RUNNING HEAD: Anisotropy on the face

Anisotropies of tactile distance perception on the face

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Abstract

The distances between pairs of tactile stimuli oriented across the width of the hand dorsum are perceived as about 40% larger than equivalent distances oriented along the hand length. Clear anisotropies of varying magnitudes have been found on different sites on the limbs and less consistently on other parts of the body, with anisotropies on the centre of the forehead, but not on the belly. Reported anisotropies on the centre of forehead, however, might reflect an artefact of categorical perception from the face midline, which might be comparable to the expansion of tactile distance perception observed for stimuli presented across joint boundaries. To test whether tactile anisotropy is indeed a general characteristic of the tactile representation of the face, we assessed the perceived distance between pairs of touches on the cheeks and three locations on the forehead: left, right and centre. Consistent with previous results, a clear anisotropy was apparent on the centre of the forehead. Importantly, similar anisotropies were also evident on the left and right sides of the forehead and both cheeks. These results provide evidence that anisotropy of perceived tactile distance is not a specific feature of tactile organization at the limbs but it also exists at the face, and further suggest that the spatial distortions found for tactile distances that extend across multiple body parts are not present for stimuli that extend across the body midline.

Keywords: distance perception, anisotropy, categorical perception, face, tactile perception.

Introduction

In one of the first systematic investigations of the sense of touch in the 19th century, Weber (1834) found that as he moved the two points of a compass across his skin it felt to him as if the distance between them increased as he moved them from a region of relatively low sensitivity (e.g., the forearm) to a region of relatively higher sensitivity (e.g., the hand). This pattern has been replicated in numerous subsequent studies (Anema, Wolswijk, Ruis, & Dijkerman, 2008; Cholewiak, 1999; Goudge, 1918; Miller, Longo, & Saygin, 2016; Taylor-Clarke, Jacobsen, & Haggard, 2004), which collectively demonstrate a systematic relation between tactile sensitivity and perceived tactile distance on the skin. Analogous illusions can also be shown for stimuli in different orientations on a single skin surface (e.g., Fiori & Longo, 2018; Green, 1982; Longo & Haggard, 2011). For example, Longo and Haggard (2011) found that tactile distances oriented across the width of the hand dorsum are perceived as about 40% larger than equivalent distances oriented along hand length.

Such anisotropies in perceived tactile distance have been reported on several skin surfaces. In addition to the hand dorsum (Canzoneri et al., 2013; Longo & Golubova, 2017; Longo & Haggard, 2011; Longo & Sadibolova, 2013; Miller, Longo, & Saygin, 2014), other studies have reported anisotropies on the forearm (Green, 1982; Le Cornu Knight, Longo, & Bremner, 2014), the thigh (Green, 1982), and the shin (Stone, Keizer, & Dijkerman, 2018). Intriguingly, in each of these cases, the direction of the anisotropy is similar, with distances perceived as larger when oriented across the width of the limbs than when oriented along their length. Longo and Haggard (2011) suggested that both the classic form of Weber’s illusion and such anisotropies could result from the geometry of tactile receptive fields in somatosensory cortex, which in addition to being smaller on sensitive skin surfaces

(Mountcastle, 2005; Sur, Merzenich, & Kaas, 1980), are generally oval-shaped on the limbs with the long axis of the receptive field aligned with the long axis of the limb (Alloway, Rosenthal, & Burton, 1989; Brooks, Rudomin, & Slayman, 1961). Interestingly, anisotropies on the glabrous skin of the palm are substantially smaller or even absent (Fiori & Longo, 2018; Le Cornu Knight et al., 2014; Longo, Ghosh, & Yahya, 2015), which is consistent with the idea that tactile receptive fields on the palm are circular, and when oval-shaped without a consistent orientation (DiCarlo & Johnson, 2002; DiCarlo, Johnson, & Hsiao, 1998). Moreover, anisotropies of tactile distance differ in magnitude across body parts, which have been found for example to be larger on the forearm than on the hand dorsum (Le Cornu Knight et al., 2014). Thus, assessing the anisotropy of tactile distance across body parts is a powerful tool to assess the structure of tactile spatial perception across the body.

Interestingly, there does not appear to be an anisotropy of tactile distance on the belly (Green, 1982; Longo, Lulciuc, & Sotakova, 2019; Marks et al., 1982), consistent with the interpretation that tactile distance anisotropy is a specific characteristic of the limbs, with their highly elongated shape. Two recent studies, however, have reported anisotropies of tactile distance perception on the face (Fiori & Longo, 2018; Longo et al., 2015). Longo, et al., (2015) used a two-alternative forced-choice paradigm and found that tactile distances oriented across the width of the forehead (i.e., the ear-to-ear axis) were perceived as about 20% larger than comparable distances oriented with the height of the forehead (i.e., the chin-to-forehead axis). Fiori and Longo (2018) asked participants to make verbal size estimates of single tactile distances, and also found an anisotropy with distance across the forehead perceived as larger. However, one notable aspect of both these studies is that they presented stimuli at the centre of the forehead. This means that stimuli presented across the width of the forehead, but not along its height, included one touch on each side of the body midline. It is therefore possible that tactile distance anisotropies on the forehead might indeed reflect an artifact of the across stimuli straddling the face midline, rather than a general characteristic of the tactile representation of the face. Several studies have found perceptual expansion of tactile distances which cross joint boundaries (de Vignemont, Majid, Jola, & Haggard, 2008; Le Cornu Knight, Cowie, & Bremner, 2017; Le Cornu Knight et al., 2014). These studies have found that pairs of tactile stimuli straddling the wrist are overestimated in distance beyond what would be expected given judgments on the adjacent regions of the forearm and hand, indicating a form of categorical perception based on segmentation of the body into discrete parts. In this regard, the body midline could – like joints – produce categorical perception effects for stimuli falling on opposite sides, given the bilateral symmetry of the human body and the fact the tactile signals from each side of the body are sent primarily to the contralateral cerebral hemisphere (Mountcastle, 1957; Penfield & Boldrey, 1937).

