Tactile distance illusions reflect a coherent stretch of tactile space

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Illusions of the perception of distance between two touches on the skin have been described since the classic work of Weber in the 19th century. The perceptual mechanisms underlying such spatial distortions, however, remain poorly understood. One potential interpretation is that the representational space of touch is related to the true structure of the skin by a geometrically simple stretch. If distortions of tactile distance perception reflect a simple stretch of tactile space, perceived distance should vary predictably as a function of the orientation of the stimulus on the skin, showing a sinusoidal pattern. Here, we tested this prediction by obtained judgments of perceived tactile distance for pairs of touches aligned with eight orientations on the skin. Across four experiments, the results were highly consistent with this prediction, showing no apparent deviation from a model of simple stretch of tactile space. Similar results were apparent on both the dorsum and palm of the hand, as well as the forehead. These results show that spatial distortions of touch are well characterized by a geometrically simple stretch of tactile space.

touch | anisotropy | tactile distance | size perception | somatosensation

The ability to perceive the spatial properties of objects through touch is a fundamental aspect of perception. Since the classic studies of Weber in the 19th century, the perception of tactile distance has been widely used to investigate the somatosensory system (1, 2). The mechanisms underlying tactile distance perception nevertheless remain poorly understood. Recent results have shown that the distance between two touches is an attribute susceptible to sensory adaptation (3), suggesting that it is a basic feature coded at relatively early stages of somatosensory processing. There is also evidence, however, that tactile perception of size and distance is modulated both from the bottom-up by basic features of somatosensory organization such as cortical magnification (1, 4–7) and receptive field (RF) geometry (2, 8), and from the top-down by factors such as illusions of body part size (5, 9–13) and tool use (14–17).

One important source of information about the mechanisms underlying tactile distance perception comes from spatial distortions in perceived distance. Weber (1), for example, found that as he moved the two points of a compass across his skin, the perceived distance between them changed. The distance felt larger on more sensitive skin surfaces (e.g., the palm) and smaller on less sensitive surfaces (e.g., the forearm), an effect known as Weber's illusion. Subsequent studies have confirmed Weber's observations and found a consistent relation between perceived tactile distance and the spatial sensitivity of skin surfaces (4–7). This pattern suggests that distortions of early somatosensory cortex, such as the well-known Penfield homunculus (18), are preserved in higher-level aspects of tactile perception. Similar perceptual distortions can also be found within a single skin surface as a function of stimulus orientation, with tactile distances in general feeling larger when oriented with the mediolateral body axis than the proximodistal axis (2, 8, 15, 19–22). For example, using a two-alternative forced-choice paradigm, Longo and Haggard (8) found that tactile distances oriented across the width of the hand dorsum were perceived as ∼40% larger than those oriented along the length of the hand. Importantly, this bias parallels the fact that tactile spatial sensitivity is also higher in the mediolateral axis (1, 23–26) and that the RFs of tactile neurons are commonly oval shaped with the long axis aligned with the proximodistal body axis (27–30).

To account for this overall pattern of distortions, we developed a "pixel model," which proposes that tactile space is comprised of a 2D grid, with the RFs in a somatotopic map forming the "pixels" of the grid (8, 31). Evidence for such a grid-like representation comes from studies showing that magnification (i.e., the number of neurons representing an area of skin) and RF size are inversely related so as to preserve a constant degree of overlap between the RFs of adjacent neurons (32). Calculation of distance would rely on a process of counting the number of RFs between two stimulated locations. Because neurons representing highly sensitive skin surfaces have smaller RFs than those representing less sensitive surfaces (27, 32), the activation peaks produced by any given tactile distance will be separated by more RFs on a sensitive than a less sensitive skin surface, consistent with Weber's illusion. Analogously, since tactile RFs are usually oval shaped and elongated in the proximodistal limb axis (27–30), tactile distances oriented across the limb will cover more RFs than the same distance oriented along the length of the limb, consistent with the anisotropies described above (2, 8).

While the pixel model is described in terms of underlying neural mechanisms, it also makes clear predictions at the purely perceptual level. A key prediction of the model is that perceptual distortions should be geometrically coherent in the sense that the layout of tactile space should be related to the actual layout of skin by simple deformations, such as stretch or compression.

Significance

Spatial illusions, such as the classic horizontal–vertical illusion, have played a major role in theories of visual organization. Although analogous illusions in touch have been known since the 19th century, they have been much less studied, and there is no general theory of their mechanistic basis. We developed and tested a model of tactile distance illusions in terms of a geometrically simple stretch of tactile space. We demonstrate that the pattern of perceived tactile distances across orientations is consistent with the model's predictions. Similar results were apparent on the hand dorsum, palm, and forehead, suggesting it is a general characteristic of tactile spatial perception. These results show that tactile distance illusions reflect a geometrically simple deformation of tactile space.

