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RUNNING HEAD: Anisotropy on the face

Anisotropies of tactile distance perception on the face

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Abstract

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

18

19 **Keywords:** distance perception, anisotropy, categorical perception, face, tactile
20 perception.

21

22

23 Introduction

24 In one of the first systematic investigations of the sense of touch in the 19th
25 century, Weber (1834) found that as he moved the two points of a compass across his
26 skin it felt to him as if the distance between them increased as he moved them from a
27 region of relatively low sensitivity (e.g., the forearm) to a region of relatively higher
28 sensitivity (e.g., the hand). This pattern has been replicated in numerous subsequent
29 studies (Anema, Wolswijk, Ruis, & Dijkerman, 2008; Cholewiak, 1999; Goudge,
30 1918; Miller, Longo, & Saygin, 2016; Taylor-Clarke, Jacobsen, & Haggard, 2004),
31 which collectively demonstrate a systematic relation between tactile sensitivity and
32 perceived tactile distance on the skin. Analogous illusions can also be shown for
33 stimuli in different orientations on a single skin surface (e.g., Fiori & Longo, 2018;
34 Green, 1982; Longo & Haggard, 2011). For example, Longo and Haggard (2011)
35 found that tactile distances oriented across the width of the hand dorsum are perceived
36 as about 40% larger than equivalent distances oriented along hand length.

37 Such anisotropies in perceived tactile distance have been reported on several
38 skin surfaces. In addition to the hand dorsum (Canzoneri et al., 2013; Longo &
39 Golubova, 2017; Longo & Haggard, 2011; Longo & Sadibolova, 2013; Miller, Longo,
40 & Saygin, 2014), other studies have reported anisotropies on the forearm (Green,
41 1982; Le Cornu Knight, Longo, & Bremner, 2014), the thigh (Green, 1982), and the
42 shin (Stone, Keizer, & Dijkerman, 2018). Intriguingly, in each of these cases, the
43 direction of the anisotropy is similar, with distances perceived as larger when oriented
44 across the width of the limbs than when oriented along their length. Longo and
45 Haggard (2011) suggested that both the classic form of Weber's illusion and such
46 anisotropies could result from the geometry of tactile receptive fields in
47 somatosensory cortex, which in addition to being smaller on sensitive skin surfaces

48 (Mountcastle, 2005; Sur, Merzenich, & Kaas, 1980), are generally oval-shaped on the
49 limbs with the long axis of the receptive field aligned with the long axis of the limb
50 (Alloway, Rosenthal, & Burton, 1989; Brooks, Rudomin, & Slayman, 1961).

51 Interestingly, anisotropies on the glabrous skin of the palm are substantially smaller or
52 even absent (Fiori & Longo, 2018; Le Cornu Knight et al., 2014; Longo, Ghosh, &
53 Yahya, 2015), which is consistent with the idea that tactile receptive fields on the
54 palm are circular, and when oval-shaped without a consistent orientation (DiCarlo &
55 Johnson, 2002; DiCarlo, Johnson, & Hsiao, 1998). Moreover, anisotropies of tactile
56 distance differ in magnitude across body parts, which have been found for example to
57 be larger on the forearm than on the hand dorsum (Le Cornu Knight et al., 2014).
58 Thus, assessing the anisotropy of tactile distance across body parts is a powerful tool
59 to assess the structure of tactile spatial perception across the body.

60 Interestingly, there does not appear to be an anisotropy of tactile distance on
61 the belly (Green, 1982; Longo, Lulciuc, & Sotakova, 2019; Marks et al., 1982),
62 consistent with the interpretation that tactile distance anisotropy is a specific
63 characteristic of the limbs, with their highly elongated shape. Two recent studies,
64 however, have reported anisotropies of tactile distance perception on the face (Fiori &
65 Longo, 2018; Longo et al., 2015). Longo, et al., (2015) used a two-alternative forced-
66 choice paradigm and found that tactile distances oriented across the width of the
67 forehead (i.e., the ear-to-ear axis) were perceived as about 20% larger than
68 comparable distances oriented with the height of the forehead (i.e., the chin-to-
69 forehead axis). Fiori and Longo (2018) asked participants to make verbal size
70 estimates of single tactile distances, and also found an anisotropy with distance across
71 the forehead perceived as larger. However, one notable aspect of both these studies is
72 that they presented stimuli at the centre of the forehead. This means that stimuli

