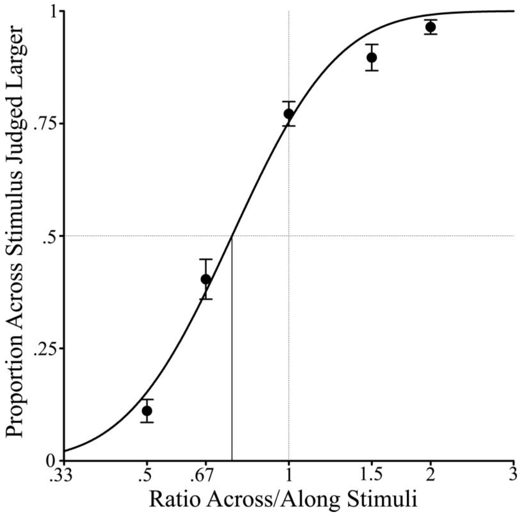

Figure 1. Results from Experiment 1. Error bars represent the standard error of the mean. Curves are cumulative Gaussian functions fit with least-squares regression. Vertical lines represent points of subjective equality (i.e., where the curve crosses 50%).

proximodistally. All 20 participants showed this bias, in that PSEs from every participant were less than 1 (range = .598–.949). Two participants were apparent outliers in terms of their IQRs. However, excluding these participants had no effect on the results, $t(17) = -11.85$, $p < .0001$.

These results demonstrate a clear bias for tactile distances to be perceived as larger when oriented mediolaterally, across the dorsum of the hand, than proximodistally, along the hand. This suggests that the aspect ratio of the hand (i.e., the ratio of width to length) is systematically larger in the body model mediating touch than on the actual hand (i.e., the hand is represented as being wider than it actually is). These results are consistent with findings of similar anisotropy on the forearm (Wong et al., 1974; Green, 1982), but contrast with previous failures to find anisotropy on the hand (Green, 1982; Cholewiak, 1999). One potential explanation of these results is that the two latter studies investigated touch on the glabrous skin of the palm of the hand, which may be represented very differently from the dorsum. To investigate this possibility, we conducted a second experiment directly comparing performance on the dorsum and the palm.

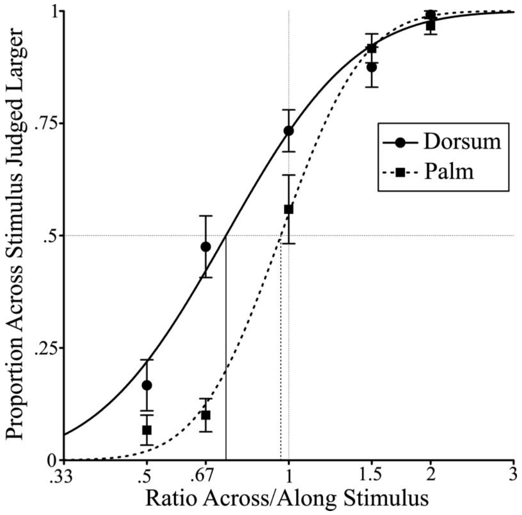

Figure 2. Results from Experiment 2. Error bars represent the standard error of the mean. Curves are cumulative Gaussian functions fit with least-squares regression. Vertical lines represent points of subjective equality.

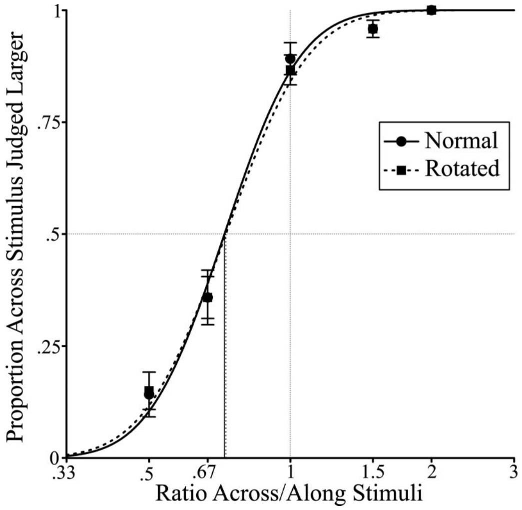

Figure 3. Results from Experiment 3. Error bars represent the standard error of the mean. Curves are cumulative Gaussian functions fit with least-squares regression. Vertical lines represent points of subjective equality