To our knowledge no previous studies have investigated a potential effect of the body midline on tactile distance perception. Note that the lack of anisotropy at the center of the belly in previous studies (Green, 1982; Longo et al., 2019; Marks et al., 1982) is not indicative per se of the lack of midline categorical effects, as these studies did not test anisotropy at the side of the belly for comparison. Hence, the reported lack of anisotropy at the center of the belly could be the net combination of positive categorical perception plus a reverse anisotropy effect, where the across stimuli is actually perceived shorter than the along.

In this study, we investigated whether there are anisotropies of perceived tactile distance on the face independent of potential categorical perception induced by the body midline, to first, clarify whether body midline can affect perception in the same way as joint boundaries can, and second, to provide a detailed description of distortions of tactile space in five regions of the face. In Experiment 1, we compared perceived tactile distances across vs. along the left and right sides of the forehead (i.e., entirely on one side of the midline) and the left and right cheeks. In Experiment 2, we directly compared stimuli presented centred on the forehead to stimuli presented entirely on the left or right sides.

Experiment 1

In the first experiment, we measured anisotropies on the left and right sides of the forehead and cheek. Because all stimuli were presented entirely on one side of the body midline, any potential effect of categorical perception based on the midline should not affect results.

Methods

Participants. Twenty-two people (11 women, mean age: 24.0 years, range: 19-35) participated for payment after giving written informed consent. Procedures were approved by the local ethics committee. Testing started on an additional participant but ended after 10 trials due to a technical problem and this participant was excluded. All the participants took part in a second experiment (not involving touch), either on the same day (following the anisotropy task) or a week apart. The data of this experiment is not considered here. Data from three participants were excluded due to poor fitting of the data in one or more conditions (see below).

The two previous studies which investigated tactile distance anisotropies on the face found effect sizes of Cohen's *d* = 1.11 (Longo et al., 2015) and 1.35 (Fiori & Longo, 2018), respectively. Averaging these numbers weighted by their sample sizes (35 and 25) gives an average effect size of Cohen's *d* = 1.21. A power analysis using G*Power 3.1 software (Faul, Erdfelder, Land, & Buchner, 2007) found that 8 participants were required for power of 0.80 and an alpha of 0.05. Our sample size is therefore well powered to identify comparable effects.

Procedures. The stimuli were pairs of wooden sticks which tapered to a point (~1mm) that were embedded in foamboard at distances of 2, 2.5, 3, or 4 cm apart, similar to those we have used in other studies (e.g., Calzolari, Azañón, Danvers, Vallar, & Longo, 2017; Fiori & Longo, 2018; Hidaka, Tucciarelli, Azañón, & Longo, 2020; Longo & Haggard, 2011). On each trial, two pairs of stimuli were applied to the participant's face, one with the two touches oriented across the width of the face (i.e., the ear-to-ear axis) and one oriented along the length of the face (i.e., the chin-to-forehead axis). Each stimulus was applied manually by an experimenter for approximately one second with an inter-stimulus interval of approximately one second. The participant's task was to judge whether the distance between the two points felt farther apart in the along or the across orientation, by making an unspeeded verbal judgment. Across trials, there were seven pairs of distances used, varying in the ratio of distances in the two orientations (across/along): 2/4 cm, 2/3 cm, 2.5/3 cm, 3/3 cm, 3/2.5 cm, 3/2 cm, 4/2 cm.

In different blocks, stimuli were applied to four different locations on the face: the left and right sides of the forehead and the left and right cheeks. On the forehead, we identified the location on each side of the forehead midway between the facial midline (i.e., an upwards continuation of the midline of the nose) and the temple, which formed the centre point for stimuli. For the cheeks, stimuli were applied roughly midway between the lateral edge of the nose and the ear tragus.

There were four experimental blocks, one for each location on the face, which were presented in random order for each participant. Each block consisted of 56 trials, 8 trials for each of the 7 ratios between the across and along distances, half with the across stimulus presented first and half with the along stimulus presented first. The 56 trials in each block were presented in random order. If a given stimulus was perceived as a single touch or as a pair of non-simultaneous touches, that trial was cancelled and repeated at the end of the condition. This procedure was added in case participants presented with a two-point discrimination threshold larger than the smaller of our stimuli (i.e., 2 cm) in a given orientation or location on the face. However, participants overall reported the perception of one (or non-simultaneous stimulation) in less than 1% of the trials (M = 0.79%), which were removed from analyses and re-tested at the end. Regardless of this, the mean two point-point discrimination threshold reported in several studies at the cheeks and forehead is well below 2 cm (Mancini et al., 2014; Sato, Okada, Miyamoto, & Fujiyama, 1999; Vriens & van der Glas, 2009; Won, Kim, Kim, & Kim, 2017). Nevertheless, it does remain possible that on some trials participants may have felt only one touch for one of the stimuli, which could affect the nature of the judgment they made. Participants were allowed to take a short break between blocks. They were blindfolded during the experiment.