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Where RFs differ in size, there should be magnification of the skin surface with smaller RFs (or, equivalently, compression of the surface with larger RFs). Where RFs are oval shaped, there should be stretch along the short axis of the RFs.

Previous studies describing anisotropies in tactile distance perception have compared stimuli oriented with the mediolateral body axis to stimuli oriented with the proximodistal axis (2, 8, 19, 20). A critical test of the pixel model, however, concerns stimuli at intermediate orientations. If distortions of perceived tactile distance reflect a geometrically coherent stretch of tactile space, perceived distance should vary systematically as a function of the cosine of the angle between the actual stimulus orientation and the axis along which tactile space is stretched, as depicted in Fig. 1. The psychophysical function relating judgments of tactile distance to stimulus orientation on the skin should thus be characterized by a sinusoidal function. The amplitude of the sinusoid should reflect the magnitude of the stretch of tactile space. The phase of the sinusoid should reflect the direction along which tactile space is stretched (i.e., the peak of the sinusoid should be directly aligned with the axis of stretch).

In this study, we tested the prediction of the pixel model that perceived tactile distance should show vary in a sinusoidal relation as a function of stimulus orientation on the skin. Pairs of simultaneous touches were applied in eight orientations on the skin, and participants made verbal estimates of the perceived distance between the two touches. Consistent with previous findings, there were clear biases to perceive distances oriented across the width of the body as bigger than those oriented along the length of the body. Critically, the perceived distance of stimuli at intermediate orientations was well characterized by a sinusoidal function, consistent with the predictions of the pixel model.

Results

Experiment 1: Spatial Distortions on the Hand Dorsum Are Well Characterized by Simple Stretch. In experiment (Exp.) 1, we investigated the perceived distance between pairs of tactile stimuli applied at different orientations on the hairy skin of the dorsum of the left hand (Fig. 2*A*). Stimuli were pairs of wooden posts mounted in foam board and separated by 2, 2.5, 3, 3.5, or 4 cm,

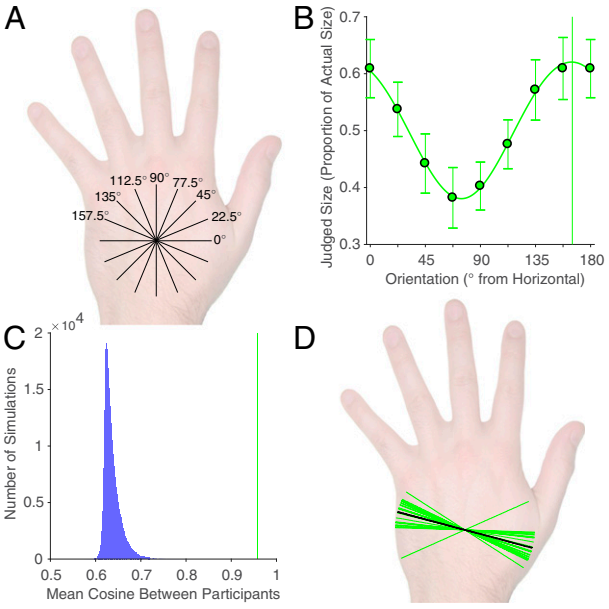

Fig. 2. (*A*) The eight stimulus orientations used in the study. (*B*) Results from Exp. 1 showing judged size as a function of stimulus orientation. The dashed green curve shows the best-fitting sinusoid. The data were fit well by this function. The vertical green line indicates the peak of the sinusoid, reflecting the orientation at which tactile distances were judged as largest (i.e., the axis in which tactile space is stretched). Error bars indicate one SE. For illustrative purposes, the same data point is shown as both 0° and 180°, although it was only included once in analyses. (*C*) Phase alignment of best-fitting curves. The green vertical line indicates the mean cosine of the angular deviation between each pair of the 25 participants. The blue histogram shows the same mean calculated for each of 1 million simulations of random data. The green vertical line was larger than any of the simulations, indicating that the phase alignment in the data was greater than would be expected by chance. (*D*) The axis of stretch. Each green line indicates the orientation of maximal stretch for a single participant. The black line indicates the average axis across participants.

