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Chang, Kai-Chien and Longo, Matthew (2022) Similar tactile distance anisotropy across segments of the arm. *Perception* 51 (5), pp. 300-312. ISSN 0301-0066.

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Similar Tactile Distance Anisotropy Across Segments of the Arm

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Abstract

A substantial literature has described anisotropy of tactile distance perception across many body parts. In general, the distance between two touches is felt as larger when the touches are oriented with the medio-lateral axis of the limbs than when oriented with the proximo-distal axis. In this study, we investigated tactile distance perception across the arm, measuring anisotropy on the upper arm, forearm, and hand dorsum. Participants made forced-choice judgments of which of two pairs of tactile distances felt larger and anisotropy was measured using the method of constant stimuli. Clear anisotropy was found on all three regions of the arm. There was no apparent difference in the magnitude of anisotropy across segments of the arm. We further measured the physical curvature of the arm and show that this cannot account of the perceptual anisotropy observed.

In his pioneering studies in the 19th century, E. H. Weber (1834) found that the perceived distance between two points on the skin seemed to change as he moved the stimulus across the skin. The distance felt bigger when applied to highly sensitive regions of the skin (e.g., the palm of the hand) than when applied to less sensitive regions (e.g., the forearm). Subsequent work has replicated this overall pattern, showing systematic relations between the sensitivity of skin surfaces and the perceived distance between pairs of tactile stimuli (Anema, Wolswijk, Ruis, & Dijkerman, 2008; Cholewiak, 1999; Fitt, 1917; Goudge, 1918; Miller, Longo, & Saygin, 2016; Taylor-Clarke, Jacobsen, & Haggard, 2004), an effect known as *Weber's illusion*. In addition, studies have reported analogous effects comparing different orientations of stimuli on individual skin surfaces (Green, 1982; Longo & Haggard, 2011), with distances across body width generally perceived as larger than those along body length or height.

Such anisotropy of tactile distance perception has been more widely studied on the hand dorsum, for which overestimation of distances across hand width compared to along hand length have been consistently found (Calzolari, Azañón, Danvers, Vallar, & Longo, 2017; Canzoneri et al., 2013; Longo & Golubova, 2017; Longo & Morcom, 2016; Longo & Sadibolova, 2013; Miller, Cawley-Bennett, Longo, & Saygin, 2017; Miller, Longo, & Saygin, 2014; Tamè, Tucciarelli, Sadibolova, Sereno, & Longo, 2021). Nevertheless, similar anisotropy has also been described on several other parts of the body, including the palm of the hand (Fiori & Longo, 2018; Le Cornu Knight, Longo, & Bremner, 2014; Longo, 2020; Longo, Ghosh, & Yahya, 2015), the forearm (Green, 1982; Le Cornu Knight et al., 2014), the face (Fiori & Longo, 2018; Longo et al., 2020; Longo, Ghosh, et al., 2015), the thigh (Green, 1982; Tosi & Romano, 2020), the shin (Stone, Keizer, & Dijkerman, 2018), the feet (Manser-

Smith, Tamè, & Longo, 2021), and the upper back (Nicula & Longo, 2021). Interestingly, across these body parts, the direction of anisotropy is consistent, with distances oriented with body width feeling larger than equally-sized distances oriented with body length or height. The only body parts which do not appear to fit this general pattern are on the torso, with no apparent anisotropy on the belly (Green, 1982; Longo, Lulciuc, & Sotakova, 2019; Marks et al., 1982), and two recent studies finding an effect in the opposite direction on the lower back (Nicula & Longo, 2021; Plaisier, Sap, & Kappers, 2020).

While anisotropy has consistently been found in the same direction on the limbs and head, the magnitude of anisotropy does appear to vary. For example, the magnitude of anisotropy is consistently smaller on the glabrous skin of the palm than on the hairy skin of the hand dorsum (for a recent meta-analysis, see Longo, 2020), a pattern which also appears to hold for the sole and dorsum of the foot (Manser-Smith et al., 2021). Two studies have also provided evidence that the magnitude of anisotropy differs between the hand and forearm. Le Cornu Knight and colleagues (Le Cornu Knight et al., 2014) found in two experiments that anisotropy on both the dorsal and volar surfaces of the forearm was larger than on the corresponding surfaces of the hand (i.e., the dorsum and palm, respectively). Miller and colleagues (2016) asked participants to judge whether tactile distances were bigger on the forearm or hand, finding a bias to perceive distances on the hand as bigger in the medio-lateral axis, but not the proximo-distal axis. While this comparison does not allow calculation of absolute anisotropy on each skin surface individually, this pattern implies that anisotropy should be larger on the forearm than on the hand, consistent with the results of Le Cornu Knight and colleagues.