Analysis. We analysed the proportion of trials in which the tactile distance across the width of the face 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 skin region 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).

The criteria for exclusion of participants was if the R_2 for the psychometric functions was less than 0.5 in any of the four skin regions, as in other recent studies from our lab (Longo, 2017; Longo et al., 2015; Longo & Morcom, 2016). Three participants were excluded on this basis.

The cumulative Gaussian curve fit to the data has two parameters, the mean and the standard deviation. The mean of the function indicates the point of subjective-equality (PSE), that is the ratio between the across and along stimuli for which participants were equally likely to say that each was bigger. If there is no anisotropy, then the PSE should on average be equal to 1 (i.e., the stimuli should feel the same when they really are the same). If there is a perceptual bias for stimuli to be perceived as bigger when oriented with face height than with face width then PSEs should on average be larger than 1 (i.e., the stimuli would be perceived as the same size when the across stimulus was bigger); in contrast, if there is a bias for stimuli to be perceived as bigger when oriented with face width than height then PSEs should be less than 1 (i.e., the stimuli would be perceived as the same size when the along stimulus was bigger). The second parameter of the psychometric function, the standard deviation is inversely related to the slope of the psychometric function, and therefore to the precision of responses.

To assess anisotropy, we conducted one-sample t-tests comparing mean PSE to a ratio of 1. Note that all statistical tests were performed on the logarithms of PSEs, which were converted back to ratios for reporting mean values. To compare the different skin surfaces, we conducted a 2x2 factorial analysis of variance (ANOVA) including region (forehead, cheek) and laterality (left, right) as within-subject factors and both PSEs and standard deviations as dependent variables.

As measures of effect size, we calculated Cohen’s *d* for one-sample t-tests, d_z for paired t-tests, and η_{p2} for F-statistics.

Results and Discussion

The results from Experiment 1 are shown in Figure 1. R_2 values indicated good fit to the data, with psychometric functions accounting for 86.2% of the variance on the forehead and 92.3% on the cheek. To investigate the presence of anisotropy on the forehead and cheek, we first compared mean PSEs to 1 collapsing across the left and right sides. There was a clear anisotropy on the forehead (*M*: 0.884), $t(18) = -4.71$, $p < 0.0005$, $d = 1.081$, with tactile distances oriented across the width of the forehead perceived as larger than those oriented along forehead height. There was also a clear anisotropy in the same direction on the cheek (*M*: 0.889), $t(18) = -3.99$, $p < 0.001$, $d = 0.915$.

An ANOVA on PSEs revealed a modest effect of laterality, $F(1, 18) = 4.63$, $p = 0.045$, $\eta_{p2} = 0.205$, with larger anisotropy on the left (*M*: 0.860) than on the right side of the face (*M*; 0.913). There was no main effect of skin region, $F(1, 18) = 0.02$, $p > 0.50$, $\eta_{p2} = 0.001$, nor an interaction of region and laterality, $F(1, 18) = 0.33$, $p > 0.50$, $\eta_{p2} = 0.018$.

An ANOVA on the standard deviations of the psychometric functions revealed a significant main effect of body part, $F(1, 18) = 16.94$, $p < 0.001$, $\eta_{p2} = 0.485$, with smaller standard deviations (i.e., higher sensitivity) on the cheek than the forehead. There was also a significant main effect of laterality, $F(1, 18) = 8.35$, $p = 0.010$, $\eta_{p2} =0.317$, with smaller standard deviations on the right side of the face than on the left side. There was no significant interaction between body part and laterality, *F*(1, 18) = 1.88, $p = 0.187$, $\eta_{p2} = 0.095$.

This experiment replicates the anisotropies on the forehead reported in previous studies (Fiori & Longo, 2018; Longo et al., 2015). Critically, because in contrast to those previous studies, stimuli were presented entirely on one side of the face midline, these results demonstrate further that this effect does not require that the across stimuli straddle the face midline.