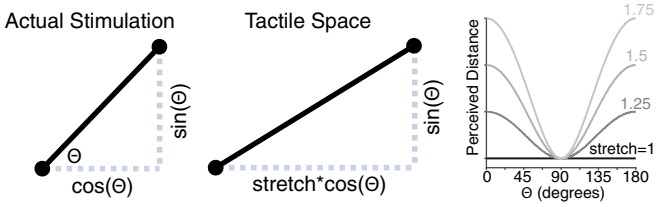

Fig. 1. The effect of stretch of tactile space on perceived tactile distance depends on stimulus orientation. (*Left*) Actual stimulation on the skin. The black barbell represents a pair of touches separated by unit length on the skin oriented at angle Θ with respect to the mediolateral body axis. The stimulus can be thought of as consisting of components with respect to the mediolateral axis [i.e., cos (Θ)] and the proximodistal axis [i.e., sin(Θ)]. The actual distance between the two points can be reconstructed from these components using the Pythagorean theorem. (*Center*) Mental representation of the stimulation in a stretched tactile space. A simple stretch of the mediolateral axis will affect the cosine component of the stimulus, but not the sine component. The stretch will thus lead to an increase in perceived distance in proportion to the cosine of the angle of the stimulus from the axis of stretch (in this case the mediolateral axis). (*Right*) Examples of how perceived distance should change as a function of stimulus orientation for four different values of the stretch parameter. For any combination of the stretch parameter and stimulus orientation (Θ), a prediction can be made about perceived distance. When stretch equals 1, there is no distortion and perceived distance is constant across orientations. As the stretch parameter increases, perceived distance varies sinusoidally with orientation, with the amplitude of the sinusoid increasing in proportion to the amount of stretch. Here, the stretch is assumed to be oriented with the mediolateral axis (0°); stretch in a different orientation would shift the phase of the sinusoid.

as in previous studies (3, 8, 15, 21). On each trial, a single tactile distance was applied at one of eight orientations (as shown in Fig. 2*A*). Participants made verbal estimates of the perceived distance between each pair of stimuli by giving a number in centimeters. The response on each trial was expressed as a proportion of actual stimulus size and averaged across the five stimulus sizes.

The results are shown in Fig. 2*B*. An ANOVA revealed that judgments differed systematically across orientations, $F(2.49, 59.79) = 25.98$, $P < 0.0001$, $\eta_p^2 = 0.52$. As in previous studies, there was a clear bias to judge stimuli oriented with the mediolateral hand axis as bigger than stimuli oriented with the proximodistal hand axis (2, 8). We measured the magnitude of this anisotropy by comparing the ratio of judgments in the mediolateral axis (0°) and the proximodistal axis (90°). The mean ratio was 1.53, significantly greater than 1, $t(24) = 8.71$, $P < 0.00001$, $d = 1.74$. (Note that for this and other tests involving ratios, the calculation of means and all statistical tests were conducted on log-transformed values, which were converted back to ratios to report mean values.)

The key question concerns what happens with intermediate stimuli, not directly aligned with the mediolateral or proximal-distal hand axes. As is clear from Fig. 2*B*, the pattern of judgments across orientations produced a clear sinusoidal pattern. We modeled this pattern by identifying the best-fitting sinusoid for each participant, using the function given in Eq. **1**. As described above in Fig. 1, we divided each stimulus into its components in the axis parallel to the stretch (i.e., the cosine component) and the axis perpendicular to the stretch (i.e., the

sine component). The predicted judgment is thus given by the Pythagorean theorem in terms of these two components with the stretch applied to the first component. We also included a third parameter, which added an overall offset to the entire function to model global underestimation or overestimation of tactile distance. Note that because judgments were expressed as a proportion of actual size, a veridical estimate, by definition, will have unit length.

$$\text{Predicted judgment} = \text{offset} + \sqrt{(\text{stretch} \times \cos(\Theta - \text{phase}))^2 + \sin(\Theta - \text{phase})^2}. \quad [1]$$

There are three parameters to this model. The stretch parameter controls the amplitude of the sinusoid, that is the amount by which judgments in the orientation parallel to the stretch differ from judgments in the perpendicular orientation. The phase parameter controls the orientation of the stretch by shifting the curve left-to-right. Finally, the offset parameter shifts the entire curve up and down to reflect any overall underestimation or overestimation of tactile distance.

The green curve in Fig. 2*B* shows the best-fitting sinusoid fit to the grand mean data, which showed extremely good fit (R^2 = 0.998). Data from individual participants was also well fit, with a mean R^2 of 0.759 (SD = 0.189, range: 0.345–0.983).

To investigate whether there was any systematic deviation from the model, we calculated the residuals (i.e., the difference between the observed and fitted values) for each participant at each orientation. A systematic deviation from the model should lead to the residuals being larger at some orientations than others. Critically, however, an ANOVA on the residuals revealed no effect of orientation, $F(4.21, 101.11) = 0.18$, not significant (*n.s.*), $\eta_p^2 = 0.01$. To determine whether this nonsignificant result provides evidential support for the null hypothesis of no actual difference, we conducted a Bayesian repeated measures ANOVA (33). The Bayes' factor associated with the effect of orientation, BF_{01} = 108.20, provided decisive evidence in favor of the null hypothesis. This provides strong evidence against there being a systematic deviation from the model.