There is also evidence that tactile spatial acuity varies systematically across the arm. Vierordt (1870) proposed a “law of mobility” for tactile sensitivity, arguing that “the acuity

of the spatial sense of the various skin areas of a body region, which is always moved as a whole, is proportional to the mean distances of these areas from all their common axes of rotation" (pg. 53). Vierordt analysed data on two-point discrimination thresholds (2PDT) across the arms, originally collected by Kottenkamp and Ullrich (1870), which he argued was consistent with this proposal. This data was discussed at some length by Boring (1942), who constructed a graph depicting these data, which clearly showed a progressive decrease in the 2PDT from the shoulder to the fingers. While the limits of 2PDT as a measure of tactile acuity are well known (Craig & Johnson, 2000) – though were not to Vierordt and Boring – it is worth noting that this gradient of acuity from the shoulder to fingertip has been replicated in recent research using more easily interpretable measures of tactile acuity (Mancini et al., 2014).

Boring's (1942) figure showing Vierordt's data collapsed across the dorsal and volar surfaces of the arm, as well as 2PDTs in the medio-lateral and proximo-distal axes, meaning that it provides no information about anisotropy of tactile acuity across the arm. However, examination of Vierordt's Table 2 suggests that there are similar gradients of acuity from the shoulder to finger for stimuli in both orientations. Sensitivity appears to be higher in the medio-lateral than in the proximo-distal orientation, but this difference does not appear dramatically different at different regions of the arm. The study of Mancini and colleagues (2014), while replicating the gradient from shoulder to fingers, only tested stimuli in the proximo-distal orientation, so provides no information about anisotropy. Another study, however, by Cody and colleagues compared tactile spatial acuity in both orientations on the hand dorsum and forearm (Cody, Garside, Lloyd, & Poliakoff, 2008). Clear anisotropy was apparent on both surfaces, the ratio of spatial discrimination thresholds in the medio-lateral and proximo-distal axes was on average .73 on the forearm and .78 on the hand. While this

difference is fairly modest, it is in the direction that would be expected given the findings described above showing larger tactile distance anisotropy on the forearm than on the hand (Le Cornu Knight et al., 2014; Miller et al., 2016). The present study, therefore, investigated tactile distance perception across the arm. We used the two-alternative forced-choice (2AFC) task we have used in several previous studies (e.g., Longo et al., 2015; Longo & Haggard, 2011; Longo & Morcom, 2016; Tamè, Bumpus, Linkenauger, & Longo, 2017) to measure tactile distance anisotropy on the dorsal surfaces of the upper arm, forearm, and hand.

One issue that arises when testing on the arm is the reference frame which participants use to determine distance between two touches. While somatotopic maps in the somatosensory cortex represent the skin as a 2-dimensional (2-D) sheet, the skin is of course stretched across a complex 3-dimensional (3-D) body. This means there are two ways in which distance between two points on the skin might be conceived. First, distance between two touches could be coded as the *Euclidean distance* between the two locations in 3-D space, taking into account the way in which the skin is stretched across the flesh of the body. Alternatively, distance could be coded as the *skin distance*, following the surface of the skin. Unless a skin surface is completely flat, the skin distance will always be larger than the Euclidean distance, and this difference may vary depending on the orientation of the stimulus on the limb. Given that the arm, as approximately cylindrical, is more highly curved in the medio-lateral than in the proximo-distal axis, it is possible that an apparent anisotropy in the perception of tactile distance could in fact reflect an anisotropy in the physical curvature of the limb.

The fact that tactile distance anisotropy has different magnitude on the palm and dorsum of the hand (Longo, 2020; Longo & Haggard, 2011) which are uncorrelated across

participants (Longo, Ghosh, et al., 2015) suggests that anisotropy arises from distinct 2-D maps of each skin surface, rather than an integrated representation of the hand as a 3-D whole. This is consistent with the finding that tactile distance adaptation aftereffects do not transfer between the palm and dorsum (Calzolari et al., 2017). However, other recent evidence has indicated that tactile localisation relies on a complex combination of reference frames based on the 2-D skin surface and the 3-D body (Sadibolova, Tamè, & Longo, 2018). To our knowledge, no published research has investigated which reference frames underlie tactile distance perception. We therefore measured the physical curvature of the skin to determine whether this could account for any perceptual anisotropy observed.

