

RUNNING HEAD: CATEGORICAL REPRESENTATION OF THE BODY

Categorical perception of tactile distance

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ABSTRACT

The tactile surface forms a continuous sheet covering the body. And yet, the perceived distance between two touches varies across stimulation sites. Perceived tactile distance is larger when stimuli cross over the wrist, compared to when both fall on either the hand or the forearm. This effect could reflect a categorical distortion of tactile space across body-part boundaries (in which stimuli crossing the wrist boundary are perceptually elongated) or may simply reflect a localised increase in acuity surrounding anatomical landmarks (in which stimuli near the wrist are perceptually elongated). We tested these two interpretations, by comparing a well-documented bias to perceive mediolateral tactile distances across the forearm/hand as larger than proximodistal ones along the forearm/hand at three different sites (hand, wrist, and forearm). According to the ‘categorical’ interpretation, tactile distances should be elongated selectively in the proximodistal axis thus reducing the anisotropy. According to the ‘localised acuity’ interpretation, distances will be perceptually elongated in the vicinity of the wrist regardless of orientation, leading to increased overall size without affecting anisotropy. Consistent with the categorical account, we found a reduction in the magnitude of anisotropy at the wrist, with no evidence of a corresponding specialized increase in precision. These findings demonstrate that we reference touch to a representation of the body that is categorically segmented into discrete parts, which consequently influences the perception of tactile distance.

KEYWORDS: SELF PERCEPTION; BODY REPRESENTATION; TACTILE PERCEPTION; CATEGORICAL PERCEPTION; TACTILE ACUITY

The spatial representation of tactile information is no mean feat. We must resolve numerous cutaneous and neural variations (Cholewiak, 1999; Hagert, Forsgren, & Ljung, 2005; Ochoa, 2010; Penfield & Boldrey, 1937), and also perceptual distortions (Cody, Gaarside, Lloyd, & Poliakoff, 2008; Green, 1982; Longo & Haggard, 2011; Weber, 1834 / 1996). There is certainly no straightforward one-to-one spatial correspondence between skin surface and neural region (Longo, Azañón, & Haggard, 2010). One potential solution to these challenges is to represent touch, not in terms of metric extent, but rather according to salient body parts and anatomical landmarks. Here, we investigated how the representation of distinct body parts affects the spatial perception of touch.

The body is not one continuous sheet: it has a clear landscape with well-defined contours and observable segments. Investigating the structuring effect of body-part boundaries on tactile distance perception, de Vignemont, Majid, Jola, and Haggard (2009) reported an intriguing perceptual warping of distance over the wrist. Tactile distances presented proximodistally along the length of the limb were perceived to be larger when they crossed over the joint in comparison to the same distances presented entirely within the bounds of either the hand or the forearm. Does the presence of distinct body parts drive this perceptual distortion of tactile distance?

These results could be explained by either of two contrasting accounts. Firstly, de Vignemont and colleagues (2009) interpret this perceptual warping as reflecting a perceptual segmentation of the body, with the joints forming the boundaries of body-part categories. This kind of categorical segmentation is comparable with the way in which colour terms influence hue discrimination (e.g., Kay & Kempton, 1984). Alternatively, these results may be based on differential acuity across the body: The distance distortion may reflect an increase in acuity in the vicinity of anatomical landmarks such as the

wrist (Cholewiak & Collins, 2003; Cody et al., 2008; Weber, 1834/1996). Given that perceived tactile distance is known to relate systematically to acuity (i.e., *Weber's illusion*, Weber, 1834/1996; Taylor-Clarke, Jacobsen, & Haggard, 2004), increased acuity in the vicinity of the wrist could cause a general increase in perceived tactile distance. Existing data do not differentiate between these two interpretations.

We developed a novel method to test whether perceptually increased tactile distance traversing the wrist reflects categorical perception of tactile distance over body-part boundaries (the categorical account) or overall increases in perceived distance in the *vicinity* of the wrist (the localised acuity account). Our method was based on the following prediction: If the categorical account is true then tactile distances should be increased whenever they cross over the wrist boundary (i.e., in the proximodistal orientation), but not when they run parallel to the wrist boundary (i.e., in the mediolateral orientation). Alternatively, if the acuity account is correct, then increases in tactile distance should be seen at the wrist, regardless of orientation. Tactile distance perception is known to exhibit anisotropies on both the forearm (Green, 1982) and the hand (Longo & Haggard, 2011), with stimuli running mediolaterally, across the limb being perceived as larger than stimuli running proximodistally, along the limb.

Therefore, the categorical account makes the critical prediction that the magnitude of anisotropy should be reduced for stimuli crossing the wrist, compared to those presented entirely on the hand or forearm. Conversely, according to the localised acuity account the anisotropy will remain constant. Therefore, a reduction in the anisotropy at the wrist is predicted by the categorical – but not the localised acuity – account. No change in the anisotropy at the wrist would suggest that the perceptual elongation of distance over the wrist as found by de Vignemont et al. (2009) may in fact be driven by a localised increase in acuity around anatomical landmarks. Figure 1

provides a visual depiction of how tactile perception would be distorted on the wrist according to the differing accounts.