The vertical green line in Fig. 2*B* indicates the axis of stretch (i.e., the peak of the sinusoid). To investigate the consistency of the axis of stretch across participants, we investigated the phase alignment of the best-fitting sinusoids in two ways. First, we applied the Rayleigh test, which tests the null hypothesis that a set of angles are uniformly distributed around the circle (34). The Rayleigh test provided clear evidence against the phases being randomly distributed, $z = 21.29$, $P < 0.00001$. Second, we quantified the similarity in phase between pairs of participants by calculating the cosine of the angle between them, a value that ranges between 1 (identical phase) and 0 (orthogonal phase). We calculated the mean cosine between the phases of the models for each of the 300 pairs of participants (vertical green line in Fig. 2*C*) with the values obtained in 1 million simulations of random data (blue histogram in Fig. 2*C*). The obtained mean value of these cosines was 0.958, which was larger than that obtained in any of the simulations ($P < 10^{-7}$).

Interestingly, the axis of stretch was not exactly aligned with the mediolateral hand axis as we had operationalized it, but was rotated on average 14.95° clockwise from this axis. A circular one-sample test for mean angle provided evidence for systematic deviation away from 0°, $P < 0.00001$.

Exp. 2: Distortions on the Palm Are also Well Characterized by Simple Stretch. Exp. 2 aimed to replicate these results and to investigate whether similar results would hold on the glabrous skin of the palm. Anisotropy for tactile distance perception is substantially smaller on the palm than on the dorsum (3, 8, 20, 21). We thus investigated whether this bias on the palm, even if smaller than on the dorsum, is also characterized by a coherent stretch of tactile space. Procedures were as in Exp. 1 except that in half the blocks, stimuli were applied to the dorsum and in half to the palm.

The results are shown in Fig. 3*A*. An ANOVA revealed a significant main effect of skin surface, $F(1, 24) = 5.10$, $P < 0.05$, $\eta_p^2 = 0.18$, with distances judged as larger on the palm than on the dorsum. This finding replicates the classic Weber illusion (1, 4, 5), given the greater sensitivity of the palm. There was also a significant main effect of orientation, $F(3.75, 90.09) = 16.39$, $P < 0.0001$, $\eta_p^2 = 0.41$, as well as an interaction, $F(4.14, 99.45) = 9.45$, $P < 0.0001$, $\eta_p^2 = 0.28$.

Separate ANOVAs conducted on each skin surface revealed clear effects of orientation, both on the dorsum, $F(3.84, 92.10) = 13.29$, $P < 0.0001$, $\eta_p^2 = 0.36$, and on the palm, $F(4.56, 109.34) = 12.81$, $P < 0.0001$, $\eta_p^2 = 0.35$. There was a clear bias to perceive stimuli oriented with the mediolateral axis as bigger than those oriented with the proximodistal axis, as ratios between stimuli at 0° and 90° were greater than 1 both on the dorsum ($M = 1.30$), $t(24) = 4.03$, $P < 0.0005$, $d = 0.81$, and on the palm ($M = 1.14$), $t(24) = 4.57$, $P = 0.0001$, $d = 0.91$. The magnitude of anisotropy was significantly greater on the dorsum than on the palm, $t(24) = 2.07$, $P < 0.05$, $d_z = 0.41$, consistent with previous findings (3, 8, 20, 21).

As is clear from Fig. 3*A*, the grand average data were very well fit by sinusoidal functions, both on the dorsum ($R^2 = 0.995$) and on the palm ($R^2 = 0.936$). Overall, there was also good fit to individual participant data both on the dorsum ($M = 0.671$, range: 0.014–0.911) and on the palm ($M = 0.628$, range: 0.142–0.919).

There was no significant effect of orientation on the magnitude of residuals on the dorsum, $F(3.43, 82.22) = 0.15$, *n.s.*, $\eta_p^2 = 0.01$, or on the palm, $F(3.98, 95.50) = 1.64$, *n.s.*, $\eta_p^2 = 0.06$. As in Exp. 1, the Bayes' factor for this effect on the dorsum, BF_{01} = 118.15, provided strong evidence in favor of the null hypothesis.