73 presented across the width of the forehead, but not along its height, included one
74 touch on each side of the body midline. It is therefore possible that tactile distance
75 anisotropies on the forehead might indeed reflect an artifact of the across stimuli
76 straddling the face midline, rather than a general characteristic of the tactile
77 representation of the face. Several studies have found perceptual expansion of tactile
78 distances which cross joint boundaries (de Vignemont, Majid, Jola, & Haggard, 2008;
79 Le Cornu Knight, Cowie, & Bremner, 2017; Le Cornu Knight et al., 2014). These
80 studies have found that pairs of tactile stimuli straddling the wrist are overestimated in
81 distance beyond what would be expected given judgments on the adjacent regions of
82 the forearm and hand, indicating a form of categorical perception based on
83 segmentation of the body into discrete parts. In this regard, the body midline could –
84 like joints – produce categorical perception effects for stimuli falling on opposite
85 sides, given the bilateral symmetry of the human body and the fact the tactile signals
86 from each side of the body are sent primarily to the contralateral cerebral hemisphere
87 (Mountcastle, 1957; Penfield & Boldrey, 1937).

88 To our knowledge no previous studies have investigated a potential effect of
89 the body midline on tactile distance perception. Note that the lack of anisotropy at the
90 center of the belly in previous studies (Green, 1982; Longo et al., 2019; Marks et al.,
91 1982) is not indicative per se of the lack of midline categorical effects, as these
92 studies did not test anisotropy at the side of the belly for comparison. Hence, the
93 reported lack of anisotropy at the center of the belly could be the net combination of
94 positive categorical perception plus a reverse anisotropy effect, where the across
95 stimuli is actually perceived shorter than the along.

96 In this study, we investigated whether there are anisotropies of perceived
97 tactile distance on the face independent of potential categorical perception induced by

98 the body midline, to first, clarify whether body midline can affect perception in the
99 same way as joint boundaries can, and second, to provide a detailed description of
100 distortions of tactile space in five regions of the face. In Experiment 1, we compared
101 perceived tactile distances across vs. along the left and right sides of the forehead (i.e.,
102 entirely on one side of the midline) and the left and right cheeks. In Experiment 2, we
103 directly compared stimuli presented centred on the forehead to stimuli presented
104 entirely on the left or right sides.

105

106

Experiment 1

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

111

112 *Methods*

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

121

122 The two previous studies which investigated tactile distance anisotropies on
123 the face found effect sizes of Cohen's $d = 1.11$ (Longo et al., 2015) and 1.35 (Fiori &
124 Longo, 2018), respectively. Averaging these numbers weighted by their sample sizes
125 (35 and 25) gives an average effect size of Cohen's $d = 1.21$. A power analysis using
126 G*Power 3.1 software (Faul, Erdfelder, Land, & Buchner, 2007) found that 8
127 participants were required for power of 0.80 and an alpha of 0.05. Our sample size is
128 therefore well powered to identify comparable effects.

129

130 *Procedures.* The stimuli were pairs of wooden sticks which tapered to a point
131 (~1mm) that were embedded in foamboard at distances of 2, 2.5, 3, or 4 cm apart,
132 similar to those we have used in other studies (e.g., Calzolari, Azañón, Danvers,
133 Vallar, & Longo, 2017; Fiori & Longo, 2018; Hidaka, Tucciarelli, Azañón, & Longo,
134 2020; Longo & Haggard, 2011). On each trial, two pairs of stimuli were applied to the
135 participant's face, one with the two touches oriented across the width of the face (i.e.,
136 the ear-to-ear axis) and one oriented along the length of the face (i.e., the chin-to-
137 forehead axis). Each stimulus was applied manually by an experimenter for
138 approximately one second with an inter-stimulus interval of approximately one
139 second. The participant's task was to judge whether the distance between the two
140 points felt farther apart in the along or the across orientation, by making an unsped
141 verbal judgment. Across trials, there were seven pairs of distances used, varying in the
142 ratio of distances in the two orientations (across/along): 2/4 cm, 2/3 cm, 2.5/3 cm, 3/3
143 cm, 3/2.5 cm, 3/2 cm, 4/2 cm.