Method

Participants

Forty members of the Birkbeck community (22 women) between 18 and 51 years of age (M : 30.4 years) participated for payment or course credit. All participants but 4 were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) (M : 72.2, SD : 47.0). Participants gave written informed consent before participating. Procedures were approved by the Department of Psychological Sciences research ethics committee at Birkbeck, and were consistent with the principles of the Declaration of Helsinki.

A weighted average of effect sizes from 15 previous experiments from our laboratory measuring tactile distance anisotropy on the hand (total $N=300$) gave an average effect size of Cohen's $d = 1.56$. A power analysis using G*Power 3.1 (Faul, Erdfelder, Land, & Buchner, 2007) with alpha of .05 and power of .95 indicated that eight participants were required. Our sample size of 5 times this number gives us substantial power to detect

potential effects on the forearm and upper arm even substantially smaller than found on the hand dorsum.

Procedure

Tactile Distance Judgments. The stimuli were wooden sticks embedded in foamboard and set at different distances apart (2.5, 3.5, and 4.5 cm), similar to those we have used in several previous studies in our lab (Calzolari et al., 2017; Fiori & Longo, 2018; Longo, Ghosh, et al., 2015; Longo & Haggard, 2011; Longo & Sadibolova, 2013). In studies on the hand, we have typically used slightly smaller stimuli (2, 3, and 4 cm). A recent study measuring spatial discrimination thresholds, however, found values on the upper arm (i.e., the shoulder) of just over 2 cm (Mancini et al., 2014). The smallest stimuli we used in this study was clearly larger than this, meaning that all stimuli were large enough to be spatially-discriminated on all three skin surfaces. The sticks were pointy, but not sharp, and tapered to a point of approximately 1mm in diameter. On each trial, two pairs of stimuli were applied, one with the touches oriented across the width of the limb (i.e., the medio-lateral axis) and one oriented along the length of the limb (i.e., the proximo-distal axis). The order of the two orientations was counterbalanced across trials. Each stimulus was applied manually by the experimenter with moderate pressure for approximately one second. The participant's task was to judge whether the distance between the two points felt farther apart in the first stimulus applied, or the second, by making an unspeeeded verbal judgment (i.e., "first" or "second"). Across trials, there were five pairs of distances use, varying in the ratio of distances in the two orientations (across/along): 2.5/4.5 cm, 2.5/3.5 cm, 3.5/3.5 cm, 3.5/2.5 cm, and 4.5/2.5 cm.

Across blocks, stimuli were applied to three different skin surfaces: the dorsum of the left hand, the left dorsal forearm, and the left dorsal upper arm. Participants lay their hand palm down on a table in front of them. For hand blocks, stimuli were applied approximately in the centre of the hand dorsum. For the forearm and upper arm blocks, stimuli were applied approximately in the centre of the dorsal surface of each body part. In each case, the exact locations were varied across trials to avoid sensitization of the skin. Each stimulus was applied manually by the experimenter for approximately 1 second with an inter-stimulus interval of approximately 1 second.

There were six experimental blocks, two for each of the body parts tested. Blocks 1-3 consisted of one repetition of each of the three body parts, counterbalanced across participants according to a Latin Square. Blocks 4-6 were in the reverse order. Each block consisted of 40 trials, eight trials for each of the five ratios between the across and along distances, half with the across stimulus presented first and half with the along stimulus presented first. The 40 trials within each block were presented in random sequence.

Measurement of Skin Curvature. After the tactile distance judgment task was completed, we made measurements of the curvature of each of the three parts of the participant's arm in both orientations. We used a set of digital calipers to make marks on each skin surface using a black pen that were 40 mm apart in Euclidean, 3-dimensional space, one set of marks separated in the across orientation and another in the along orientation. We then used a tailor's tape measure to determine the distance between the marks on the surface of the skin.