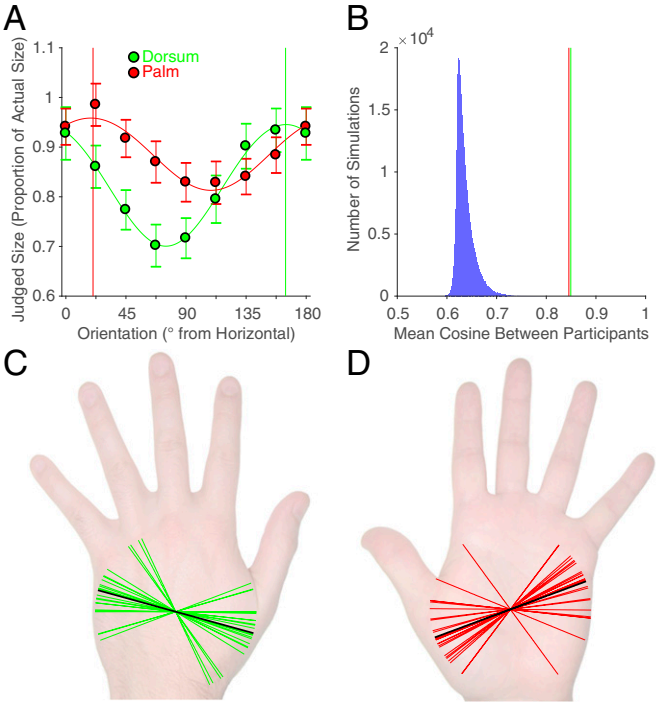

Fig. 3. (*A*) Results from Exp. 2 showing judged size as a function of stimulus orientation for the dorsum (green) and palm (red). Although anisotropy is smaller on the palm, judgments on both skin surfaces are well characterized by a sinusoidal function. (*B*) Phase alignment of best-fitting curves on the dorsum (green line) and palm (red line). Alignment on both surfaces was higher than in any of the simulations. (*C* and *D*) Axes of stretch for individual participants on the dorsum (*C*) and palm (*D*). The black lines indicate the average axis across participants.

The Bayes' factor on the palm, $BF_{01} = 2.66$, also provided some evidence in favor of the null hypothesis, although much less decisively than on the dorsum.

The Rayleigh test revealed clear evidence of phase-alignment across participants, both on the dorsum, $z = 13.40$, $P < 0.00001$, and on the palm, $z = 13.48$, $P < 0.00001$. The average value of the cosines between the phases of pairs of participants (vertical lines in Fig. 3*B*) was larger than that obtained in any of the one million simulations (blue histogram in Fig. 3*B*) both on the dorsum ($M = 0.849$) and the palm ($M = 0.846$; both P values $<10^{-7}$).

The lower images of Fig. 3 shows the orientation of the axis of maximal stretch for individual participants on the dorsum (Fig. 3*C*) and the palm (Fig. 3*D*). As in Exp. 1, the axis of maximal stretch deviated significantly from 0° as assessed by the circular one-sample test for mean angle, both on the dorsum ($M = -15.43°$), $P < 0.005$, and the palm ($M = 20.35°$), $P < 0.0005$. Visually, it looks like the direction of stretch is very different on the dorsum and palm. Note, however, that this results from the fact that the dorsum and palm are effectively mirror reflections of one another. On both surfaces, the axis of maximal stretch runs broadly from the base of the little finger to the base of the thumb.

Exp. 3: Stretch Is Defined in a Skin-Centered Reference Frame. At different times, we experience the location of touch in a skin-centered reference frame (e.g., "I feel an itch on my arm") or in an external reference frame (e.g., "I feel the table in front of me"). Transformations between these reference frames can occur within 200 ms of stimulus onset (35). In Exp. 3, we investigated whether stretch of tactile space is defined in a skin-centered or in an external reference frame by comparison of tactile distance judgments with the hand in two postures. In the normal posture, the stimulated left hand rested with the fingers pointing away from the participant, as in Exps. 1 and 2. In the rotated posture, the hand was turned 90° with the fingers pointing to the right. If the effects seen in the first two experiments are defined with respect to the skin, similar results should be found in both postures. If, in contrast, the effects are defined in a reference frame defined by the head, eyes, or torso, the effects should be phase-shifted by 90° in the rotated posture.

The results are shown in Fig. 4*A* and revealed highly similar results in the two postures. There was no main effect of hand posture, $F(1, 24) = 0.01$, *n.s.*, $\eta_p^2 = 0.00$, suggesting that overall perception of tactile distance was unaffected by hand posture. There was a clear effect of stimulus orientation, $F(4.21, 100.92) = 17.74$, $P < 0.0001$, $\eta_p^2 = 0.43$. There was also a modestly significant interaction between hand posture and orientation, $F(7, 168) = 2.16$, $P = 0.04$, $\eta_p^2 = 0.08$. Fig. 4*A* indicates that this interaction may reflect the magnitude of anisotropy being smaller in the normal than in the rotated posture. This could reflect tactile distance being calculated, at least partly, in an external frame of reference. However, it is also important to note that previous studies have found no evidence for a change in the magnitude of anisotropy with hand rotation (3, 8).

Separate ANOVAs conducted on each posture revealed clear effects of orientation both in the normal posture, $F(4.80, 115.28) = 9.88$, $P < 0.0001$, $\eta_p^2 = 0.29$, and the rotated posture, $F(7, 168) = 13.50$, $P < 0.0001$, $\eta_p^2 = 0.36$. Clear anisotropies were apparent in both postures comparing the ratios between stimuli at 0° and 90°, both in the normal posture ($M = 1.16$), $t(24) = 4.09$, $P < 0.0005$, $d = 0.82$, and the rotated posture ($M = 1.24$), $t(24) = 6.44$, $P < 0.0001$, $d = 1.29$. The magnitude of anisotropy on the two surfaces was correlated, $r(23) = 0.669$, $P < 0.0005$.