Experiment 2: Comparison of Dorsum Versus Palm

Method

Participants. Twelve volunteers (9 female) between 18 and 30 years of age participated. Participants were generally right-handed, as assessed by the Edinburgh Inventory (M = 43.0, range = −79.0–100), and reported no known abnormalities of touch perception and normal or corrected-to-normal vision. They gave written informed consent and were paid for their participation.

Materials. Stimuli were similar to Experiment 1 but were made of wooden posts, which were found to be more comfortable for the participant. As with the metal posts used in Experiment 1, the stimuli tapered to a point but were not sharp.

Procedure. Procedures were identical to Experiment 1, except that stimuli were delivered to the dorsum or the palm of the left hand in separate blocks. Each block consisted of 50 trials, 10 of each stimulus pair. The order of along and across stimuli was counterbalanced within each stimulus pair, the order of trials was randomized, and the order of blocks was counterbalanced across participants.

Results and Discussion

Two participants showed extremely low R-squared values in the dorsum condition (.189 and .344), and so were excluded from subsequent analyses. For the remaining 10 participants, the average R-squared for the dorsum condition was .946 (range = .773–1) and for the palm condition was .989 (range = .949–1), indicating good fit to the data. IQRs were significantly lower for stimuli presented on the palm (.159) than on the dorsum (.326), $t(9) = 2.68$, $p < .05$, indicating, unsurprisingly, that sensitivity was better on the palm.

As in Experiment 1, PSEs for stimuli presented on the dorsum were again significantly less than 1 for all participants ($M = 0.739$, range = .624–.892), $t(9) = -9.43$, $p < .0001$ (see Figure 2), again indicating a bias for the hand to be represented as wider than it actually is. Also as in Experiment 1, all participants showed this bias (i.e., had PSEs less than 1). Further, the magnitude of bias was similar in the two experiments. In contrast, no such bias was observed for stimuli delivered to the palm ($M = 0.967$, range = .849–1.225), $t(9) = -0.72$, *n.s.* There was significantly less bias on the palm than on the dorsum, $t(9) = -4.11$, $p < .005$. Although there was slight overlap of the ranges of PSEs on the dorsum and palm, all participants had smaller PSEs on the dorsum than on the palm.

These results replicate the anisotropy on the hand dorsum found in Experiment 1 and reveal a dramatic dissociation between the representation of the dorsum and the palm. The hairy skin of the hand dorsum is represented as being substantially wider than it actually is (this study), like the hairy skin of the forearm (Wong et al., 1974; Green, 1982), whereas no anisotropy is apparent on the palm (Green, 1982; Cholewiak, 1999; this study).

We have interpreted the biases in Experiments 1 and 2 as reflecting a bias in perception depending on stimulus orientation on the hand surface. However, in Experiments 1 and 2 the participant's hand was always in the same posture, with fingers pointing away from the body. Thus, orientation on the hand was confounded with orientation relative to the torso and the eyes. Could the biases we have found reflect biases in torso- or eye-centered reference frames? The absence of anisotropy on the palm argues against this hypothesis, because biases in torso- or eye-centered coordinates ought to have affected performance in that condition as well as on the dorsum. Nevertheless, to conclusively rule out this possibility, we conducted a third experiment in which the posture of the stimulated hand was rotated relative to the rest of the body, decoupling orientation on the hand from orientation in other coordinate reference frames.

Experiment 3: Reference Frame of Biases

Method

Participants. Fourteen volunteers (10 female) between 18 and 28 years of age participated. Participants were all right-handed, as assessed by the Edinburgh Inventory (Oldfield, 1971, $M = 79.3$, range = 33.3–100), and reported no known abnormalities of touch perception and normal or corrected-to-normal vision. They gave written informed consent and were paid for their participation.