If the skin is curved, then the distance measured with the tape measure should be greater than 40 mm, as shown in Figure 1. For a given pair of tactile stimuli (the black circles

in Figure 1), there are two ways in which participants might conceive of the distance between them. The *Euclidean distance* between the points in 3-dimensional space (dotted lines in Figure 1) follows the most direct path between the two points, in most cases passing through the flesh of the arm. The *skin distance*, in contrast, is the most direct path following the surface of the skin (dashed lines in Figure 1). Unless the surface of the arm is completely flat, the skin distance will always be greater than the Euclidean distance. The magnitude of this difference reflects the amount of curvature of the arm, as reflected in the differences between the left and right panels. We quantified this by taking the ratio of skin distance to Euclidean distance, which we call the *Curvature Index*. The curvature index was calculated for each of the two orientations on all three skin surfaces.

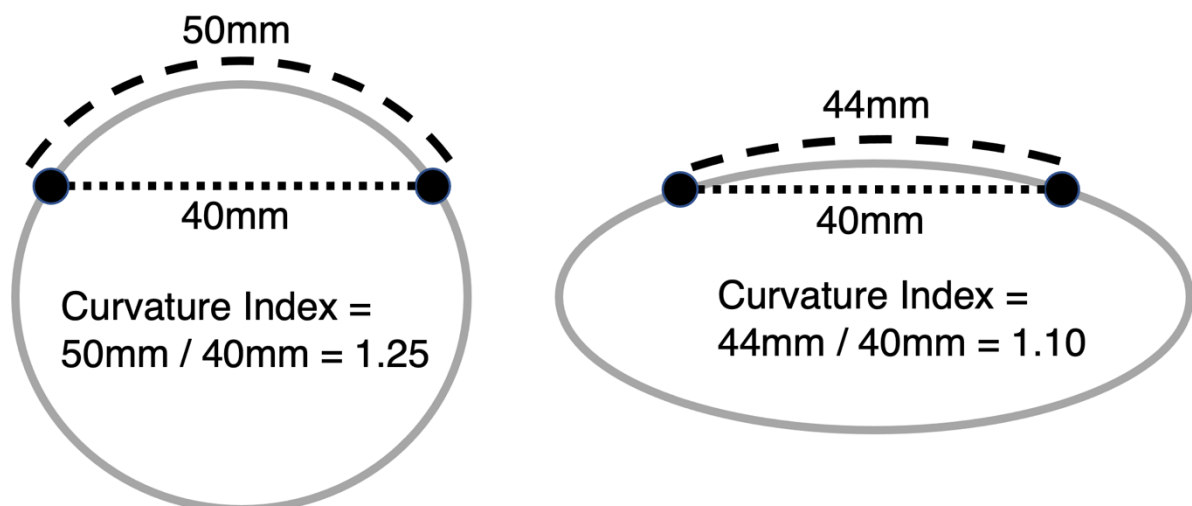


Figure 1: Measurement of skin curvature. The two grey ovals represent two hypothetical coronal cross-sections through the arm, reflecting plausible shapes of the upper arm (left panel) and hand (right panel). A pair of calipers was used to make marks with a pen (black circles) that were 40 mm apart in *Euclidean distance* (dotted lines). We then used a tailor's tape measure to determine the *skin distance* between the points (dashed lines). This procedure was applied both in the medio-lateral and proximo-distal axes. The curvature index is defined as the ratio of the skin distance to the Euclidean distance. The ratio of curvature indices in the two orientations quantifies the anisotropy that would be expected if participants code distance using skin distance, even if there were no perceptual anisotropy.

If the distance between two touches is calculated based on skin distance, rather than Euclidean distance, then an anisotropy in the curvature index itself could produce an apparent anisotropy in perceived tactile distance. By taking the ratio of curvature indices in the medio-lateral and proximo-distal orientations, we estimated the anisotropy in tactile distance perception that would be produced purely by curvature of the skin itself, if participants' responses were based on skin distance. This allows us to essentially 'correct' perceptual estimates of tactile distance anisotropy from the perceptual confounding influence of anisotropy of the shape of the skin itself.

Analysis

We analysed the proportion of trials in which the tactile distance across the width of the arm was judged as larger as a function of the ratio of the across and along stimuli, plotted logarithmically to produce a symmetric distribution around a ratio of 1 (i.e., the ratio at which the two distances were the same size). Data from each body part in each participant was fit with a cumulative Gaussian function using maximum-likelihood estimation with the Palamedes toolbox (Prins & Kingdom, 2009) for MATLAB (Mathworks, Natick, MA, USA).

We excluded participants from analysis if the R^2 for the psychometric functions was less than .5 in any of the three body parts, as in other studies from our lab. Six participants were excluded on this basis.