An ANOVA on the residuals revealed no effect of posture, $F(1, 24) = 0.01$, *n.s.*, $\eta_p^2 = 0.00$, orientation, $F(3.91, 93.88) = 0.65$, *n.s.*, $\eta_p^2 = 0.03$, nor an interaction, $F(4.17, 100.18) = 1.84$, *n.s.*, $\eta_p^2 = 0.07$. As in the previous experiments, the Bayes' factor associated with the effect of orientation, $BF_{01} = 72.68$, provided strong evidence again systematic deviations from the model.

The Rayleigh test revealed clear evidence for phase-alignment across participants, both in the normal posture, $z = 10.29$, $P < 0.0001$, and the rotated posture, $z = 15.24$, $P < 0.00001$. The

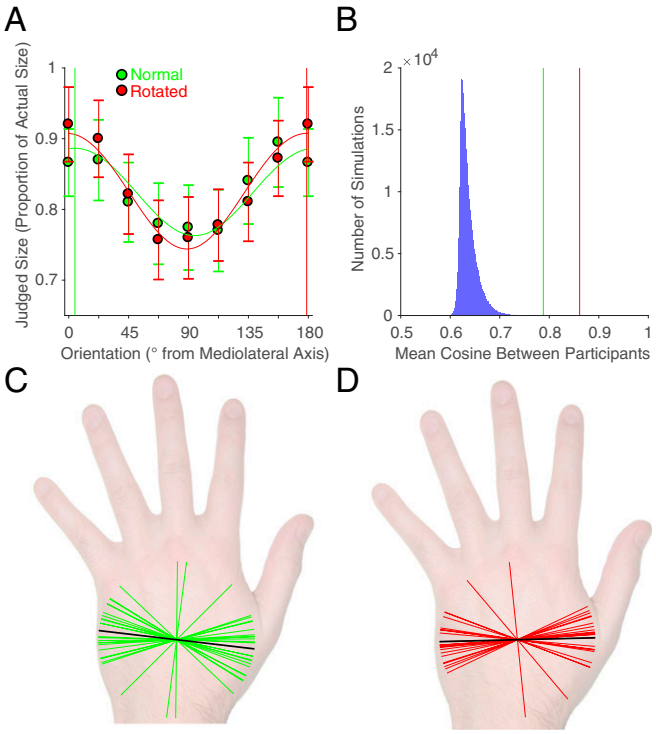

Fig. 4. (*A*) Results from Exp. 3 showing judged size as a function of stimulus orientation for the normal (green) and rotated (red) postures. Judgments in both orientations are well characterized by a sinusoidal function. (*B*) Phase alignment of best-fitting curves in the normal (green line) and rotated (red line) postures. Alignment in both postures was higher than the vast majority of the simulations. (*C* and *D*) Axes of stretch for individual participants in the normal (*C*) and rotated (*D*) postures. The black lines indicate the average axis across participants.

average value of the cosines between the phases of pairs of participants (vertical lines in Fig. 4*B*) was larger than that obtained in any of the 1 million simulations in the rotated posture ($M = 0.861$, $P < 10^{-7}$) and all but 20 in the normal posture ($M = 0.788$, $P = 0.00002$). The axis of maximal stretch (Fig. 4 *C* and *D*) was on average rotated clockwise from 0°, but this did not reach significance by a circular one-sample test on either the normal posture ($M = -6.71°$), *n.s.*, or the rotated posture ($M = 0.03°$), *n.s.*

Exp. 4: Distortions on the Forehead Are also Well Characterized by Simple Stretch. The preceding experiments all investigated the hands. In Exp. 4, we investigated whether the coherent stretch we have reported generalizes to other body parts. Recent results have revealed an anisotropy in tactile distance on the forehead, with tactile distance oriented across the width of the forehead perceived as larger than those oriented along the vertical axis (20). We thus tested whether this anisotropy reflects a coherent stretch of tactile space. Procedures were similar to Exp. 1 except that stimuli were applied on the forehead.

The results are shown in Fig. 5*A*, showing a clear sinusoidal pattern. There was a significant effect of orientation, $F(2.22, 53.26) = 39.58$, $P < 0.0001$, $\eta_p^2 = 0.62$. There was significant anisotropy comparing judgments of stimuli at 0° and 90°, ($M = 1.83$), $t(24) = 6.74$, $P < 0.0001$, $d = 1.35$. The grand-average data were fit extremely well by a sinusoid ($R^2 = 0.991$). Overall, there was good fit to individual participants' data as well ($M = 0.795$, range: 0.170–0.980).

An ANOVA on the residuals showed no significant effect of orientation, $F(3.42, 81.98) = 1.15$, *n.s.*, $\eta_p^2 = 0.05$. The Bayes' factor associated with this effect, $BF_{10} = 9.57$, provided evidence against there being systematic deviations from the model.