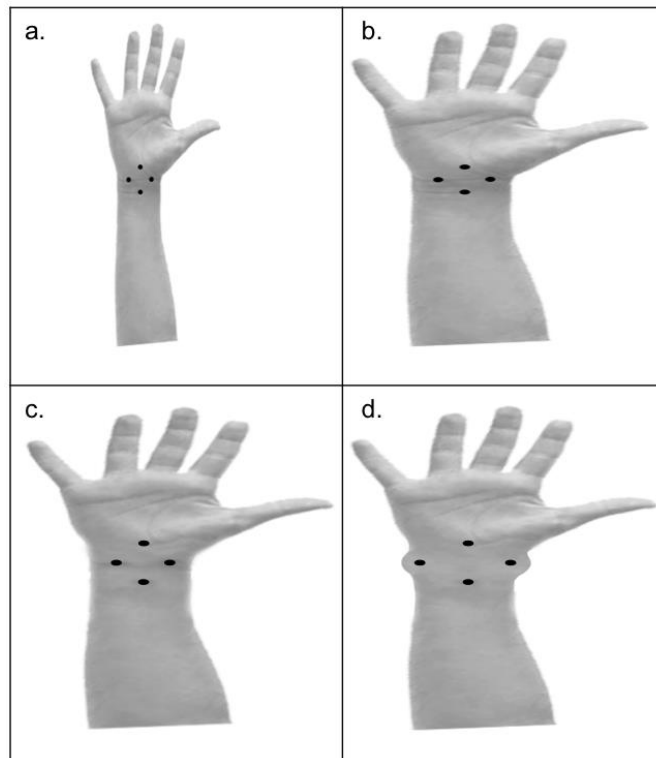


Figure. 1. An image depicting example points of stimulation across and along the ventral wrist (a). (b) indicates how these would be perceived according to the known mediolateral bias. We also illustrate perceptual distortions at the wrist according to the two accounts being investigated in this paper (over and above the mediolateral bias): the categorical account (c) shows a selective proximodistal elongation, whereas the localised acuity account (d) assumes a perceived increase in distance in both axes at the wrist.

In order to separate these accounts, participants were asked to judge which of two tactile distances, one in each axis (mediolateral vs. proximodistal), was larger. These two-alternative forced-choice trials were presented on the hand, wrist, and forearm in order to compare anisotropic effects. In addition, we investigated both the dorsal and ventral surfaces of the limb in order to allow for a satisfactory comparison of our findings with previous effects which have been found on different surfaces of the limb (cf. de Vignemont et al., 2009; Longo & Haggard, 2011). **In two experiments we**

show that the bias to perceive stimuli running across the limb as larger than those running along the limb (tactile anisotropy, cf. Longo & Haggard, 2011) is reduced at the wrist, supporting the categorical account described above. Experiment 2 refined some aspects of Experiment 1 in order to provide a more robust demonstration of this effect. Whereas Experiment 1 compared anisotropies on ventral and dorsal surfaces between participant groups, Experiment 2 made this comparison within participants, thus doubling the number of trials for each participant.

Experiment 1

Method

Participants. Twenty-eight healthy participants (eighteen female), aged between 20 and 31 years, participated. All participants reported they were right-handed. One participant was excluded from the analyses (see Results). Prior to testing, ethical approval was gained covering both Experiment 1 and 2 from the Department of Psychology Research Ethics Committee at Goldsmiths, University of London. All participants gave informed consent prior to testing.

Materials and procedure. Participants were blindfolded and seated at a table with their left hand extended comfortably in front of them. The tactile stimuli comprised two plastic pins with rounded points (~1mm tip width) fixed at distances of 2, 3, and 4 cm. In each trial two pairs of punctuate stimuli were presented sequentially (one in each orientation, both centred on the same presentation point). The experimenter presented stimuli manually ensuring that the two points of each pair touched the skin simultaneously. Each presentation lasted approximately one second, with an inter-stimulus interval (ISI) of approximately one second. Participants indicated which of the pairs they perceived to be larger by verbally responding either “first” or “second”.

Half of the participants were stimulated on the dorsal and the other half on the ventral surface of the limb. For each of group, stimuli were presented on three body parts (forearm, wrist, and hand). The midpoint between the two stimuli for the wrist was taken as the narrowing between the ulna bone and the hand. The midpoint for the hand was taken as approximately the centre of the palm/dorsum. The midpoint for the forearm was placed at an equal distance from wrist to hand midpoints, towards the elbow. The mediolateral dimension of the midpoints were visually estimated as the central point across the body part.

Presentation of the tactile stimuli on the three body parts was made in blocks of 20 trials using an ABCCBA design. The order of body parts was counterbalanced across participants. Each block included 5 sets of stimuli presented 4 times in a pseudo-randomised order. The 5 sets within each block were selected according to the relative size of each orientation (Mediolateral:Proximodistal); 2:4, 2:3, 3:3, 3:2, 4:2 cm.

Statistical analyses. We measured the proportion of responses in which the across stimulus was judged to be larger, as a function of the ratio of the length of the across to the along stimuli. Cumulative Gaussian curves were fit to the data using R 2.8.0. Points-of-Subjective-Equality (PSEs) were calculated as the ratio of across and along stimuli at which the psychometric function crossed 50%. PSEs give a measure of the anisotropy of tactile distance perceived along vs. across the hand/wrist/forearm. For statistical analysis PSE ratios were log-transformed. The interquartile range (IQR) – that is the difference between the points on the x-axis where the curve crosses 25% and 75% - was calculated as a measure of the precision of participants' judgements.

Results

One participant from the Dorsal group was excluded due to extremely low R-squared scores for forearm and hand conditions (0.15 and 0.45 respectively). The

remaining R-squared scores, averaged across participants, showed a good fit to the data. These were 0.92, 0.98, and 0.95 (Dorsal group), and 0.96, 1.00, and 0.99 (Ventral group), for forearm, wrist, and hand respectively. Figure 2 (Panels a and b) illustrates the cumulative Gaussian functions fitted to the data across Body Part conditions and between Surface groups.