The cumulative Gaussian curves fit to the data have two parameters, the mean and the slope (i.e., the inverse of the standard deviation of the Gaussian). The mean of the function indicates the point of subjective-equality (PSE), the ratio between the across and along stimuli such that the participant was equally likely to say that each stimulus was

bigger. An anisotropy for across stimuli to be judged as larger than along stimuli would result in the PSE being smaller than 1 (i.e., the stimuli are judged as equal in size when the across stimulus is in fact smaller); conversely, and anisotropy for along stimuli to be judged as larger than across stimuli would result in the PSE being larger than 1. The second parameter (the slope) is the inverse of the standard deviation of the Gaussian, and reflects the precision of discrimination of tactile distance between orientations.

To assess overall anisotropy on each body part, we conducted one sample t-tests comparing the mean PSE to a ratio of 1. All statistical tests on PSE were conducted on the logarithms of the PSEs, which were converted back to ratios for reporting mean values. To compare the body parts, we conducted a one-way repeated-measures analysis of variance (ANOVA). As measures of effect size, we report Cohen's d for one-sample t-tests and η_p^2 for F-statistics.

As noted above, we calculated the curvature indices for each orientation on all three body parts. These were compared to a ratio of 1 using one-sample t-tests. We then assessed the presence of anisotropy of curvature on each region of the arm by taking the ratio between the curvature indices in the proximo-distal and medio-lateral axes, which were again compared to a ratio of 1 using one-sample t-tests. We also compared the magnitude of these ratios across the arm using a one-way repeated measures ANOVA. As with PSEs, analyses were conducted on the logarithm of these ratios, which were converted back to a ratio for reporting mean values. Finally, we used these measures of anisotropy of actual arm curvature to 'correct' the PSE values from the perceptual task, by comparing PSEs to the value that would be expected just based on the physical shape of the arm if participants responses entirely based on skin-distances rather than Euclidean distances. We calculated paired t-tests comparing the PSE at each skin surface with the corresponding ratio of

curvature indices (rather than a value of 1, as in the analysis above). Finally, we also ran an ANOVA to compare the magnitude of these corrected PSE values across regions of the arm.

Results

The results are shown in Figure 2. R^2 values showed good fit to the data, with psychometric functions accounting for 92.3% of the variance in the data on the hand, 88.2% on the forearm, and 89.8% on the upper arm. To investigate the presence of anisotropy, we first conducted one-sample t-tests to compare mean PSEs to 1. There was clear anisotropy on all three regions of the arm, the hand ($M: 0.727$), $t(33) = -9.10$, $p < .0001$, $d = 1.560$; the forearm ($M: 0.687$), $t(33) = -9.28$, $p < .0001$, $d = 1.591$; and the upper arm ($M: 0.698$), $t(33) = -7.32$, $p < .0001$, $d = 1.256$. An ANOVA found no evidence that the magnitude of anisotropy varied across the three regions of the arm, $F(2, 66) = 0.65$, $p = .525$, $\eta_p^2 = .019$. An ANOVA on slopes of the psychometric functions also showed no significant differences between regions, $F(2, 66) = 2.07$, $p = .135$, $\eta_p^2 = 0.059$.