144 In different blocks, stimuli were applied to four different locations on the face:
145 the left and right sides of the forehead and the left and right cheeks. On the forehead,
146 we identified the location on each side of the forehead midway between the facial

147 midline (i.e., an upwards continuation of the midline of the nose) and the temple,
148 which formed the centre point for stimuli. For the cheeks, stimuli were applied
149 roughly midway between the lateral edge of the nose and the ear tragus.

150 There were four experimental blocks, one for each location on the face, which
151 were presented in random order for each participant. Each block consisted of 56 trials,
152 8 trials for each of the 7 ratios between the across and along distances, half with the
153 across stimulus presented first and half with the along stimulus presented first. The 56
154 trials in each block were presented in random order. If a given stimulus was perceived
155 as a single touch or as a pair of non-simultaneous touches, that trial was cancelled and
156 repeated at the end of the condition. This procedure was added in case participants
157 presented with a two-point discrimination threshold larger than the smaller of our
158 stimuli (i.e., 2 cm) in a given orientation or location on the face. However,
159 participants overall reported the perception of one (or non-simultaneous stimulation)
160 in less than 1% of the trials ($M = 0.79\%$), which were removed from analyses and re-
161 tested at the end. Regardless of this, the mean two point-point discrimination
162 threshold reported in several studies at the cheeks and forehead is well below 2 cm
163 (Mancini et al., 2014; Sato, Okada, Miyamoto, & Fujiyama, 1999; Vriens & van der
164 Glas, 2009; Won, Kim, Kim, & Kim, 2017). Nevertheless, it does remain possible that
165 on some trials participants may have felt only one touch for one of the stimuli, which
166 could affect the nature of the judgment they made. Participants were allowed to take a
167 short break between blocks. They were blindfolded during the experiment.

168 *Analysis.* We analysed the proportion of trials in which the tactile distance
169 across the width of the face was judged as larger as a function of the ratio of the
170 across and along stimuli, plotted logarithmically to produce a symmetric distribution
171 around a ratio of 1 (i.e., the ratio at which the two distances were the same size). Data

172 from each skin region in each participant was fit with a cumulative Gaussian function
173 using maximum-likelihood estimation with the Palamedes toolbox (Prins & Kingdom,
174 2009) for MATLAB (Mathworks, Natick, MA).

175 The criteria for exclusion of participants was if the R^2 for the psychometric
176 functions was less than 0.5 in any of the four skin regions, as in other recent studies
177 from our lab (Longo, 2017; Longo et al., 2015; Longo & Morcom, 2016). Three
178 participants were excluded on this basis.

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

193 To assess anisotropy, we conducted one-sample t-tests comparing mean PSE
194 to a ratio of 1. Note that all statistical tests were performed on the logarithms of PSEs,
195 which were converted back to ratios for reporting mean values. To compare the
196 different skin surfaces, we conducted a 2x2 factorial analysis of variance (ANOVA)

197 including region (forehead, cheek) and laterality (left, right) as within-subject factors
 198 and both PSEs and standard deviations as dependent variables.

199 As measures of effect size, we calculated Cohen's d for one-sample t-tests, d_z
 200 for paired t-tests, and η_p^2 for F-statistics.