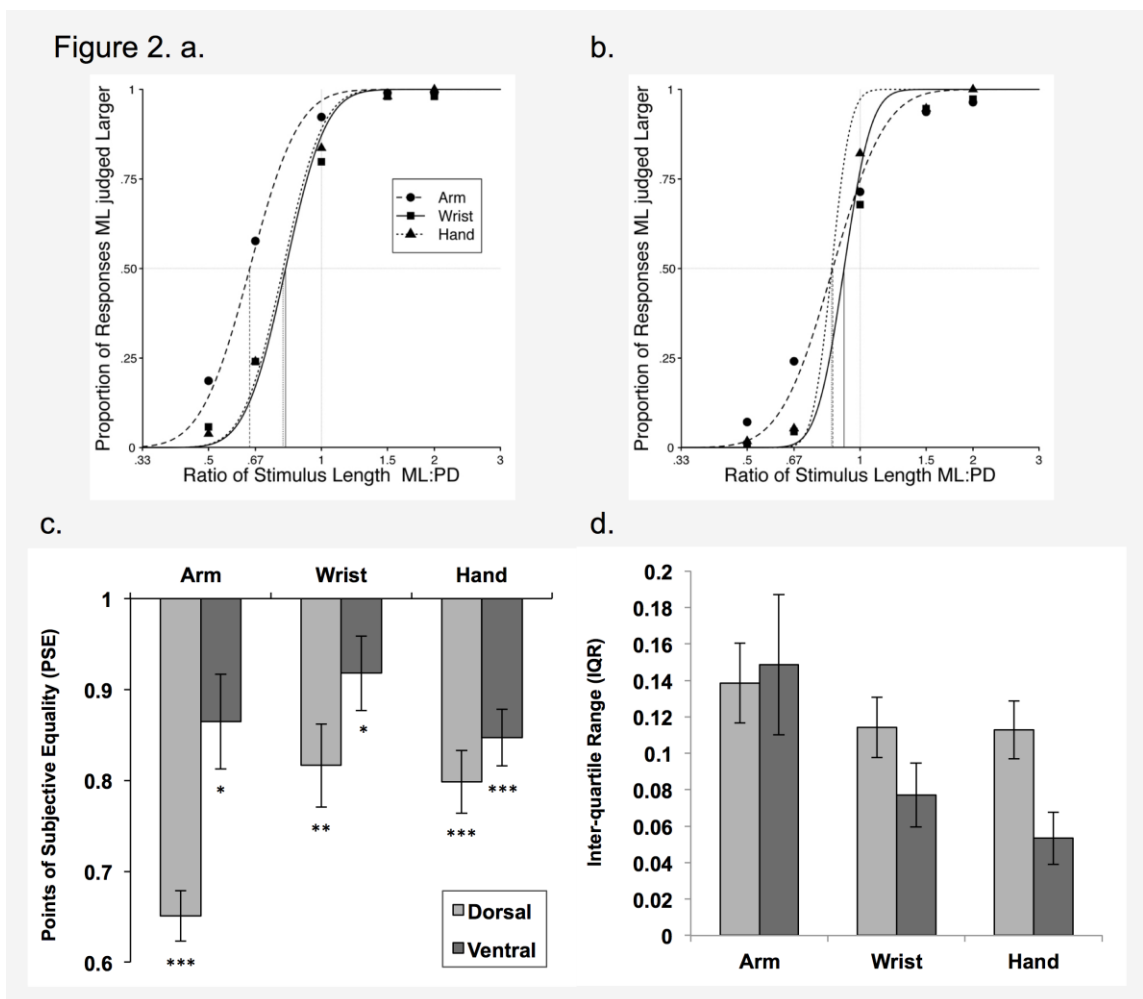


Figure 2. Results of Experiment 1. Panels a to c present raw PSE scores before log-transformation for analysis. Panels (a) and (b) present the proportion of mediolateral (ML) distances judged to be larger plotted as a function of the stimulus ratio (mediolateral:proximodistal, ML:PD): on the dorsal (a) and ventral (b) surfaces.

Stimulus ratios are plotted logarithmically on the x-axis so that the point 1 represents where the PSE would be veridical, i.e. the ratio of ML and PD response is accurate. The PSE is the point at which the psychometric function crosses the y-axis at .50. Panel (c) presents points of subjective equality (PSEs) for Arm, Wrist, and Hand, split between the Ventral and Dorsal Surfaces. Here PSE values below 1 represent more bias towards ML being perceived to be larger than PD. Panel (d) presents interquartile ranges (IQRs) for the Arm, Wrist and Hand between Ventral and Dorsal Surfaces. Asterisks illustrate values that are significantly different from 1 at a level $p < .001$ (***) and $p < .01$ (**) and $p < .05$ (*).

Points of subjective equality (PSEs). Log transformed points of subjective equality (PSEs) across all body parts and surfaces were compared against a ratio of 0 (veridical perception) with t-tests using Holm's sequential Bonferroni correction in order to detect significant anisotropies. PSE values significantly below 0 indicate a tendency to perceive distance running across the body part as larger than those presented along the body part, while those greater than 0 indicate the opposite. Figure 2 (Panel c) shows these findings and indicates which PSEs demonstrate a significant anisotropy. All PSEs were reliably less than 0 (indicating significant mediolaterally biased anisotropies; all p 's $< .04$, all t 's > 2.23). This replicates Longo and Haggard's (2011) finding that tactile distances are perceived as longer across than along the hand, and show that this anisotropy extends down the forearm (see also Green, 1982).