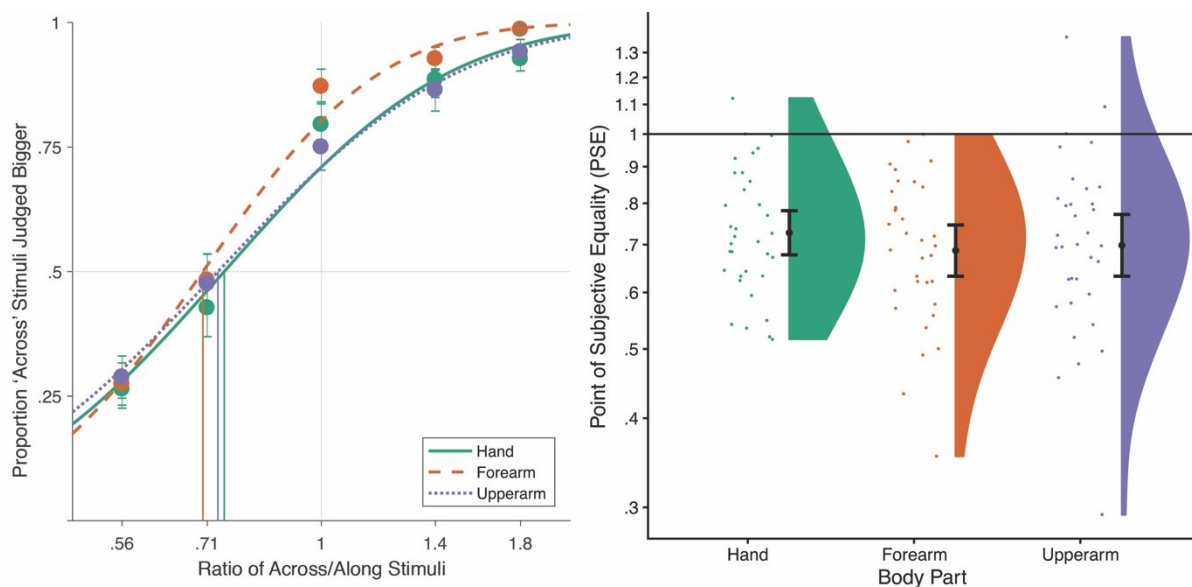


Figure 2: *Left panel:* Proportion of trials in which the 'across' stimulus was judged as larger than the 'along' stimulus as a function of the ratio between stimuli (across/along). Curves are cumulative Gaussian functions. Error bars indicate one standard error. Vertical lines indicate the point-of-subjective equality (PSE), the ratio

between across and along stimuli which participants perceive as equal. Clear anisotropy was apparent on all three skin surfaces, with distances across arm width overestimated relative to distances along arm length. *Right panel:* Raincloud plots (Allen et al., 2021) showing PSE values for the three regions of the arm.

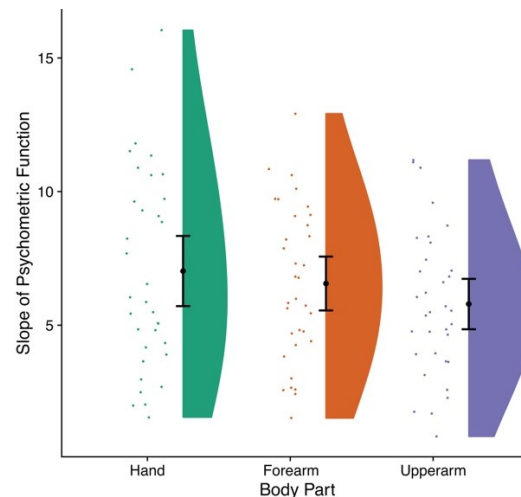


Figure 3: Slopes of the psychometric function across skin surfaces. Error bars indicate one standard error.

The curvature indices for both orientations on each of the three skin surfaces are shown in Table 1. All curvature indices were significantly greater than 1 (all $ps < .0001$), which indicates (unsurprisingly) that the body is not flat. The most important question concerns whether the magnitude of curvature differs in the two orientations. The bottom row of Table 1 shows the ratio of curvature indices in the proximo-distal and medio-lateral axes. This indicates the magnitude of anisotropy that would be expected on the tactile distance judgment task if participants responded based on skin distance in the absence of any perceptual anisotropy. No evidence for an anisotropy of curvature was present on the hand dorsum ($M: 0.996$), $t(33) = -0.46$, $p = .647$, $d = 0.079$. There was, however, evidence for an anisotropy of curvature on both the forearm ($M: 0.962$), $t(33) = -5.27$, $p < .001$, $d = 0.905$, and the upper arm ($M: 0.958$), $t(33) = -4.25$, $p < .001$, $d = 0.729$. Thus, there are differences in curvature of the forearm and upper arm across axes, a finding which is unsurprising given that the arm is approximately cylindrical. Importantly, however, the magnitude of this

anisotropy in skin shape itself is small in comparison to the perceptual anisotropies reported above. An ANOVA on anisotropy of curvature (i.e., the log ratio of curvature indices in the proximo-distal to medio-lateral axis) values across the three regions showed a significant difference, $F(1.67, 55.04) = 6.28, p < .01, \eta_p^2 = .160$. Follow-up t-tests using Holm-Bonferroni correction for multiple comparisons showed that anisotropy was significantly smaller on the hand than on either the forearm, $t(33) = 3.05, p < .05, d_z = 0.523$, or the upper arm, $t(33) = 2.70, p < .05, d_z = 0.051$. There was no significant difference in anisotropy, however, between the forearm and upper arm, $t(33) = 0.44, p = .664, d_z = 0.075$.