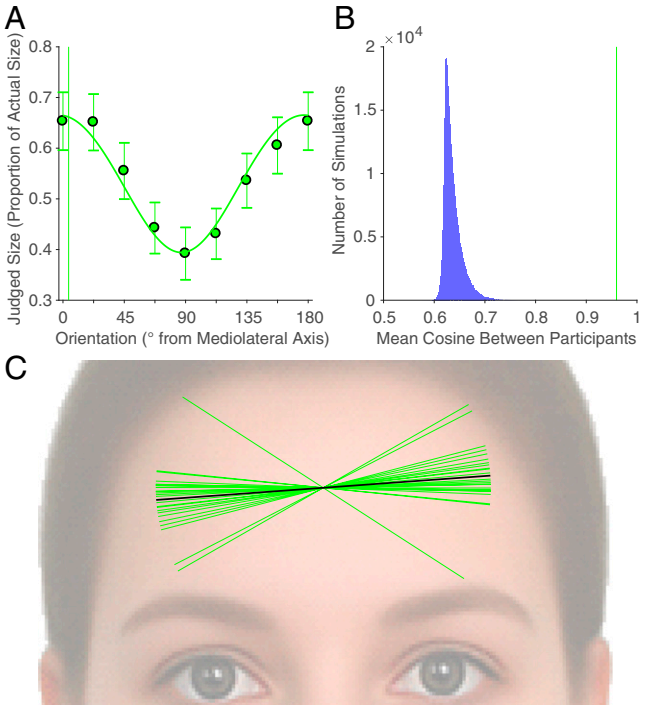

Fig. 5. (*A*) Results from Exp. 4 showing judged size as a function of stimulus orientation on the forehead. Judgments in both orientations were well characterized by a sinusoidal function. (*B*) Phase alignment of best-fitting curves (vertical green line). Alignment was higher than in any of the simulations. (*C*) Axes of stretch for individual participants. The black line indicates the average axis across participants.

The Rayleigh test revealed clear evidence of phase-alignment across participants, $z = 21.46$, $P < 0.00001$. Fig. 5*B* shows the mean cosine between the phases of pairs of participants (vertical line; $M = 0.960$), which was greater than that seen in any of the simulations, $P < 10^{-7}$. Fig. 5*C* shows the axes of maximal stretch for individual participants. On average, the axis of maximal stretch was rotated 4.01° counterclockwise from the mediolateral axis, which was not statistically significant as assessed by the circular one-sample test for mean angle.

Discussion

Spatial distortions in the perception of tactile distance have been known since the classic investigations of Weber (1) in the 19th century. The mechanisms producing these effects, however, remain poorly understood. The present results contribute to an understanding of these mechanisms by showing that the pattern of distortions across orientations is consistent with what would be expected if tactile space were related to the actual shape of the skin by simple stretches. We found consistent patterns on three different skin surfaces: the hand dorsum, palm, and forehead. Moreover, this pattern does not change when the stimulated skin surface is rotated in external space, indicating that the stretch is determined in a skin-centered reference frame.

These results are consistent with the predictions of the pixel model (8, 31), which proposes that tactile space consists of a 2D array in which individual RFs form the pixels. Since RFs representing sensitive skin surfaces are smaller than those representing less sensitive surfaces (32, 36), perceived tactile distances should be expanded on sensitive skin surfaces, consistent with Weber's illusion. Since RFs representing the limbs are typically oval shaped with the long axis aligned with the proximodistal limb axis (27–30), perceived tactile distances should be expanded when oriented across the width of the limbs, consistent with reported anisotropies (2, 8). In both cases, perceptual distortions should be characterized by geometrically coherent stretches of tactile space. These results are consistent with this prediction.

Anisotropies in tactile distance perception (2, 8) have some analogy to anisotropies in visual size perception, such as the well-known "horizontal-vertical" illusion (37, 38) in which vertical lines are perceived as longer than horizontal ones. The canonical form of the illusion, with an inverted "T" shape, is known to reflect both an orientational anisotropy and a bias for bisected line segments to appear shorter (37–39). Intriguingly, the orientational anisotropy in vision does not appear to be consistent with a coherent stretch of visual space. Specifically, lines appear longest not when exactly vertical, but when oriented ∼20–30° in either direction from vertical (40–43). This pattern, with two separate peaks, is inconsistent with the sinusoidal pattern predicted by a simple stretch of visual space. Thus, despite their superficial similarity, tactile distance anisotropies and the visual horizontal-vertical illusion appear to result from qualitatively different underlying mechanisms. Spatial distortions in touch, unlike those in vision, appear consistent with simple stretches of perceptual space.