We conducted a 3 x 2 mixed ANOVA [Body Part x Surface] on the PSEs. There was a main effect of Body Part, $F(2, 50) = 7.56$, $p < .01$, $\eta_p^2 = .23$. A polynomial within-participants trend analysis showed this effect is both linear, $F(1, 25) = 7.40$, $p < .05$, $\eta_p^2 = .23$ and quadratic, $F(1, 25) = 7.70$, $p < .01$, $\eta_p^2 = .24$. Critically, this quadratic effect indicates that, whilst there is a progressive linear reduction in anisotropy from forearm to hand, the anisotropy at the wrist is reduced over and above what one would expect given this linear change. We explored this relationship further using focussed t-tests (p values were subjected to the Holm-Bonferroni correction), which confirmed that

the anisotropy at the arm was larger than both the wrist, $t(26) = 3.16, p < .001, d = .68$, and the hand, $t(26) = 2.31, p < .03, d = .49$. Despite a trend towards a greater anisotropy on the hand than the wrist, this comparison did not reach significance, $t(26) = 1.40, p = .09, d = .29$.

Consistent with previous findings (Longo & Haggard, 2011), there was also a Surface effect, $F(1, 25) = 9.56, p < .01, \eta_p^2 = .28$, with larger anisotropies on the dorsal than the ventral surface. Finally, there was a significant interaction between Body Part and Surface, $F(2, 50) = 4.08, p < .05, \eta_p^2 = .14$. In order to explore this interaction further we performed a series of six focussed t-tests (using Holm-Bonferroni correction $p < .008$) comparing each body part against the others separately between Surface. On the dorsal surface the anisotropy at the arm was larger than both the wrist, $t(14) = 3.96, p < .001, d = 1.10$, and the hand, $t(14) = 3.89, p < .001, d = 1.08$. There was no reliable difference between the anisotropy at the wrist and the hand, $t(14) = .35, p = .37, d = .10$. On the ventral surface, there were no statistically reliable differences in the PSE values (all t 's $< 1.51, p$'s $> .08$). The interaction between Body Part and Surface appears to be driven by the extremely large anisotropy found on the dorsal forearm.

Interquartile ranges (IQRs). The inter-quartile range (IQR) was calculated as the difference in stimulus ratios where the curve crosses 25% and 75%. This was taken as a measure of precision (see Figure 2, Panel d). A 3 x 2 Mixed ANOVA [Body Part x Surface] revealed a significant effect of Body Part $F(2, 50) = 4.63, p < .05, \eta_p^2 = .16$. A polynomial trend analysis revealed a linear contrast effect of Body Part in the proximodistal dimension, $F(1, 25) = 6.19, p < .05, \eta_p^2 = .20$. The IQRs therefore indicate a linear change in precision; judgements were least sensitive at the forearm but became increasingly more so towards the hand. This is consistent with the previously found proximodistal tactile acuity gradient, which increases linearly from trunk to

extremity (Hamburger, 1980; Weinstein, 1968). Importantly, the lack of a quadratic effect does not correspond with that found in the PSEs, which one might predict if the reduction of the PSE at the wrist was driven solely by changes in tactile acuity. No other effects or interactions were statistically reliable (Surface, $F(1, 25) = 1.88, p > .05, \eta_p^2 = .07$; Body Part by Surface, $F(2, 50) = 1.43, p > .05, \eta_p^2 = .05$).

Discussion

In Experiment 1, we found that the bias to perceive stimuli running across the hand as larger than those running along it (tactile anisotropy, cf. Longo & Haggard, 2011) is also observed farther up the forearm. Crucially however, this tactile spatial anisotropy is smallest at the wrist, as seen in a quadratic trend in this anisotropy of perceived tactile distance observed from arm to wrist to hand. This quadratic trend is consistent with the categorical account - an increase in perceived tactile distances *across* the wrist boundary due to a categorical segmentation of tactile space - rather than a localised and non-specific increase in acuity in the region of the wrist. Indeed, this non-linear trend in anisotropy was not matched by measures of overall sensitivity to differences in tactile distance which increased linearly from the arm to the hand. Nonetheless, whilst, the significant effect of body part on the anisotropy demonstrated a reliable reduction between the arm and the wrist, the trend for a further increase from wrist to hand did not reach significance. In order to attempt to obtain a more robust demonstration of the selective decrease in tactile anisotropy at the wrist we conducted a second experiment in which each participant received twice as many trials. Each participant completed both a dorsal and a ventral surface condition, and so surface was compared within participants in Experiment 2.

Experiment 2

Method

Participants. Fifteen healthy participants (eleven female), aged between 20 and 35 years, participated. All participants, bar two were right handed.

Materials and procedure. The procedure and stimuli were repeated as in Experiment 1 with one change. Namely, each participant took part in both ventral and dorsal surface conditions.

Each participant took part in 12 blocks of trials. These 12 blocks were made up of the six unique combinations of Body Part (Arm, Wrist, Hand) and Surface (Dorsal, Ventral), each of which was presented twice. The 12 blocks were presented in a pseudo-randomised order. Block order was counterbalanced across participants. Each block included 20 trials, in which the 5 distance comparisons were each presented 4 times in a pseudo-randomised order. The 5 distance comparisons compared distances in the mediolateral and proximodistal axes in the following stimulus pairs: 2:4, 2:3, 3:3, 3:2, 4:2 cm.

Statistical analyses. Statistical analyses were the same as those used in Experiment 1 with two exceptions. Firstly, the factor of surface was compared within participants rather than between participants. Secondly, supported by the results of Experiment 1, the critical comparisons to make were those between body parts for each surface separately. For the purpose of this experiment we were not interested in focussed differences in PSEs between each surface for each body part. Therefore given a main effect of Body Part (as predicted by Experiment 1.) we planned to perform two comparisons between PSEs at the wrist and the forearm, and the wrist and the hand. Given a significant interaction between Body Part and Surface (as predicted by Experiment 1.) we planned a series of four comparisons consisting of the above two planned comparisons within each surface separately.