201

202 *Results and Discussion*

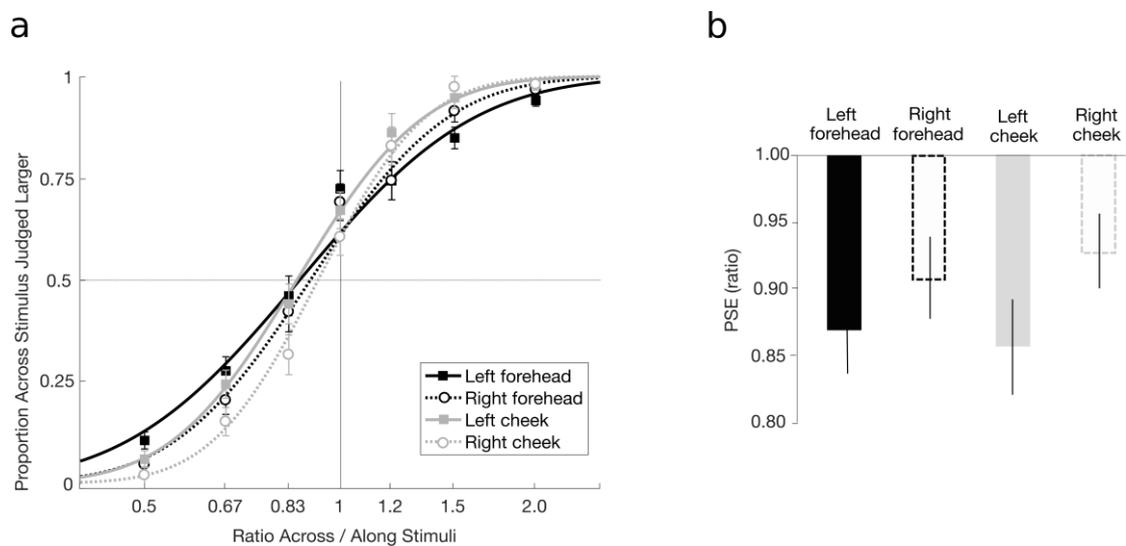
203 The results from Experiment 1 are shown in Figure 1. R^2 values indicated
 204 good fit to the data, with psychometric functions accounting for 86.2% of the variance
 205 on the forehead and 92.3% on the cheek. To investigate the presence of anisotropy on
 206 the forehead and cheek, we first compared mean PSEs to 1 collapsing across the left
 207 and right sides. There was a clear anisotropy on the forehead ($M: 0.884$), $t(18) = -$
 208 4.71 , $p < 0.0005$, $d = 1.081$, with tactile distances oriented across the width of the
 209 forehead perceived as larger than those oriented along forehead height. There was
 210 also a clear anisotropy in the same direction on the cheek ($M: 0.889$), $t(18) = -3.99$, p
 211 < 0.001 , $d = 0.915$.

212 An ANOVA on PSEs revealed a modest effect of laterality, $F(1, 18) = 4.63$, p
 213 $= 0.045$, $\eta_p^2 = 0.205$, with larger anisotropy on the left ($M: 0.860$) than on the right
 214 side of the face ($M: 0.913$). There was no main effect of skin region, $F(1, 18) = 0.02$,
 215 $p > 0.50$, $\eta_p^2 = 0.001$, nor an interaction of region and laterality, $F(1, 18) = 0.33$, $p >$
 216 0.50 , $\eta_p^2 = 0.018$.

217 An ANOVA on the standard deviations of the psychometric functions revealed
 218 a significant main effect of body part, $F(1, 18) = 16.94$, $p < 0.001$, $\eta_p^2 = 0.485$, with
 219 smaller standard deviations (i.e., higher sensitivity) on the cheek than the forehead.
 220 There was also a significant main effect of laterality, $F(1, 18) = 8.35$, $p = 0.010$, η_p^2
 221 $= 0.317$, with smaller standard deviations on the right side of the face than on the left

222 side. There was no significant interaction between body part and laterality, $F(1, 18) =$
 223 $1.88, p = 0.187, \eta_p^2 = 0.095$.

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



229 **Figure 1.** Results from Experiment 1. a) Proportion of “across” stimuli judged larger as a function of
 230 the presented ratio (Across/Along). Curves are cumulative Gaussian function fits of the data. All four
 231 locations showed anisotropy, with tactile distances oriented across the width of the face perceived as
 232 larger than those oriented along height of the face (all points of subjective equality < 1 ; all $p < 0.025$).
 233 b) Ratio between the across and along stimuli for which participants were equally likely to say that
 234 each was bigger at each condition (i.e., point of subjective equality, PSE). Error bars represent the
 235 standard error of the mean.
 236

237

238 Experiment 2

239 The results from Experiment 1 demonstrate that tactile distance anisotropy on
 240 the forehead exists independent of any potential effect of categorical perception from
 241 the face midline. However, the magnitude of anisotropy found on the sides of the

242 forehead in Experiment 1 (M : 0.887) is somewhat smaller in magnitude than that
243 found previously on the centre of the forehead (M : 0.818; Longo et al., 2015). This is
244 consistent with the possibility that there may be a categorical perception effect from
245 the face midline that modulates the magnitude of anisotropy. To investigate this
246 possibility, Experiment 2 compared anisotropy at the centre of the forehead and on the
247 right and left sides of the forehead in the same participants.