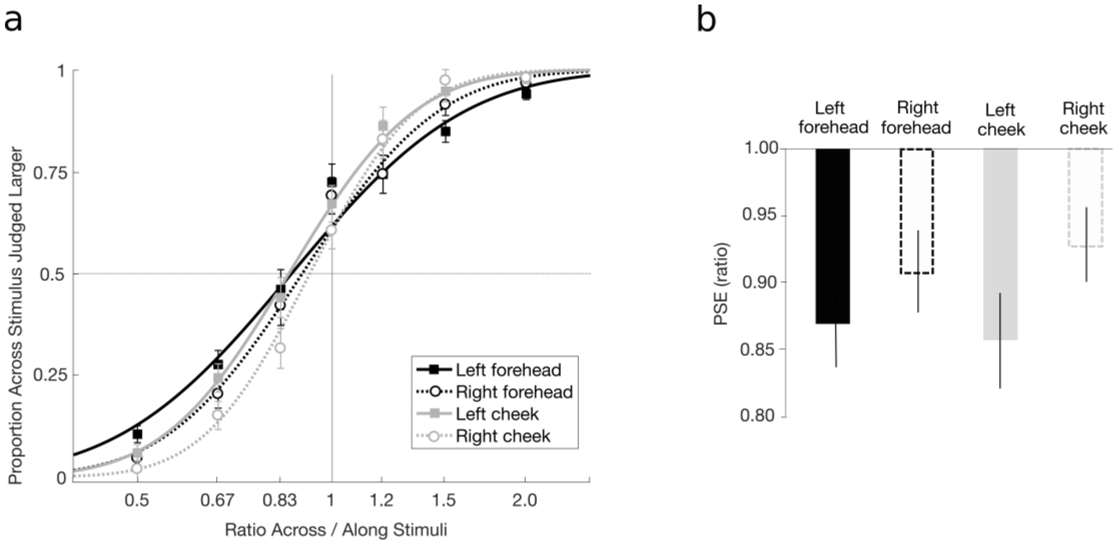

Figure 1. Results from Experiment 1. a) Proportion of "across" stimuli judged larger as a function of the presented ratio (Across/Along). Curves are cumulative Gaussian function fits of the data. All four locations showed anisotropy, with tactile distances oriented across the width of the face perceived as larger than those oriented along height of the face (all points of subjective equality < 1; all $p < 0.025$). b) Ratio between the across and along stimuli for which participants were equally likely to say that each was bigger at each condition (i.e., point of subjective equality, PSE). Error bars represent the standard error of the mean.

Experiment 2

The results from Experiment 1 demonstrate that tactile distance anisotropy on the forehead exists independent of any potential effect of categorical perception from the face midline. However, the magnitude of anisotropy found on the sides of the forehead in Experiment 1 (*M*: 0.887) is somewhat smaller in magnitude than that found previously on the centre of the forehead (*M*: 0.818; Longo et al., 2015). This is consistent with the possibility that there may be a categorical perception effect from the face midline that modulates the magnitude of anisotropy. To investigate this possibility, Experiment 2 compared anisotropy at the centre of the forehead and on the right and left sides of the forehead in the same participants.

Participants

Thirty people (18 women, mean age: 27.6 years, range: 20-45) participated after giving written informed consent. To our knowledge there are five previous experiments which have measured categorical perception effects on tactile distance (all at the wrist): Experiments 1 and 2 of de Vignemont and colleagues (2008), Experiments 1 and 2 of Le Cornu Knight and colleagues (2014), and the single experiment reported by Le Cornu Knight and colleagues (2017). For each of these experiments, we calculated the effect size (Cohen's d_z) for the key comparison of stimuli crossing the wrist to stimuli on the hand. We calculated an average of these effect sizes weighted by the sample size of each experiment, which yielded a mean effect size of Cohen's $d_z = 0.590$. A power analysis using G*Power 3.1 for a two-tailed t-test with this effect size, power of 0.80, alpha of 0.05, indicated that 25 participants were required. Our sample is therefore appropriately powered to identify a comparable effect of the body midline.

Methods

Stimuli were similar to those used in Experiment 1. Across trials, stimuli were presented at three locations on the forehead. The left and right forehead locations were defined as in Experiment 1, while the centre location was in the middle of the forehead, straddling the facial midline, consistent with the location of stimuli in the two other studies that investigated tactile distance on the face (Fiori & Longo, 2018; Longo et al., 2015). There were five pairs of distances used (across/along): 2/4 cm, 2/3 cm, 3/3 cm, 3/2 cm, 4/2 cm, as in previous studies from our lab (e.g., Calzolari et al., 2017; Longo et al., 2015; Longo & Haggard, 2011). The participant's task was to judge whether the distance between the two touches felt bigger for the first or for the second stimulus, rather than indicating whether the along or the across stimulus was larger (as in Experiment 1). This change reduces the likelihood that any biases observed in Experiment 1 might have been due to response bias, to preferentially respond 'across', rather than perceptual bias.

There were 7 blocks of 30 trials each. Each block included 2 repetitions of each pair of distances (14 in total), one with the across stimulus first another with the along stimulus first, at each of the three forehead locations. The order of trials was randomised in each block. Again, a trial was repeated (at the end of the block), if the participant reported feeling one touch rather than two or two asynchronous touches (0.38%).

Analysis

The analysis was similar to that of Experiment 1. We applied the same exclusion criteria (i.e., $R_2 < 0.5$ in any condition), but no participant was excluded. One-sample t-tests were used to compare mean PSE in each condition to a ratio of 1. A one-way repeated-measures analysis of variance (ANOVA) was used to compare the three conditions. Mauchley's test revealed no violation of the sphericity assumption.

Results and Discussion

The results from Experiment 2 are shown in Figure 2. Overall, the psychometric functions showed good fit to the data, with mean R_2 indicating that they accounted for 95.4%, 94.7%, and 96.5% of the variance in the centre, left, and right locations, respectively.