Results

The R-squared scores, averaged across participants, showed a good fit to the data. For dorsal presentations these were 0.84, 0.90 and 0.92 for forearm, wrist, and hand respectively. For ventral presentations these were 0.91, 0.93 and 0.96 for forearm, wrist, and hand respectively. Figure 5 illustrates the cumulative Gaussian functions fitted to the data across Body Part and Surface conditions.

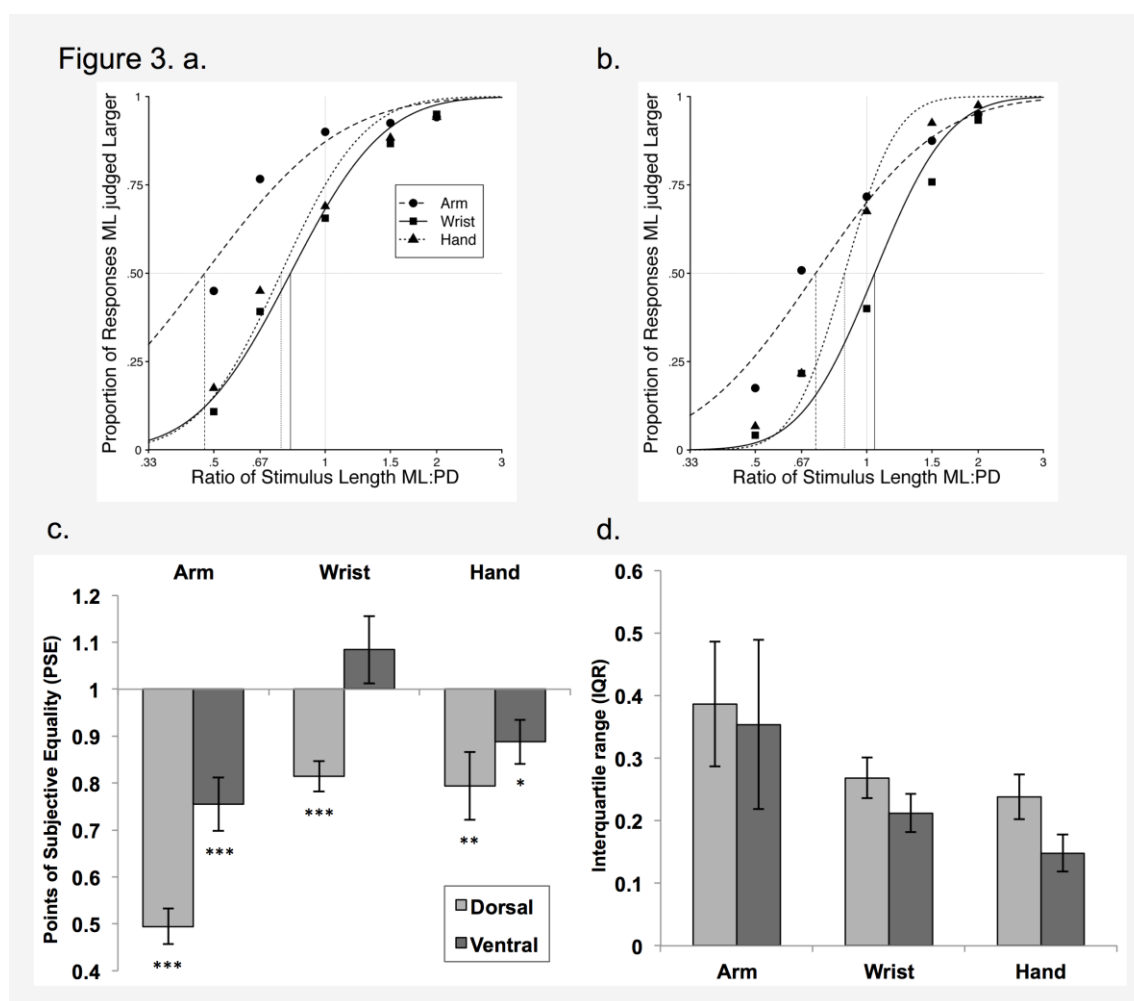


Figure 3. Results of Experiment 2. Panels a to c present raw PSE scores before log-transformation for analysis. Panels (a) and (b) present the proportions of mediolateral (ML) distances judged to be larger plotted as a function of the stimulus ratio (mediolateral:proximodistal, ML:PD): on the dorsal (a) and ventral (b) surfaces. The PSE is the point at which the psychometric function crosses the y-axis at .50. Panel (c) presents points of subjective equality (PSEs) for Arm, Wrist and Hand, split between the Ventral and Dorsal Surfaces. Log-transformed values are presented so that the point 1

on the y-axis represents where the PSE would be veridical, i.e. the ratio of ML and PD response is accurate. Here PSE values below 1 represent more bias towards ML being perceived to be larger than PD. Panel (d) presents Inter-quartile ranges (IQRs) for the Arm, Wrist and Hand between Ventral and Dorsal Surfaces. Asterisks illustrate values that are significantly different from 1 at a level $p < .001$ (***) , $p < .01$ (**) and $p < .05$ (*).

Points-of-Subjective-Equality (PSEs). As in Experiment 1, PSE ratios were log-transformed for further analysis. PSEs were compared against a ratio of 0 using t-tests with Holm's sequential Bonferroni correction in order to detect significant anisotropies, across all body parts and surfaces. Figure 3 (Panel c) shows these findings and indicates which PSEs demonstrate a significant anisotropy. As in Experiment 1, PSEs were less than 0 (indicating significant mediolaterally biased anisotropies; all p 's $< .02$, all t 's > 2.71) on all but the ventral wrist condition ($t = 1.17$, $p = .26$, $d = .30$). On the ventral wrist the PSE was a positive value suggesting a proximodistally-biased anisotropy however this did not reach significance.