248

249 *Participants*

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

263

264 *Methods*

265 Stimuli were similar to those used in Experiment 1. Across trials, stimuli were
266 presented at three locations on the forehead. The left and right forehead locations

267 were defined as in Experiment 1, while the centre location was in the middle of the
268 forehead, straddling the facial midline, consistent with the location of stimuli in the
269 two other studies that investigated tactile distance on the face (Fiori & Longo, 2018;
270 Longo et al., 2015). There were five pairs of distances used (across/along): 2/4 cm,
271 2/3 cm, 3/3 cm, 3/2 cm, 4/2 cm, as in previous studies from our lab (e.g., Calzolari et
272 al., 2017; Longo et al., 2015; Longo & Haggard, 2011). The participant's task was to
273 judge whether the distance between the two touches felt bigger for the first or for the
274 second stimulus, rather than indicating whether the along or the across stimulus was
275 larger (as in Experiment 1). This change reduces the likelihood that any biases
276 observed in Experiment 1 might have been due to response bias, to preferentially
277 respond 'across', rather than perceptual bias.

278 There were 7 blocks of 30 trials each. Each block included 2 repetitions of
279 each pair of distances (14 in total), one with the across stimulus first another with the
280 along stimulus first, at each of the three forehead locations. The order of trials was
281 randomised in each block. Again, a trial was repeated (at the end of the block), if the
282 participant reported feeling one touch rather than two or two asynchronous touches
283 (0.38%).

284

285 *Analysis*

286 The analysis was similar to that of Experiment 1. We applied the same
287 exclusion criteria (i.e., $R^2 < 0.5$ in any condition), but no participant was excluded.
288 One-sample t-tests were used to compare mean PSE in each condition to a ratio of 1.
289 A one-way repeated-measures analysis of variance (ANOVA) was used to compare
290 the three conditions. Mauchley's test revealed no violation of the sphericity
291 assumption.

292

293 *Results and Discussion*

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

298 A significant anisotropy was apparent at the centre of the forehead ($M: 0.919$),
299 $t(29) = -2.38, p < 0.05, d = 0.435$. Critically, similar anisotropies were also found on
300 the left side of the forehead ($M: 0.857$), $t(29) = -4.41, p < 0.0001, d = 0.806$, and the
301 right side ($M: 0.912$), $t(29) = -2.39, p < 0.05, d = 0.437$. An ANOVA revealed no
302 significant differences between the three locations, $F(2, 58) = 2.50, p = 0.09, \eta_p^2 =$
303 0.079 . It is worth noting that of the three testing locations, the numerical magnitude of
304 anisotropy was actually smallest on the centre of the forehead, a trend if anything
305 opposite to what would be expected if there were an effect of categorical perception.