Materials. Materials were identical to Experiment 2 materials.

Procedure. Procedures were similar to Experiment 1, except that the participant's left hand was positioned on the table with the fingers pointing either straight ahead (normal posture condition), as in Experiments 1 and 2, or with the hand rotated 90° relative to the body with the fingers pointing to the right (rotated posture condition). The rotation of the arm involved movements of the shoulder and elbow joints, but left the wrist in a similar relaxed position as the normal posture. The two postures were tested in separate blocks of 50 trials each, 10 trials of each stimulus pair. The order of along and across stimuli was counterbalanced within each stimulus pair, the order of trials was randomized, and the order of blocks was counterbalanced across participants.

One additional change was that rather than indicating whether the along or the across stimulus was larger, as in Experiments 1 and 2, participants were simply asked to judge whether the first or the second stimulus was larger. This change reduces the likelihood that any biases observed in the first two experiments might have been due to response bias, rather than perceptual bias.

Results and Discussion

R-squared values were similar in the normal ($M = .982$, range = .936–1) and rotated ($M = .969$, range = .913–.999) postures. IQRs were similar in the normal ($M = .155$; range = .037–.433) and rotated ($M = .171$; range = .043–.295) postures, $t(11) = .651$.

PSEs were significantly less than 1 for all participants in both the normal ($M = .719$, range = .510–.928), $t(11) = -8.42$, $p < .0001$, and rotated postures ($M = .729$, range = .596–.921), $t(11) = -10.03$, $p < .0001$, which did not differ significantly, $t(11)$, $-.36$, *n.s* (see Figure 3). These biases, furthermore, were significantly correlated across participants, $r(11) = .531$, $p < .05$ (one-tailed). That is, it is the orientation of stimuli *on the hand* that is driving the effect, not the orientation in egocentric (i.e., eye- or torso-centered) space. This suggests that this effect reflects a bias in the implicit representation of hand shape, rather than a bias in the representation of egocentric space in general or any kind of foreshortening of visual imagery.

Furthermore, given that participants in this experiment judged whether the first or second stimulus was larger, the results of this experiment suggest that the effects in the first two experiments do not reflect any simple response bias. Although this does not definitively rule out all forms of response bias (cf. Schneider & Bavelier, 2003; Spence & Parise, 2010), it does control for any simple, first-order bias to preferentially respond 'across.'

These results demonstrate that the biases we observed in Experiments 1 and 2 reflect anisotropy in tactile size perception on the surface of the hand dorsum, rather than torso- or eye-centered reference frames[1].

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[1] One potential concern about all the experiments reported here relates to experimenter bias. As the experimenter was not naïve to the experimental hypotheses, subtle differences in stimulus strength or duration could conceivably have influenced the present findings. As one part of a separate study, we collected data using a paradigm identical to Experiment 3. For that dataset, the experimenter was unaware of the experimental hypotheses. Data from those 10 participants revealed a clear anisotropy ($M = .681$, range = .307–.996), $t(9) = -3.96$, $p < .005$. This suggests that the results in the present dataset are unlikely to be due to experimenter bias.

Between-Experiment Analysis of Sex

Given known sex differences in tactile sensitivity (e.g., Peters, Hackeman, & Goldreich, 2009) and susceptibility to body image distortions (e.g., Mohr, Porter, & Benton, 2007), we ran an additional analysis to investigate potential sex differences in our results. Females predominated in our sample, making analysis of potential sex differences difficult in each experiment analyzed individually. However, given that similar PSE effects were found in all three experiments on the dorsum, we conducted a further analysis collapsing the dorsum condition of each experiment (normal posture condition of Experiment 3). PSEs were significantly lower than 1 for both males ($M = .736$, range = .624–.850), $t(7) = -11.05$, $p < .0001$, and females ($M = .744$, range = .510–.949), $t(33) = -14.04$, $p < .0001$. There was no hint of any sex difference in the magnitude of this anisotropy, $t(36) = .32$, *n.s.*