We conducted a 3 x 2 ANOVA [Body Part x Surface] on the PSEs. There was a main effect of Body Part, $F(2, 28) = 21.85$, $p < .0001$, $\eta_p^2 = .61$. A polynomial within-subjects trend analysis revealed this effect is both linear, $F(1, 14) = 16.41$, $p < .002$, $\eta_p^2 = .54$ and quadratic, $F(1, 14) = 32.36$, $p < .0001$, $\eta_p^2 = .70$. Critically, the quadratic effect has the strongest effect size and indicates that, whilst there is a progressive linear reduction in anisotropy from forearm to hand, the anisotropy at the wrist is reduced over and above what one would expect given this linear change. This interpretation was confirmed using two focussed t-tests, collapsed across Surface, which showed that the anisotropy on the wrist was significant smaller than that on the forearm, $t(14) = 5.72$, $p < .0001$, $d = 1.48$, and that on the hand, $t(14) = 2.65$, $p < .02$, $d = .69$. The latter of these two tests pits the quadratic variation in anisotropy against that which would be predicted by a linear change in anisotropy. This supports the categorical account, indicating that

perceived tactile distance is specifically elongated proximodistally over the wrist boundary.

There was also a main effect of Surface, $F(1, 14) = 29.94, p < .0001, \eta_p^2 = .68$, with greater PSEs on the ventral surface than on the dorsal surface. This indicates that the bias to perceive distances as being larger in the mediolateral axis was greater on the dorsal than the ventral surface and is consistent with previous findings (Longo and Haggard, 2011).

Finally, there was a significant interaction between Body Part and Surface, $F(2, 28) = 4.24, p < .05, \eta_p^2 = .23$. Consequently we performed the crucial series of four planned comparisons outlined above, comparing the PSE at the wrist against both the hand and the forearm for each Surface condition. Reliably greater anisotropies were observed on the arm than on the wrist [Dorsal, $t(14) = 6.40, p < .0001, d = 1.65$; Ventral, $t(14) = 3.69, p < .01, d = .95$] for both surfaces. A reliable reduction in the anisotropy at the wrist compared to the hand was observed on the ventral surface only [$t(14) = 2.16, p < .05, d = .56$; Dorsal, $t(14) = 1.08, p = .298, d = .28$]. Thus, differences in the PSE on the ventral skin surface reveal a reduction in the PSE at the wrist over and above that predicted by the overall reduction in PSEs as locations move proximodistally down the arm. This pattern of effects falls in line with the predictions made by the categorical account of perceived tactile distance over the wrist. On the dorsal surface however PSEs at the hand and wrist were not reliably different. Figure 3c. indicates that the PSE at the forearm (i.e., greater mediolateral bias) is far greater than either the hand or wrist, this echoes the finding of a large anisotropy specifically on the dorsal forearm in Experiment 1.

2.2. Interquartile ranges (IQRs)

The inter-quartile range (IQR) is calculated as the difference in stimulus ratios where the response curve crosses 25% and 75%. This was taken as a measure of precision (see Figure 3, Panel d). A 3 x 2 Mixed ANOVA [Body Part x Surface] found no significant main effects nor was the interaction significant (all $F_s < 2.05$, $p_s > .17$).

General discussion

Tactile distances are perceived as larger when they cross over the wrist, not whenever they are near the wrist. In two experiments we have found that the bias to perceive stimuli running across the limb as larger than those running along the limb (tactile anisotropy, cf. Longo & Haggard, 2011) is reduced at the wrist. Furthermore, we find no evidence of a corresponding decrease in our measure of precision at the wrist, which one might expect if the effect was solely driven by changes in acuity across the skin surface. These results provide strong support for an account of body representation which argues that tactile space is structured around, and distorted by, body parts and the boundaries between them (see de Vignemont et al., 2006). Put another way, the modulation of tactile distance, such that it is increased over body parts boundaries, demonstrates that tactile space is structured by its categorical properties rather than solely metric ones.

In line with existing data finding that overall tactile acuity is greatest on the fingertip reducing linearly towards the trunk (Hamburger, 1980; Weinstein, 1968), we find a linear relationship in our precision measure. This also appears to be reflected in the magnitude of the anisotropy, showing an inverse linear relationship such that as precision increases anisotropy decreases. The key finding here however is that the anisotropy is further reduced at the wrist, in the absence of a corresponding additional increase in precision. This anisotropy of tactile perception at the wrist is best explained in terms of the categorical segmentation account set out in the introduction. Crossing

category boundaries increases perceived distance, in this case stimuli crossing over the wrist are perceptually elongated. Stimuli which are presented on the wrist but do not cross category boundaries (across stimuli) are unaffected. The elongation of perceived distance in the proximodistal axis only leads to a reduction in the overall mediolateral bias.

We find smaller anisotropies across all body parts on the ventral than on the dorsal surface of the arm and hand. This is likely due to key physiological differences between the two surfaces, the most pertinent here being the higher proportion of mechanoreceptors with small receptive fields on the glabrous skin of the ventral surface (Vallbo, Olausson, Wessberg, & Kakuda, 1995). These receptors are more attuned to processing fine-grained discriminative properties of touch, encompassing tactile distance estimation, and are unsurprisingly found in regions requiring more sensitive tactile acuity such as the fingertip or palm (Edin & Abbs, 1991; Johansson, Trulsson, Olsson, & Westberg, 1988). Conversely, the mechanoreceptors of the hairy skin are characterised by rapidly adapting units with large receptive fields, more proficient with the perception of flutter or gentle strokes. Larger anisotropies across all body parts on the dorsal surface may be a consequence of the less precise discriminative capacity of hairy skin. This may explain the notably larger anisotropy found on the dorsal forearm, which has a similar physiological profile to that of the trunk (Vallbo, Olausson, Wessberg, & Norrsell, 1993) than even the hairy surface of the hand.