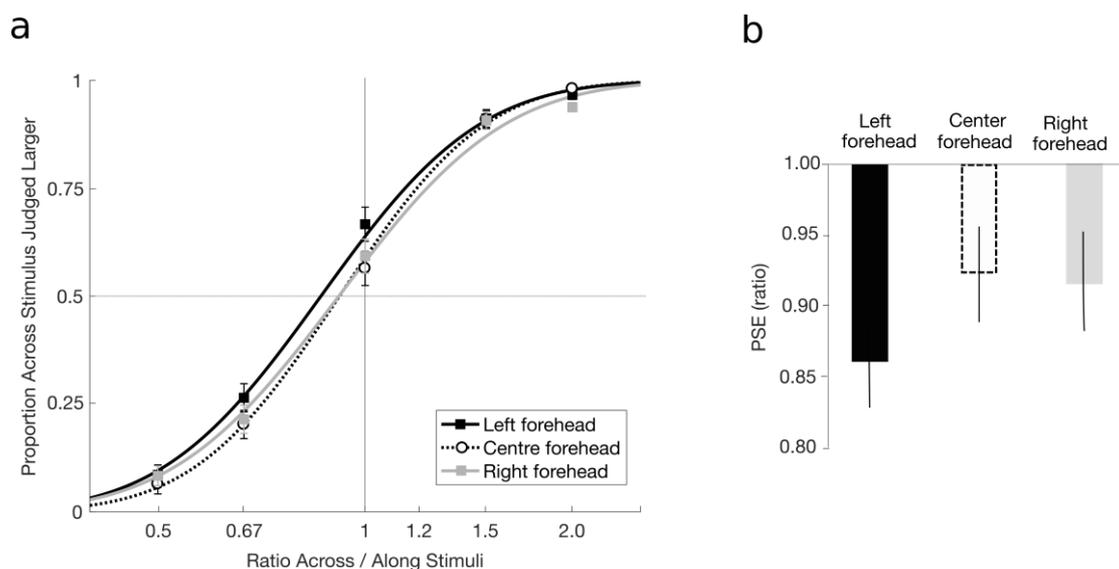
306 Given the laterality effect observed in Experiment 1, we also compared the
307 magnitude of anisotropy on the left and right forehead. This difference was not
308 statistically significant, $t(29) = -1.64, p = 0.111, d_z = 0.300$, but the trend was in the
309 same direction as observed in Experiment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

310 An ANOVA on the standard deviation of the psychometric function revealed a
311 significant effect of stimulus location, $F(2, 58) = 5.89, p < 0.01, \eta_p^2 = 0.169$. Standard
312 deviations were significantly smaller at the centre of the forehead than on the left,
313 $t(29) = -2.37, p < 0.05, d_z = 0.432$, or the right, $t(29) = -3.07, p < 0.005, d_z = 0.560$,
314 side. Thus, while there was no evidence that perceptual distances are expanded for
315 stimuli straddling the face midline, sensitivity does appear to be higher *near* the
316 midline. Given the laterality effect on standard deviations found in Experiment 1, we

317 also compared the left and right sides directly, which did not differ significantly, $t(29)$
 318 $= 1.20$, $p > 0.20$, $d_z = 0.218$, with the trend going in the opposite direction to that seen
 319 in Experiment 1.

320 The results of this experiment provide further evidence for the existence of
 321 tactile distance anisotropies on the forehead. There was no evidence, however, for a
 322 categorical perception effect on tactile distance for stimuli crossing the facial midline.
 323 This is in interesting contrast to studies which have reported such effects for stimuli
 324 crossing joint boundaries (de Vignemont et al., 2008; Le Cornu Knight et al., 2017,
 325 2014).

326



327

328

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

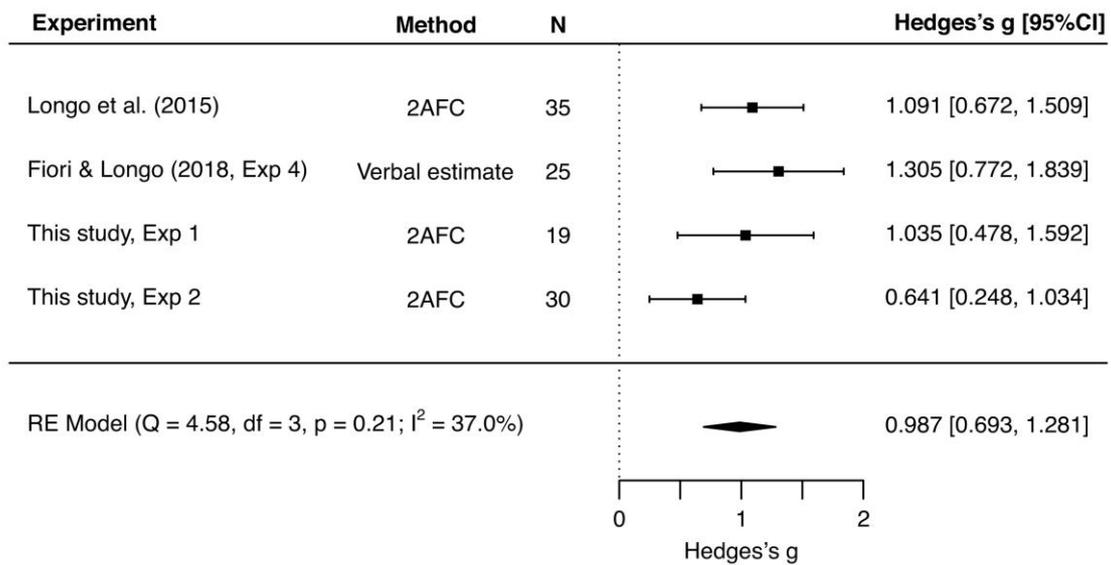
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336 *Meta-Analysis of Studies Investigating Anisotropy on the Forehead*