A significant anisotropy was apparent at the centre of the forehead (M: 0.919), $t(29) = -2.38$, $p < 0.05$, $d = 0.435$. Critically, similar anisotropies were also found on the left side of the forehead (M: 0.857), $t(29) = -4.41$, $p < 0.0001$, $d = 0.806$, and the right side (M: 0.912), $t(29) = -2.39$, $p < 0.05$, $d = 0.437$. An ANOVA revealed no significant differences between the three locations, $F(2, 58) = 2.50$, $p = 0.09$, $\eta_{p2} = 0.079$. It is worth noting that of the three testing locations, the numerical magnitude of anisotropy was actually smallest on the centre of the forehead, a trend if anything opposite to what would be expected if there were an effect of categorical perception.

Given the laterality effect observed in Experiment 1, we also compared the magnitude of anisotropy on the left and right forehead. This difference was not statistically significant, $t(29) = -1.64$, $p = 0.111$, $d_z = 0.300$, but the trend was in the same direction as observed in Experiment 1.

An ANOVA on the standard deviation of the psychometric function revealed a significant effect of stimulus location, $F(2, 58) = 5.89$, $p < 0.01$, $\eta_{p2} = 0.169$. Standard deviations were significantly smaller at the centre of the forehead than on the left, $t(29) = -2.37$, $p < 0.05$, $d_z = 0.432$, or the right, $t(29) = -3.07$, $p < 0.005$, $d_z = 0.560$, side. Thus, while there was no evidence that perceptual distances are expanded for stimuli straddling the face midline, sensitivity does appear to be higher *near* the midline. Given the laterality effect on standard deviations found in Experiment 1, we also compared the left and right sides directly, which did not differ significantly, *t*(29) = 1.20, $p > 0.20$, $d_z = 0.218$, with the trend going in the opposite direction to that seen in Experiment 1.

The results of this experiment provide further evidence for the existence of tactile distance anisotropies on the forehead. There was no evidence, however, for a categorical perception effect on tactile distance for stimuli crossing the facial midline. This is in interesting contrast to studies which have reported such effects for stimuli crossing joint boundaries (de Vignemont et al., 2008; Le Cornu Knight et al., 2017, 2014).

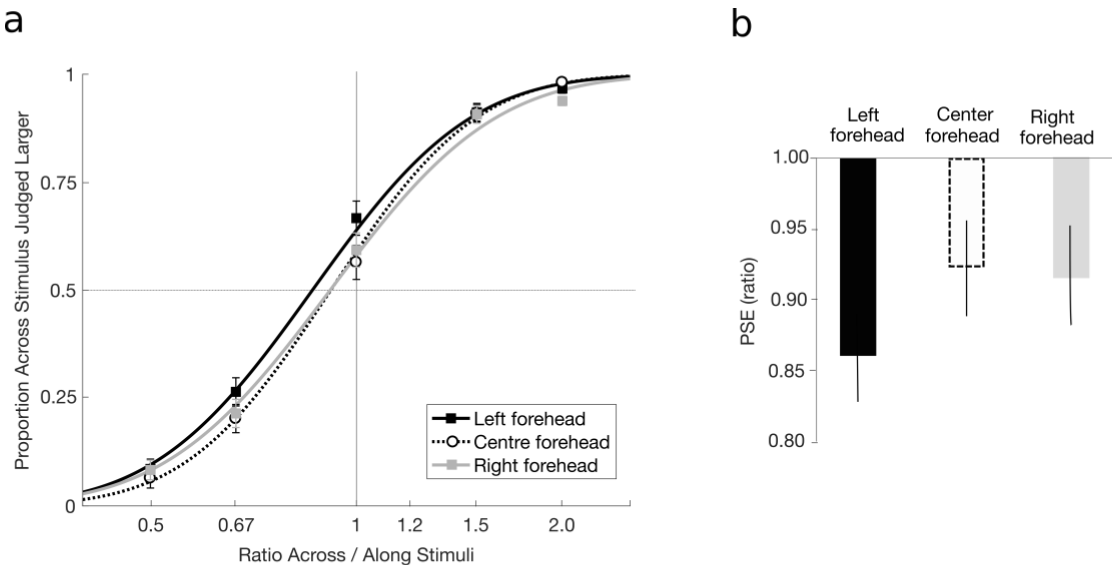

Figure 2. Results from Experiment 2. a) Proportion of "across" stimuli judged larger as a function of the presented ratio (Across/Along). Curves are cumulative Gaussian function fits of the data. All three locations on the forehead showed anisotropy (all points of subjective equality < 1; all $p < 0.05$). b) Ratio between the across and along stimuli for which participants were equally likely to say that each was bigger at each condition (i.e., point of subjective equality, PSE). Error bars represent the standard error of the mean.

Meta-Analysis of Studies Investigating Anisotropy on the Forehead

Four experiments, to our knowledge, have now investigated tactile distance anisotropy on the forehead, the two experiments reported here and two previous studies (Fiori & Longo, 2018; Longo et al., 2015). To aggregate information across these studies, we therefore conducted a random-effects meta-analysis using the *metafor* package (Viechtbauer, 2010) for R 3.4.3 software. The study of Longo and colleagues (2015) used a two-alternative forced-choice method, with anisotropy quantified as the PSE of the psychometric function, as in the two studies reported here. In contrast, in the study of Fiori and Longo (2018) participants made verbal estimates of the size of stimuli in different orientations, with anisotropy quantified as the ratio of judged size in the across and along orientations. Because of this difference in methods, we conducted the meta-analysis on standardised means. Because Cohen's d produces a slight upwards estimation bias, corrected effect sizes (Hedges's g) were used (Borenstein, Hedges, Higgins, & Rothstein, 2009). In each case, positive values of Hedges's g indicate a bias to judge stimuli as larger in the across orientation, and negative values a bias to judge stimuli as larger in the along orientation. The different stimulus locations in the two experiments reported here were collapsed for this analysis.