General Discussion

Objects touching the dorsum of the hand are perceived as approximately 30%-40% larger when they are oriented mediolaterally (across the hand) than proximodistally (along the hand). This bias was observed in all participants tested (Experiments 1–3), was not observed on the palm (Experiment 2), and was independent of the orientation of the hand relative to the body (Experiment 3). Intriguingly, this bias mirrors the known anisotropies in tactile acuity on the dorsum (Weber, 1834/1996; Cody et al., 2008) and in the shape of tactile RFs (e.g., Powell & Mountcastle, 1959; Brooks et al., 1961; Brown et al., 1975), suggesting that the present results, like the classic Weber's illusion between two skin surfaces, reflect distortions characteristic of primary somatosensory representations.

As we have argued elsewhere (Taylor-Clarke et al., 2004; Longo et al., 2010), accurate tactile size perception requires referencing to a mental body model specifying the true proportions of body parts. Indeed, changes in the perceived size of body parts alter tactile size perception (Taylor-Clarke et al., 2004; de Vignemont et al., 2005; Berryman et al., 2006). Nevertheless, the magnitude of the illusion is far less than would be expected on the basis of the variation in acuity across skin regions: Taylor-Clarke et al. (2004) estimated that Weber's illusion is just 10% of what would be predicted from differences in tactile acuity alone. The lack of quantitative data on the exact proportions of tactile RFs, especially on the hairy skin and in humans, makes it difficult to compare the magnitude of the present illusion to the magnitude of anisotropies in RF geometry. Nevertheless, some evidence suggests that the long axis of RFs on the hairy skin of the limbs may be more than twice as long as the short axis (e.g., Brown et al., 1975). This would suggest that the present illusion, like the classical form of Weber's illusion, is substantially smaller than would be expected on the basis of sensitivity, cortical magnification, or RF geometry alone. These observations suggest two main points. First, the fact that the illusion is markedly attenuated relative to differences in acuity and cortical magnification suggests a process of *tactile size constancy* that corrects for these distortions (cf. Taylor-Clarke et al., 2004). Second, the fact that some residual illusion nevertheless exists suggests that the body model mediating touch either inherits (in attenuated form) distortions characteristic of the somatosensory homunculus or compensates for such distortions only incompletely.

Several somatosensory processes besides tactile size perception also require referencing to stored representations of body size and shape (Longo et al., 2010). We recently investigated the body representation underlying position sense of the hand (Longo & Haggard, 2010), finding large distortions of the size and shape of the hand, consistent with those found in the present study for tactile size perception. Specifically, the representation of the hand dorsum underlying position sense was found to be substantially wider than it really is, and the length of the fingers was represented as being shorter than they really are. That similar distortions of hand shape appear to characterize the body representations underlying both position sense (Longo & Haggard, 2010) and tactile size perception (this study) suggests that these perceptual abilities may be mediated by a common implicit representation of body size and shape. In contrast, participants showed highly accurate conscious knowledge of what their hands are like in a 'template matching' (cf. Gandevia & Phegan, 1999) task in which they selected from an array of hand images the one most similar in shape to their own hand (Longo & Haggard, 2010). This suggests that the distorted hand representation underlying position sense (Longo & Haggard, 2010) and tactile size perception (this study) are distinct from the conscious body image.

There are two basic possibilities regarding how illusions such as the classic Weber illusion and the present effect could arise from such a body model. First, the initial tactile percept might be fully subject to the characteristic distortions of the sensory homunculus. This initial representation would then be interpreted with reference to an essentially veridical model of the body by a rescaling process. If the gain on this rescaling process were too low, it would result in systematic *underconstancy* of size for touch, as found in Weber's illusion experiments. A second, alternative model rejects the idea of initial distortion and subsequent veridical representation, suggesting that afferent inputs are coded within a body model that retains homuncular distortions, but in attenuated form. Neither the present data nor previous studies of the classic Weber illusion directly contradict either model, but several considerations favor the second model. Whereas the first model posits two distinct representations of the size of a single tactile object, the second model is simpler in positing only one; indeed, we know of no evidence for two such distinct size representations. Further, the first model implies that there is an initial, uncorrected, percept of tactile size based entirely on homuncular proportions. It is unclear, however, how any representation of tactile size could arise before referencing to a body model, because in some sense *any* percept of tactile size presupposes referencing to a body model. Lastly, the paradigm we recently used to investigate the body model mediating position sense, which provides a more direct measure of hand shape, found a similar pattern of distortions (Longo & Haggard, 2010), further suggesting that the present effects arise from a distorted representation of hand shape.