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

354 Figure 3 shows a forest-plot of the results from the meta-analysis. Overall,
355 there was clear evidence for anisotropy on the forehead, with an overall meta-analytic
356 estimate of a large effect size ($M: 0.987$), $z = 6.58$, $p < 0.0001$, 95% CI = [0.693 –
357 1.281]. There was no evidence for heterogeneity, $Q(3) = 4.58$, $p > 0.20$, $I^2 = 37.0\%$,
358 indicating that the variability between experiments was not larger than would be
359 expected by chance.

360



361

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

367

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General Discussion

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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.

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

397 Several recent studies have found categorical perception effects of joint
398 boundaries on tactile distance, with tactile distances straddling the wrist boundary
399 overestimated compared to stimuli on the adjacent regions of the forearm and hand
400 (de Vignemont et al., 2008; Le Cornu Knight et al., 2017, 2014). In the current study,
401 not only was the anisotropy in tactile distance perception on the forehead found not to
402 be an artefact of categorical perception from the face midline, we found no evidence

403 for such categorical perception effects at all. This suggests that whereas joint
404 boundaries may induce discontinuities into tactile perceptual experience, the body
405 midline may not.

406 It is important to note that in the case of joints, continuous motion provides
407 repeated sensory feedback about the categorical distinction between body parts, which
408 could explain the altered and biased perception across joints, while this is not the case
409 for the two adjacent skin regions separated through the midline. On the other hand,
410 the lack of categorical perception across the midline may be related to inter-
411 hemispheric communication between somatosensory regions and to the distribution of
412 ipsilateral projections of tactile afferent signals. Neurophysiological studies have
413 found that both ipsilateral responses (Conti, Fabri, & Manzoni, 1986; Dreyer, Loe,
414 Metz, & Whitsel, 1975; Iwamura, 2000; Jones & Powell, 1969a) and callosal
415 projections (Jones & Powell, 1969b; Killackey, Gould, Cusick, Pons, & Kaas, 1983;
416 Shanks, Pearson, & Powell, 1985) are stronger for regions close to the midline on
417 both the torso and the face. Analogous results have been reported in humans using
418 both fMRI (Fabri, Polonara, Salvolini, & Manzoni, 2005) and psychophysical (Tamè
419 & Longo, 2015) methods. This pattern has been traditionally interpreted as a
420 mechanism for binding the representations of the two hemi-bodies (Jones & Powell,
421 1969b; Pandya & Vignolo, 1969), a process of “midline fusion” (Manzoni, Barbaresi,
422 Conti, & Fabri, 1989) analogous to that seen in the visual system to merge the two
423 visual hemi-fields (Hubel & Wiesel, 1967). The absence of categorical perception
424 effects related to the midline may therefore be a result of a specific aspect of
425 somatosensory organisation designed to avoid perceptual discontinuities at the
426 midline.

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

439 The finding of anisotropy on both the cheek and forehead, innervated
440 respectively by the maxillary and ophthalmic branches of the trigeminal nerve, is
441 notable in light of evidence that the representation of the upper and lower regions of
442 the face may be represented differently. Woolsey and colleagues (Ullrich & Woolsey,
443 1954; Woolsey, Marshall, & Bard, 1942) reported that trigeminal inputs in monkeys
444 are represented in two distinct regions of the somatosensory cortex, a main trigeminal
445 region and an “upper head area”. Detailed somatotopic maps of the face have found
446 clear segregation of neurons responsive to each of the three divisions of the trigeminal
447 nerve (Dreyer et al., 1975). Similar separation has also been found in the map of the
448 face in New World monkeys (Jain, Qi, Catania, & Kaas, 2001), with separate areas
449 representing the upper and lower face. In humans, studies using fMRI have found
450 inconsistent patterns of activations with regard to the representations of the face in the
451 primary somatosensory cortex (SI). For instance, Iannetti and colleagues (2003),