Figure 3 shows a forest-plot of the results from the meta-analysis. Overall, there was clear evidence for anisotropy on the forehead, with an overall meta-analytic estimate of a large effect size (M: 0.987), $z = 6.58$, $p < 0.0001$, 95% CI = [0.693 – 1.281]. There was no evidence for heterogeneity, $Q(3) = 4.58$, $p > 0.20$, $I_2 = 37.0\%$, indicating that the variability between experiments was not larger than would be expected by chance.

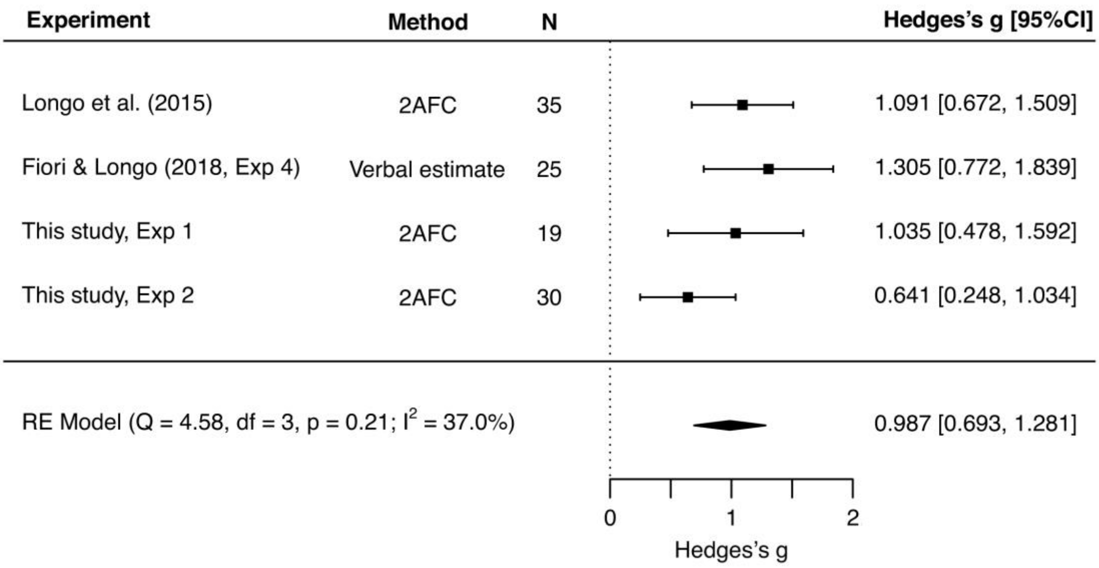

Figure 3: Forest plot showing results from a random-effects meta-analysis of experiments investigating tactile distance anisotropy on the forehead. Positive values of Hedges's g indicate a bias to judge tactile distances as larger when oriented across the width of the forehead. Collectively, these results provide strong evidence for anisotropy on the forehead.

General Discussion

The present results provide clear evidence for anisotropies of tactile distance perception on the face, both on the forehead and the cheek. These results converge with other recent studies (Fiori & Longo, 2018; Longo et al., 2015) in showing that tactile distances oriented across the width of the face (i.e., the ear-to-ear axis) are perceived as larger than distances oriented along the length of the face (i.e., the chin-to-forehead axis). The present results further demonstrate that such effects on the face are not an artefact of the across stimuli straddling the face midline, as clear anisotropies were found for stimuli on both the forehead and cheeks that were entirely on one side of the midline.

These results add to a growing literature showing tactile distance anisotropies across a wide range of skin regions. In addition to the forehead and cheek, biases to judge tactile distance as larger when aligned with body width than with body length have also been found on the hand dorsum (Longo & Golubova, 2017; Longo & Haggard, 2011), the forearm (Green, 1982; Le Cornu Knight et al., 2014), the thigh (Green, 1982), and the shin (Stone et al., 2018). Similar effects have also been found on the palm in a few studies (Fiori & Longo, 2018; Le Cornu Knight et al., 2014; Longo et al., 2015) whereas other studies have found no anisotropy (Green, 1982; Longo & Golubova, 2017; Longo & Haggard, 2011). Even when an anisotropy has been found on the palm, however, it has always been substantially smaller than on the dorsum. The one body part on which no anisotropy has been consistently found in healthy participants is the belly (Green, 1982; Longo et al., 2019; Marks et al., 1982), although recent studies suggest that anisotropy on the belly may occur in conditions such as anorexia nervosa (Engel & Keizer, 2017; Keizer et al., 2011; Keizer, Smeets, Dijkerman, van Elburg, & Postma, 2012; Spitoni et al., 2015) and obesity (Mölbert et al., 2016; Scarpina, Castelnuovo, & Molinari, 2014). The presence of anisotropy on the face is therefore notable in that it is the one non-limb body part on which anisotropy has been consistently found. This demonstrates that anisotropy is not a specific characteristic of the limbs, with their highly elongated shape.