*** INSERT TABLE 1 AROUND HERE ***

Because anisotropy of curvature on the actual arm was calculated for each participant on each arm region, the tactile distance anisotropy obtained perceptually can be compared to the anisotropy in actual skin shape, rather than an anisotropy of 0. This allows the anisotropy in actual arm shape to be 'corrected'. This analysis showed clear perceptual anisotropy over and above what could potentially be explained by arm curvature on the hand ($M: 0.731$), $t(33) = 9.05, p < .0001, d = 1.552$, the forearm ($M: 0.713$), $t(33) = 8.78, p < .0001, d = 1.51$, and the upper arm ($M: 0.729$), $t(33) = 6.30, p < .0001, d = 1.081$. An ANOVA again showed no significant differences in the magnitude of anisotropy across the three regions of the arm, $F(2, 66) = 0.13, p = .880, \eta_p^2 = .004$.

Discussion

Clear tactile distance anisotropies were found at all three locations on the arm, the hand dorsum, the forearm, and the upper arm. In each case, tactile distances oriented

across the width of the arm were judged as larger than those oriented along the length of the arm. The magnitude of anisotropy was similar across all three locations, and cannot be accounted for (at least not fully) by differences between orientations in the actual curvature of the arm.

Our manipulation of the distance between pairs of touches was based on distances defined in 3-D Euclidean space. However, given that the arm is not a flat surface, the distance between touches across the surface of the skin is even larger. Importantly, we showed that this difference between Euclidean distance and skin distance is itself anisotropic on the upper arm and forearm (but notably not on the hand dorsum). This is not surprising given that the arm is approximately cylindrical, but is important to take into account in assessing perceptual anisotropy. It is unclear whether participants' judgments of distance are based on Euclidean or skin distance (or some combination of the two). Instructions in this study, as in every study of tactile distance of which we are aware, make no mention of this distinction, and no participant in our studies has ever asked for clarification on this point. Critically, however, the present results show that even if participants are basing their judgments on skin distance, the magnitude of anisotropy in actual body shape is far too small to account for the magnitude of perceptual anisotropy observed. Thus, while it remains an interesting question for future research what frame of reference tactile distance judgments are defined in, this does not provide an alternate explanation for the perceptual anisotropy observed in this and previous studies.

In general, tasks used to measure perceived body part size have not taken into account the fact that the body is a 3-D, volumetric objects. Longo and Haggard (2012) suggested that nearly all existing methods for assessing perceived body part size can be grouped into one of two classes: *metric* methods in which the perception of some distance on

the body is compared to a 1-D metric standard, and *depictive* methods in which the perception of the body is compared to a 2-D image of a body. Recently, a few studies have attempted to measure body perception in 3-D. For example, Tavacioglu, Azañón, and Longo (2019) measured the perception of finger size in 3-D by asking participants to judge whether each finger would be able to fit through rings of various sizes. The size of the fingers (other than the thumb) was underestimated, with the magnitude of underestimation decreasing from the index to little finger. Another study investigated perception of the volume of body parts, finding systematic distortions across the body (Sadibolova, Ferrè, Linkenauger, & Longo, 2019). Finally, another study investigated the effects of perceived gravity on perceived body part weight, showing that experimental alterations of gravity using a short-arm centrifuge and parabolic flight produced rapid and systematic changes in the perceived weight of body parts (Ferrè, Frett, Haggard, & Longo, 2019). In the present study, we measured actual and not perceived curvature. It will be interesting in future research to investigate whether there are systematic distortions in people's perception of the curvature of their body, which could provide a novel window onto perception of the body as a 3-D object.

This study adds the upper arm to the list of body parts on which tactile distance anisotropy has been reported, and provides further evidence for anisotropy on the forearm (Green, 1982; Le Cornu Knight et al., 2014) and hand dorsum (Fiori & Longo, 2018; Longo & Golubova, 2017; Longo & Haggard, 2011). Notably, the anisotropy on all three main segments of the arm is mirrored by anisotropy on all three segments of the leg: the thigh (Green, 1982; Tosi & Romano, 2020), the shin (Stone et al., 2018), and the foot (Manser-Smith et al., 2021). Clear anisotropy has also been described on the face (Fiori & Longo, 2018; Longo et al., 2020; Longo, Ghosh, et al., 2015). Thus, qualitatively similar anisotropies

involving overestimation of distances across body width have been found on essentially every part of the body aside from the torso, which shows a more complicated pattern. While there does appear to be overestimation of distances across the width of the upper back (Nicula & Longo, 2021), this pattern appears to be reversed on the lower back (Nicula & Longo, 2021; Plaisier et al., 2020), and there does not appear to be any anisotropy on the belly (Green, 1982; Longo et al., 2019; Marks et al., 1982).