When differences in the anisotropies at each body part are considered for each skin surface separately the categorical effect remains for the ventral surface only. This is inline with the findings from de Vignemont's (2009) study, in which the effect was investigated on the ventral surface only. There are a number of reasons that may explain why the categorical effect is more evident on the ventral surface; here we will briefly

discuss visual and functional accounts. Andersen (1978; see also, Biederman, 1987; Brown, 1976) proposes that the mental representation of the body is broken down into visuospatial geons. If body part categories are based on visual discontinuities, those between hand and arm are more evident on the ventral surface; the wrist is typically visibly marked by a number lines segmenting the hand and the arm. Cody et al. (2008) suggest that the joints are more salient than parts as they are regions of increased mechanosensation. The authors suggest that wrist articulation produces agitation of neighbouring receptors along the joint during movement. Following this line of argument the wrist largely moves between its rest position and palm towards ventral arm; rarely do we move our dorsal hand towards dorsal forearm. Therefore increases in mechanosensation around the joint would be expected more on the ventral surface, emphasising the boundary between the body parts.

Here, we find that tactile space is influenced by a category boundary. Whilst category boundaries introduce some bias in how stimuli are perceived they also improve the accuracy of perceptual judgements (Huttenlocher, Hedges, Lourenco, Crawford & Corrigan, 2007). For stimulus-pair judgements, stimuli are made more distinct by category boundaries (Goldstone, 1996; Huttenlocher et al., 2007; Roberson & Davidoff, 2000), leading, for instance, to a perceptual elongation of tactile distance relative to those that fall within a category set (reported here; also de Vignemont et al., 2009). However, for single-stimulus judgements, stimuli close to the boundary become more accurate because they benefit from a more precise comparison of stimulus and boundary information. This very effect is found in tactile localisation studies (Cholewiak & Collins, 2003). Indeed, Cody et al. (2008) find evidence of enhanced localisation at the wrist, though, particularly pertinent for this investigation, only in the proximodistal axis (i.e. the axis which crosses the boundary). These findings corroborate those

presented in this report in indicating that the wrist serves as a category boundary such that tactile space is elongated across the wrist in the proximodistal axis only. Therefore tactile perception is modulated by body-part boundaries (de Vignemont et al., 2006; de Vignemont et al., 2009).

It seems we have an overall propensity to perceive body parts as relatively wider than veridical (Longo & Haggard, 2010, 2011). However, it would appear we also have a construct of the body, segmented into body part categories, which leads to a perceptual elongation of tactile distance over the boundaries/joints. Stimuli within one category set gravitate towards one another. Those that cross the category boundary appear perceptually farther from one another. Although surprising this finding is not implausible. Categorical perception has been shown to produce a perceptual warping effect in a variety of domains (Bornstein, 1990; Harnad, 1990; Inverson & Kuhl, 1995; Regan, 1990; Robertson & Davidoff, 2000). So what are the potential driving forces behind body part categories?

Body part categories are doubtless constructed from a variety of corresponding modes of information. Firstly, category set may be consolidated through linguistics as suggested by Majid, Enfield and Van Staden (2006; also de Vignemont et al., 2009). Action provides further non-arbitrary boundaries that are, perhaps not coincidentally, in parallel to the way we segment the body in thought and speech (Bermudez, 1998). Through limb articulation we perceive the forearm and hand as two separate entities connected by a hinge, and receive additional mechanoreceptive feedback. Furthermore, the hand and arm have different functional roles: the hand, a grasping tool employed more during fine motor functions; the arm, an extender more appropriate for gross motor movements. Supporting this is the remarkable amount of plasticity following active functional use found in the topographic arrangement within the somatosensory cortex

(Hamilton & Pascual-Leone, 1998; Braun, Schweizer, Elbert, Birbaumer, & Taub, 2000). Indeed, neurological cases such as autopagnosia (Buxbaum, Giovannetti, & Libon, 2000) and ideomotor apraxia disrupt topological aspects of body representation. Such disorders lead to specific impairments in processing the structural mereology of the human body in the absence of motor deficits or part relation knowledge of external objects. Last but not least, body parts have very different visual profiles (Biederman, 1987). These various modalities segment the body in an analogous manner, which may in part explain how a categorical representation of the body is robust enough to influence tactile perception.

Recent work on embodied cognition (for review, see Barsalou, 2008) has focused on the idea that cognition is shaped by the milieu of the body. The present results suggest that the relationship between the body and the mind is not a one-way street: Representation of the body is likewise shaped by cognition. This study suggests that tactile information is also referenced to a representation of the body arranged topologically in terms of its parts.

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REFERENCES

- Andersen, E. S. (1978). Lexical universals of body-part terminology. In J. H. Greenberg (Ed.), *Universals of human language* (pp. 335-368). Stanford: Stanford University Press.
- Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, *59*, 617-645.
- Bermudez, J. L. (1998). *The paradox of self-consciousness*. Cambridge, MA: MIT Press.
- Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, *94*, 115–147.
- Bornstein, M. H. (1990). Perceptual categories in vision and audition. In Harnad, S. (Ed.), *Categorical Perception: The groundwork for cognition*. New York: Cambridge University Press.
- Braun, C., Schweizer, R., Elbert, T., Birbaumer, N., & Taub, E. (2000). Differential activation in somatosensory cortex for different discrimination tasks. *Journal of Neuroscience*, *20*, 446–450.
- Brown, C. H. (1976). General principles of human anatomical partonomy and speculations on the growth of partonomic nomenclature. *American Ethnologist*, *3*(3), 400–424.
- Buxbaum, L. J., Giovannetti, T., & Libon, D. (2000). The role of the dynamic body schema in praxis: Evidence from primary progressive praxia. *Brain and Cognition*, *44*, 166-191.
- Cholewiak, R. W. (1999). The perception of tactile distance: Influences of body site, space, and time. *Perception*, *28*, 851-875.
- Cholewiak, R. W., & Collins, A. A. (2003). Vibrotactile localization on the arm: Effects of place, space, and age. *Perception & Psychophysics*, *65*, 1058-1077.