Several recent studies have found categorical perception effects of joint boundaries on tactile distance, with tactile distances straddling the wrist boundary overestimated compared to stimuli on the adjacent regions of the forearm and hand (de Vignemont et al., 2008; Le Cornu Knight et al., 2017, 2014). In the current study, not only was the anisotropy in tactile distance perception on the forehead found not to be an artefact of categorical perception from the face midline, we found no evidence for such categorical perception effects at all. This suggests that whereas joint boundaries may induce discontinuities into tactile perceptual experience, the body midline may not.

It is important to note that in the case of joints, continuous motion provides repeated sensory feedback about the categorical distinction between body parts, which could explain the altered and biased perception across joints, while this is not the case for the two adjacent skin regions separated through the midline. On the other hand, the lack of categorical perception across the midline may be related to inter-hemispheric communication between somatosensory regions and to the distribution of ipsilateral projections of tactile afferent signals. Neurophysiological studies have found that both ipsilateral responses (Conti, Fabri, & Manzoni, 1986; Dreyer, Loe, Metz, & Whitsel, 1975; Iwamura, 2000; Jones & Powell, 1969a) and callosal projections (Jones & Powell, 1969b; Killackey, Gould, Cusick, Pons, & Kaas, 1983; Shanks, Pearson, & Powell, 1985) are stronger for regions close to the midline on both the torso and the face. Analogous results have been reported in humans using both fMRI (Fabri, Polonara, Salvolini, & Manzoni, 2005) and psychophysical (Tamè & Longo, 2015) methods. This pattern has been traditionally interpreted as a mechanism for binding the representations of the two hemi-bodies (Jones & Powell, 1969b; Pandya & Vignolo, 1969), a process of “midline fusion” (Manzoni, Barbaresi, Conti, & Fabri, 1989) analogous to that seen in the visual system to merge the two visual hemi-fields (Hubel & Wiesel, 1967). The absence of categorical perception effects related to the midline may therefore be a result of a specific aspect of somatosensory organisation designed to avoid perceptual discontinuities at the midline.

In contrast to the lack of effects of stimulus location on the forehead on anisotropy, there was an effect on the standard deviation of the psychometric functions. Sensitivity of discriminating tactile distances was higher for stimuli presented at the centre of the forehead than on either the left or right side. Thus, the facial midline may be associated with higher tactile precision, without inducing any spatial distortions. This may be related to the finding that tactile acuity and the precision of tactile localisation are higher in the vicinity of joints than in the centre of limbs (e.g., Boring, 1942; Cody, Garside, Lloyd, & Poliakoff, 2008; Weber, 1834). It is also possible that this enhanced sensitivity near the midline might result directly from the mechanisms described in the previous paragraph. Stimuli near the midline may be processed by mechanisms in both the left and right somatosensory cortices, whereas more lateral stimuli may be processed more exclusively contralaterally.

The finding of anisotropy on both the cheek and forehead, innervated respectively by the maxillary and opthalamic branches of the trigeminal nerve, is notable in light of evidence that the representation of the upper and lower regions of the face may be represented differently. Woolsey and colleagues (Ullrich & Woolsey, 1954; Woolsey, Marshall, & Bard, 1942) reported that trigeminal inputs in monkeys are represented in two distinct regions of the somatosensory cortex, a main trigeminal region and an “upper head area”. Detailed somatotopic maps of the face have found clear segregation of neurons responsive to each of the three divisions of the trigeminal nerve (Dreyer et al., 1975). Similar separation has also been found in the map of the face in New World monkeys (Jain, Qi, Catania, & Kaas, 2001), with separate areas representing the upper and lower face. In humans, studies using fMRI have found inconsistent patterns of activations with regard to the representations of the face in the primary somatosensory cortex (SI). For instance, Iannetti and colleagues (2003), found a large overlap, within both SI and the secondary somatosensory cortex (SII), of the foci activated by mechanical stimulation of the forehead (ophthalmic trigeminal division) and lower lip (mandibular trigeminal division). Moulton and colleagues (2009), on the other hand, found that facial areas stimulated with a brush within an onion-skin layer (i.e., segmenting the face through concentric oval shapes from rostral to caudal), even though at separate stimulation sites and innervated by different branches of the trigeminal nerve, e.g., a section of the forehead and cheek, were closely represented in the cortex (see also Dasilva et al., 2002). On the motor side, there are clear double dissociations for apraxia for the lower and upper face (Bizzozero et al., 2000). Perceptual studies of self-face representation based on the relative localisation of different face parts have identified independent representations of the upper and lower face (Fuentes, Runa, Blanco, Orvalho, & Haggard, 2013) which show different patterns of distortion (Mora, Cowie, Banissy, & Cocchini, 2018). In the present study, however, we found no difference in the nature or magnitude of tactile distance anisotropy on the lower and upper face.