One potentially relevant factor in shaping the difference between the limbs and the torso could be the organisation of the spinal dermatomes across the body (Head, 1893; Keegan & Garrett, 1948; Sherrington, 1893). While the dermatomes on the arms and legs generally run along the proximo-distal axis of the limb, the dermatomes on the torso are organised as a set of thin bands running around the circumference of the torso. Thus, on the limbs, pairs of touches oriented across the width of the limb are more likely to fall in different dermatomes than touches oriented along limb length. This pattern is not true on the torso, however. It remains unclear whether dermatomal organisation has any relevance for higher-level aspects of perception, such as measured in this study. It is noteworthy in this context, though, that the global pattern of somatotopy in somatosensory cortex does mirror the sequence of dermatomes in the spinal cord (Dietrich et al., 2017; Werner & Whitsel, 1973).

The comparable magnitude of anisotropy across the regions of the arm was unexpected given two previous studies which suggested that anisotropy should be bigger on the forearm than on the hand dorsum (Le Cornu Knight et al., 2014; Miller et al., 2016). The reasons for this difference are not clear. However, it is notable that the similar anisotropy on the forearm and hand found in this study is consistent with evidence from distortions of proprioceptive maps measured using a localisation task (Longo, 2017) which were of similar

magnitude on the two body parts. Similarly, measures of anisotropy of tactile acuity have shown only modest differences across the arm (Cody et al., 2008; Vierordt, 1870). The very fact that such consistent anisotropy has been found across the body may suggest that it is based on some coordinating factor across the entire body, rather than on idiosyncratic features of the representation of each individual skin surface. In this light, it is notable that one recent study of neurons in area 2 of primary somatosensory cortex found that responses appeared related to the coordinated movements of the entire arm, rather than of any individual segment (Chowdhury, Glaser, & Miller, 2020).

The present results add to a growing literature across a wide variety of domains showing that body width tends to be overestimated relative to body length or height (Longo, 2022). Beyond the consistent findings in tactile distance perception discussed in this paper, similar biases have been found in the geometry of tactile receptive fields in somatosensory cortex (Alloway, Rosenthal, & Burton, 1989; Brooks, Rudomin, & Slayman, 1961), tactile spatial acuity (Cody et al., 2008; Schlereth, Magerl, & Treede, 2001), the precision of tactile localisation (Boring, 1930; Margolis & Longo, 2015; Medina, Tamè, & Longo, 2018), proprioceptive body maps (Ganea & Longo, 2017; Longo & Haggard, 2010; Longo, Mancini, & Haggard, 2015), perception of the relative locations of body parts (Fuentes, Longo, & Haggard, 2013; Fuentes, Pazzaglia, Longo, Scivoletto, & Haggard, 2013; Fuentes, Runa, Blanco, Orvalho, & Haggard, 2013), and explicit judgments of body part size (Dolan, Birtchnell, & Lacey, 1987; Dolce, Thompson, Register, & Spana, 1987; Longo & Haggard, 2012).

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Table 1: Curvature indices (i.e., the ratio of skin distance to Euclidean distance), for the three arm regions in the medio-lateral axis (*top row*), and the proximo-distal axis (*middle row*). The anisotropy of curvature (i.e., the ratio of curvature indices in the proximo-distal and medio-lateral axes) is shown in the bottom row.

	Hand	Forearm	Upperarm
Curvature Index – Medio-Lateral Axis	1.053 $t(33) = 8.27$	1.097 $t(33) = 14.77$	1.082 $t(33) = 9.64$
Curvature Index – Proximo-Distal Axis	1.049 $t(33) = 6.20$	1.056 $t(33) = 8.47$	1.036 $t(33) = 6.21$
Ratio of CIs (anisotropy of curvature)	0.996 $t(33) = -0.46$	0.962 $t(33) = -5.27$	0.958 $t(33) = 4.25$