In previous studies, which compared perceived tactile distance in just two orientations (2, 8, 19–21), the specific orientations chosen were based on operational definitions of the mediolateral and proximodistal limb axes. Similar operational definitions were used in the present study to assign numerical labels to each orientation. However, the phase of the best-fitting sinusoids could vary continuously, giving a data-driven estimate of the actual axis along which tactile space is stretched. While clear anisotropy was apparent comparing stimuli in the orientations we labeled "mediolateral" and "proximodistal," stimuli were in fact judged as largest which rotated slightly from the mediolateral axis. Specifically, the axis of maximal stretch was aligned approximately with a line connecting the bases of the little finger and thumb. Although unexpected, this result may provide a potential clue to the mechanisms underlying these effects. Given that the alignment of stretch is along the axis in which the fingers are individuated, it is possible that spatial distortions in touch may function to increase the perceptual distinctiveness of the digits, a form of categorical perception. It is also interesting to note that opposable movements of the thumb in precision grips involve rotation of the thumb broadly along this same axis (44). However, the fact that similar anisotropy is also apparent on the forehead suggests that more general mechanisms may also be involved.

In addition to the distortions of tactile distance perception, which motivated the present study, spatial distortions have also been reported for several other aspects of bodily perception, including position sense (45), tactile localization of stimuli in space (46), and even the subjective body image (47, 48). It is notable that in each of these cases, the general bias is to overestimate distances in the mediolateral body axis, relative to the proximodistal axis. It is an intriguing possibility that the distorted perceptual map of tactile space we describe here may have broad effects on a range of somatosensory abilities, and even on our conscious experience of our own body.

Our study shows that spatial distortions in the perception of tactile distance are well characterized by geometrically simple deformations. In his classic work, Thompson (49) argued that many differences between the size and shape of biological organisms could be described by geometrically simple transformations. The present results provide a psychological analog to this idea. We show that the mental representation of the skin appears to reflect a geometrically simple transformation of the actual structure of the skin.

Methods

Participants. One hundred members of the Birkbeck community participated after giving written informed consent, 25 in each of the four experiments (*SI Methods*). Procedures were approved by the Birkbeck Department of Psychological Sciences Research Ethics Committee and were in accordance with the principles of the Declaration of Helsinki.

Exp. 1: Hand Dorsum. In Exp. 1, a set of eight lines was marked with a pen on the dorsum of the participant's left hand using a plastic stencil, as shown in

Fig. 2*A*. The orientation marked 90° was drawn along the line connecting the center of the participant's wrist to the knuckle of their middle finger. The other lines were spaced at intervals of 22.5°, forming a compass rose indicating different orientations on the hand. The point of intersection of the lines was approximately in the center of the dorsum. Participants were not allowed to see the lines on their hand until after the experiment and were not told what the configuration of marks was that would be drawn on their hand. They were blindfolded during the experiment.

Stimuli were pairs of wooden posts mounted in foamboard and separated by 20, 25, 30, 35, or 40 mm, similar to those used in previous experiments in our laboratory (8, 15, 19–21). Each post tapered to a point ∼1 mm in diameter. On each trial, one tactile distance was applied to the participant's hand by the experimenter, aligned with one of the eight orientations. Stimuli were applied for approximately 1 s with a moderate pressure, which was easily perceivable, but not painful. Participants make unspeeded verbal judgments of the perceived distance between the two touches by giving a number in centimeters. Participants were allowed to respond using inches if they were more comfortable doing so. Participants were instructed to be as precise as possible in their judgments and to consider using decimal responses (e.g., 2.4 cm rather than just 2 cm). They were allowed to give a response of 0 cm if they felt only one touch. There were 280 trials formed by seven repetitions of each combination of the eight orientations and five stimulus sizes. The trials were presented in random order and were divided into four blocks of 70 trials. Participants were allowed to take a short break between blocks.

Exp. 2: Hand Dorsum Versus Palm. Exp. 2 was similar to Exp. 1 except that stimuli were applied either to the dorsum or the palm of the left hand in different blocks. A set of lines was marked on the palm as on the dorsum, with 90° corresponding to a line connecting the center of the wrist and the center of the crease at the base of the palmar surface of the middle finger. There were 240 trials, 120 on each skin surface, formed by three repetitions of each combination of orientation and stimulus size. There were four blocks of 60 trials, two for each skin surface. The 120 trials on each skin surface were presented in random order. The conditions were counterbalanced in ABBA fashion, with the first condition counterbalanced across participants.

Exp. 3: Reference Frame Underlying Distortions. Exp. 3 was similar to Exp. 1 except that the left hand was in two different postures. In the normal posture, the left hand rested on the table with the fingers pointing away from the body, as in Exps. 1 and 2. In the rotated posture, the hand was rotated 90° clockwise, so that the fingers pointed toward the participant's right. There were 240 trials, 120 in each posture, formed by three repetitions of each combination of orientation and stimulus size. There were four blocks of 60 trials, two of each posture. The 120 trials in each posture were presented in random order. The postures were counterbalanced in ABBA fashion, with the first posture counterbalanced across participants.

Exp. 4: Forehead. Procedures were as in Exp. 1 except that stimuli were applied to the forehead, rather than the hand. The same stencil was used to make a set of eight lines on the center of the forehead. The 0° orientation was aligned with the vertical (i.e., chin-nose) face axis and the 90° orientation with the horizontal (i.e., ear-to-ear) face axis.

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