Of course, the anisotropies observed on the cheek and forehead are also similar to those reported on the hand in a number of studies. The qualitatively similar anisotropies found on the face and the hand are intriguing in light of the potential similarities across the shape of receptive fields, as well as functional connections between the representations of these body parts. With regard to the shape of facial receptive fields, there has been several studies focusing on the somatosensory representation of head and face of both monkeys, using invasive electrophysiology (Cusick, Wall, & Kaas, 1986; Dreyer et al., 1975; Manger, Woods, & Jones, 1995) and humans, using microneurography during natural facial behaviors and/or tactile stimulation (Johansson, Trulsson, Olsson, & Abbs, 1988; Nordin & Thomander, 1989; M Trulsson & Essick, 2010; Mats Trulsson & Johansson, 2002). However, the inferred shape of facial receptive fields across the face is sparse and variable, and little is known with regard to the forehead. With regard to potential functional connections, several lines of evidence have shown functional linkages between sensori-motor representations of the face and hands (Gandevia & Phegan, 1999; Gentilucci, Benuzzi, Gangitano, & Grimaldi, 2001; Muret et al., 2014; Ramachandran, Rogers-Ramachandran, Stewart, & Pons, 1992; Serino, Padiglioni, Haggard, & Làdavas, 2009). One recent study of tool-use induced plasticity, however, found no transfer of effect on tactile distance judgments from the hand to the face (Miller, Cawley-Bennett, Longo, & Saygin, 2017). Two other studies that measured plasticity induced by vibration-induced illusions of finger elongation (de Vignemont, Ehrsson, & Haggard, 2005) and by arm immobilization (Bassolino, Finisguerra, Canzoneri, Serino, & Pozzo, 2015) used the face as a comparison region for tactile distances on the hand. Because clear effects were found in both studies comparing the hand and face, any transfer between hand and face could not have been more than partial. Indeed, we are not aware of any studies that have reported transfer of effects on tactile distance judgments between the hand and the face. Moreover, while qualitatively similar anisotropies were reported on the forehead and hands by Longo and colleagues (2015), there was no correlation between these. Thus, the exact relation between anisotropies found on different body parts remains unclear.

The belly is the only body part that has been tested so far were no anisotropy has been found (Green, 1982; Longo et al., 2019; Marks et al., 1982). One could argue that tactile anisotropy is due to the use of a frame of reference within which the applied distances are estimated and compared, using for instance neighboring anatomical landmarks, which are absent in the belly. However, even if landmarks such as joints or facial features may affect tactile distance perception in general, it seems implausible that their use could produce the same type of anisotropies in body parts with very different type of landmarks, such as limbs and faces. Furthermore, there is empirical evidence that the magnitude of anisotropy is not necessarily correlated with the presence or absence of landmarks. For example, anisotropy is substantially smaller (or even absent) on the glabrous skin of the palm compared to the hairy skin of the hand dorsum (Longo, 2019; Longo et al., 2015; Longo & Haggard, 2011), despite the number and location of landmarks being similar on both sides of the hand. Similarly, the magnitude of anisotropy is bigger on the forearm than on the hand dorsum (Le Cornu Knight et al., 2014), though there are more landmarks on the hand.

The distortions of tactile distance perception on the face may be related to other perceptual distortions. Studies of explicit body size estimation have generally reported overestimation of face width, using a range of measures including the moving caliper procedure (Dolan, Birtchnell, & Lacey, 1987; Halmi, Goldberg, & Cunningham, 1977), the image marking procedure (Meermann, 1983), and the adjustable light-beam apparatus (Dolce, Thompson, Register, & Spana, 1987; Thompson & Thompson, 1986). Overestimation of the width of the face has also been reported using a range of other tasks (Bianchi, Savardi, & Bertamini, 2008; D'Amour & Harris, 2017; Fuentes et al., 2013; Mora et al., 2018). It is an intriguing possibility that perceptual distortions such as the ones we have reported here may be linked to distortions of the conscious body image. Indeed, previous studies have provided evidence that tactile distance perception may be linked to higher-level body representations by showing that illusions of body size (de Vignemont et al., 2005; Tajadura-Jiménez et al., 2012; Taylor-Clarke et al., 2004) and tool-use (Canzoneri et al., 2013; Miller et al., 2014; Miller, Longo, & Saygin, 2017) produce corresponding modulations in tactile distance perception.

In Experiment 1 there was a significant effect of laterality, with larger anisotropy on the left side of the face than on the right side. This effect was unpredicted, only marginally significant, and was not replicated in Experiment 2 (which did, however, find a non-significant trend in the same direction). Thus, we do not feel that any strong conclusion about laterality can be drawn. To our knowledge, only one previous study has compared tactile distance perception on the left and right sides of the body. Longo and colleagues (2015) found highly similar anisotropies on the left and right hands, with strong correlations between the two hands, and no hint of a laterality effect. The absence of a laterality effect for tactile distance on the hands mirrors the more general lack of differences between the two hands in tactile spatial acuity (Sathian & Zangaladze, 1996; Vega-Bermudez & Johnson, 2001).

Open Practices Statement

The data for the experiments reported here is available at https://osf.io/y2gmf/ (Open Science Framework). None of the experiments were preregistered.

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Acknowledgments

This study was supported by European Research Council grant ERC-2013-StG-336050 under the FP7 granted to M.R.L. and by European Union Seventh Framework Programme (FP7-PEOPLE-2011-IEF, 302277) granted to E.A.