- Cody, F. W. J., Gaarside, R. A. D., Lloyd, D., & Poliakoff, E. (2008). Tactile spatial acuity varies with site and axis in the human upper limb. *Neuroscience Letters*, 433, 103-108.
- Edin, B. B., & Abbs, J. H. (1991). Finger movement responses of cutaneous mechanoreceptors in the dorsal skin of the human hand. *Journal of Neurophysiology*, 65, 657-670.
- Goldstone, R. L. (1996). Isolated and interrelated concepts. *Memory & Cognition*, 24, 608-628.
- Green, B. E. (1982). The perception of distance and location for dual tactile pressures. *Perception and Psychophysics*, 31, 315-323.
- Hagert E., Forsgren S., & Ljung B. O. (2005). Differences in the presence of mechanoreceptors and nerve structures between wrist ligaments may imply differential roles in wrist stabilization. *Journal of Orthopaedic Research*, 23, 757-763.
- Hamburger, H. I. (1980). *Locognosia: The ability to localize tactile stimuli on the body surface*: PhD thesis. Amsterdam: Universiteit van Amsterdam.
- Hamilton, R.H., & Pascual-Leone, A. (1998). Cortical plasticity associated with Braille learning. *Trends in Cognitive Sciences*, 2, 168-174.
- Harnad, S. (1990). *Categorical Perception: The groundwork for cognition*. New York: Cambridge University Press.
- Huttenlocher, J., Hedges, L. V., & Prohaska, V. (1988). Hierarchical organization in ordered domains: Estimating the dates of events. *Psychological Review*, 95, 471-484.

- Huttenlocher, J., Hedges, L. V., Lourenco, S. F., Crawford, L. E., & Corrigan, B. (2007). Estimating stimuli from contrasting categories: Truncation due to boundaries. *Journal of Experimental Psychology: General*, *136*, 502-519.
- Iverson, P., & Kuhl, P.K. (1995). Mapping the perceptual magnet effect for speech using signal detection theory and multidimensional scaling. *Journal of the Acoustical Society of America*, *97*, 553-562.
- Johansson, R. S., Trulsson, M., Olsson, K.A., & Westberg, K. G. (1988). Mechanoreceptor activity from the human face and oral mucosa. *Experimental Brain Research*, *72*, 204-208.
- Kay, P., & Willett, K. (1984). What Is the Sapir-Whorf Hypothesis? *American Anthropologist*, *86*, 65–79.
- Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: Body representation beyond primary somatosensory cortex. *Neuropsychologia*, *48*, 655-668.
- Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences, U.S.A.*, *107*, 11727-11732.
- Longo, M. R., & Haggard, P. (2011). Weber's illusion and body shape: Anisotropy of tactile size perception on the hand. *Journal of Experimental Psychology: Human Perception and Performance*, *37*, 720-726.
- Majid, A., Enfield, N. J., & van Staden, M. (2006). Parts of the body: Cross-linguistic categorisation. *Language Sciences*, *28*, 2–3.
- Mancini, F., Longo, M., R., Iannettic, G. D., & Haggard, P. (2011). A supramodal representation of the body surface. *Neuropsychologia*, *49*, 1194-1201.

- Ochoa, J. L. (2010). Intra-neural microstimulation in humans. *Neuroscience Letters*, 470, 162-167.
- Roberson, D. M. J., & Davidoff, J. (2000). The “categorical perception” of colors and facial expressions: The effect of verbal interference. *Memory & Cognition*, 28, 977–986.
- Taylor-Clarke, M., Jacobsen, P., & Haggard, P. (2004). Keeping the world a constant size: Object constancy in human touch. *Nature Neuroscience*, 7, 219-220.
- Vallbo, A. B., Olausson, H., Wessberg, J., & Norrsell, U. (1993). A system of unmyelinated afferents for innocuous mechanoreception in the human skin. *Brain Research*, 628, 301-304.
- Vallbo, A. B., Olausson, H., Wessberg, J., & Kakuda, N. (1995). Receptive characteristics of tactile units with myelinated afferents in hairy skin of human subjects. *Journal of Physiology*, 483, 783-795.
- de Vignemont, F., Tsakiris, M., & Haggard, P. (2006). Body mereology. In G. Knoblich, I. Thornton, M. Grosjean, & M. Shiffrar (Eds.), *Human body perception from the inside out* (pp. 147-170). New York, NY: Oxford University Press.
- de Vignemont, F., Majid, A., Jola, C., & Haggard, P. (2008). Segmenting the body into parts: Evidence from biases in tactile perception. *Quarterly Journal of Experimental Psychology*, 62, 500-512.
- Weber, E. H. (1996). *De subtilitate tactus* (H. E. Ross, Trans.). In H. E. Ross & D. J. Murray (Eds.), *E. H. Weber on the tactile senses, 2nd ed* (pp. 21-128). London: Academic Press. (Original work published 1834).
- Weinstein, S. (1968). Intensive and extensive aspects of tactile sensitivity as a function of body part, sex, and laterality. In D.R. Kenshalo (Ed.), *The skin senses* (pp. 195-222). Springfield, IL: Charles C Thomas.