Thus, we suggest that the evidence favors the second model that the body model mediating touch retains some minor degree of homuncular distortion, though this remains an important topic for future research. On this second interpretation, the classic form of Weber's illusion provides evidence for distortions in the relative *size* of skin surfaces in the implicit body model mediating touch. Our present results now provide evidence for analogous distortions in the *shape* of the body in this model. Specifically, the dorsum of the hand (though not the palm) appears to be represented as substantially wider and squatter than it actually is. Our data allow us to calculate an aspect ratio for different skin regions within the body representation. The aspect ratio of the palm representation appears to be approximately veridical, whereas that of the dorsum shows a 30%-40% extension of width relative to length. Thus, the mental model of the overall body does not appear to be a coherent representation of the body as a volumetric object in the physical world, but a potentially fragmented and inconsistent representation of individual skin surfaces.

What causes the underlying distortion producing Weber's illusion? Weber (1834/1996) related the effect to the density of peripheral receptors. However, several other aspects of somatosensation are very tightly correlated with receptor density, such as RF size, tactile acuity, and cortical magnification. Separating the respective contributions of each of these factors is difficult, given their systematic interrelations. Importantly, however, the finding of anisotropy provides a means of addressing this issue. Both peripheral receptor density and cortical magnification are fundamentally *areal* measures, which cannot, by definition, be anisotropic. Receptor density is defined as the number of receptors per unit *area* in the skin and cannot be different in the proximodistal and mediolateral axes, because every receptor has a position along both axes. Potentially, the arrangement (rather than density, as such) of peripheral receptors could produce anisotropy, for example, if receptors were arranged in a grid, with the intercolumn spacing being smaller in one orientation than the other (cf. Gibson & Craig, 2005). Existing data on mechanoreceptors in the hairy skin of humans, however, have not revealed any such patterns (Vallbo, Olausson, Wessberg, & Kakuda, 1995). Similarly, cortical magnification is defined as the relative *area* of cortex responsive to touches on a given area of skin. Cortical magnification can only be considered with respect to an *area* of skin, and not to a particular axis of or orientation on the skin.

In contrast, the *geometry* of tactile RFs can be—and is—anisotropic. The pattern of anisotropy of RFs on the hand, furthermore, mirrors the anisotropy in size judgments observed in this study. To recap, RFs on the hairy skin of the limbs are generally oval-shaped, with the long axis running proximodistally, both in the spinal cord (e.g., Brown et al., 1975) and in SI (e.g., Brown et al., 1975; Alloway et al., 1989). Those on the glabrous skin are generally both smaller and more circular (Powell & Mountcastle, 1959). Moreover, when RFs on glabrous skin are elongated, the orientation of the long axis tends to be distributed uniformly in all directions (DiCarlo et al., 1998; Vega-Bermudez & Johnson, 1999; DiCarlo & Johnson, 2002). This suggests that Weber's illusion between different orientations on a single skin surface may arise as a consequence of RF geometry: the size of objects touching the skin would be inversely proportional to the size of RFs along the orientation of the stimulus. Indeed, the key information for computing tactile distance may be the number of RFs between the two stimulated locations. Importantly, this account also provides a natural explanation for the classical Weber's illusion between two different skin surfaces, because RF size is inversely correlated with tactile acuity (Brown, Koerber, & Millecchia, 2004).

Wheat and Goodwin (2000), discussing the role of receptor *location* in tactile perception, point out that there are two basic strategies that the somatosensory system could adopt in interpreting peripheral input: it could maintain a stored representation of the absolute location of receptors, or it could assume a uniform distribution of receptor locations in the skin. In their computational model, similar sensitivity was found on either assumption. There is an exact analogy regarding RF *geometry*. As with absolute location on the skin, no afferent signal specifies RF size and shape. The somatosensory system, then, could either maintain a representation of true RF dimensions (though it is unclear how such a representation would arise), or it could assume uniformity of RF geometry. Such an assumption of uniformity would produce perceptual distortions of exactly the sort observed as a function of body part (in the classic form of Weber's illusion) and of orientation (in the present study). This process is shown in Figure 4. If RF dimensions are incorrectly represented as uniform, objects touching skin surfaces with smaller RFs (e.g., the glabrous skin of the palm) would be interpreted as systematically oversized relative to identical objects touching skin surfaces with larger RFs (e.g., the forehead), as in Figure 4A, producing the classic form of Weber's illusion. Moreover, objects touching skin surfaces with anisotropic RF geometries would be interpreted as systematically distorted, stretched along the minor axis of the RFs, see Figure 4B, producing the orientational Weber's illusion reported here.

Thus, we suggest that RF geometry may play a fundamental role in the construction of the implicit body model mediating tactile size and shape perception. Essentially, the body model would be composed of individual 'pixels,' each corresponding to a RF location on the skin. Crucially, the pixels would be represented as isotropic forms (e.g., circles), even though the RFs might have anisotropic shapes (e.g., ovals). Tactile distance judgments, then, would be determined by essentially 'counting' the number of RFs between the stimulated RFs, without regard to their shape. Because more RFs intervene in a given tactile distance in a mediolateral

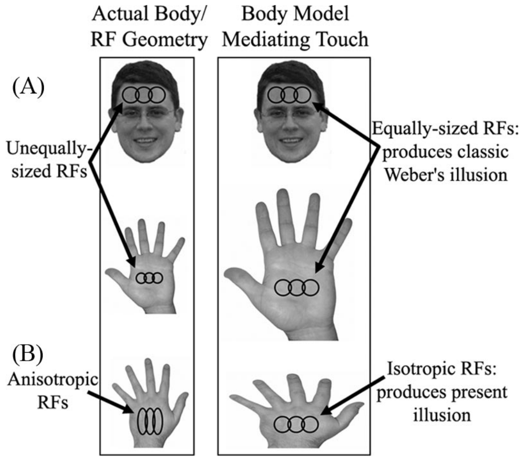

Figure 4. Schematic representation of 'pixel' model of how RF geometry could shape the body model used for tactile size/distance perception. RFs varying in size and shape are interpreted as if they were equally sized and roughly circular. In the case of RFs that differ in actual size, such as those on the palm of the hand and on the forehead (A), this would result in a relative increase in the size of the palm in the body model mediating touch, which would produce the classic form of Weber's illusion (i.e., identical touches are perceived as larger on the palm than on the forehead). In the case of RFs that are elongated along one axis, such as on the dorsum of the hand (B), this would result in stretching of the dorsum along the mediolateral axis in the body model mediating touch. This would produce the orientation-dependent illusion reported here.

direction than in a distal-proximal orientation, mediolateral distances appear correspondingly larger.

This view suggests a strong linkage between early somatosensory representations and more abstract cognitive models of the body itself. It therefore differs from alternative models in which cognitive body models arise primarily from nonsomatosensory signals, such as vision (e.g., Brugger et al., 2000). Intriguingly, this hypothesis of pixelated representation based on RFs bears a striking resemblance to the finding of so-called *segregates*: regions of cortex in which RFs, though varying widely in size and shape, are all nonetheless centered on a single skin area, producing a 'mosaic' representation of the body surface (Favorov, Diamond, & Whitsel, 1987).

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Received November 19, 2009
Revision received August 11, 2010
Accepted September 2, 2010 ■