452 found a large overlap, within both SI and the secondary somatosensory cortex (SII),
453 of the foci activated by mechanical stimulation of the forehead (ophthalmic trigeminal
454 division) and lower lip (mandibular trigeminal division). Moulton and colleagues
455 (2009), on the other hand, found that facial areas stimulated with a brush within an
456 onion-skin layer (i.e., segmenting the face through concentric oval shapes from rostral
457 to caudal), even though at separate stimulation sites and innervated by different
458 branches of the trigeminal nerve, e.g., a section of the forehead and cheek, were
459 closely represented in the cortex (see also Dasilva et al., 2002). On the motor side,
460 there are clear double dissociations for apraxia for the lower and upper face
461 (Bizzozero et al., 2000). Perceptual studies of self-face representation based on the
462 relative localisation of different face parts have identified independent representations
463 of the upper and lower face (Fuentes, Runa, Blanco, Orvalho, & Haggard, 2013)
464 which show different patterns of distortion (Mora, Cowie, Banissy, & Cocchini,
465 2018). In the present study, however, we found no difference in the nature or
466 magnitude of tactile distance anisotropy on the lower and upper face.

467 Of course, the anisotropies observed on the cheek and forehead are also
468 similar to those reported on the hand in a number of studies. The qualitatively similar
469 anisotropies found on the face and the hand are intriguing in light of the potential
470 similarities across the shape of receptive fields, as well as functional connections
471 between the representations of these body parts. With regard to the shape of facial
472 receptive fields, there has been several studies focusing on the somatosensory
473 representation of head and face of both monkeys, using invasive electrophysiology
474 (Cusick, Wall, & Kaas, 1986; Dreyer et al., 1975; Manger, Woods, & Jones, 1995)
475 and humans, using microneurography during natural facial behaviors and/or tactile
476 stimulation (Johansson, Trulsson, Olsson, & Abbs, 1988; Nordin & Thomander,

477 1989; M Trulsson & Essick, 2010; Mats Trulsson & Johansson, 2002). However, the
478 inferred shape of facial receptive fields across the face is sparse and variable, and
479 little is known with regard to the forehead. With regard to potential functional
480 connections, several lines of evidence have shown functional linkages between
481 sensori-motor representations of the face and hands (Gandevia & Phegan, 1999;
482 Gentilucci, Benuzzi, Gangitano, & Grimaldi, 2001; Muret et al., 2014;
483 Ramachandran, Rogers-Ramachandran, Stewart, & Pons, 1992; Serino, Padiglioni,
484 Haggard, & Làdavas, 2009). One recent study of tool-use induced plasticity, however,
485 found no transfer of effect on tactile distance judgments from the hand to the face
486 (Miller, Cawley-Bennett, Longo, & Saygin, 2017). Two other studies that measured
487 plasticity induced by vibration-induced illusions of finger elongation (de Vignemont,
488 Ehrsson, & Haggard, 2005) and by arm immobilization (Bassolino, Finisguerra,
489 Canzoneri, Serino, & Pozzo, 2015) used the face as a comparison region for tactile
490 distances on the hand. Because clear effects were found in both studies comparing the
491 hand and face, any transfer between hand and face could not have been more than
492 partial. Indeed, we are not aware of any studies that have reported transfer of effects
493 on tactile distance judgments between the hand and the face. Moreover, while
494 qualitatively similar anisotropies were reported on the forehead and hands by Longo
495 and colleagues (2015), there was no correlation between these. Thus, the exact
496 relation between anisotropies found on different body parts remains unclear.

497 The belly is the only body part that has been tested so far where no anisotropy
498 has been found (Green, 1982; Longo et al., 2019; Marks et al., 1982). One could
499 argue that tactile anisotropy is due to the use of a frame of reference within which the
500 applied distances are estimated and compared, using for instance neighboring
501 anatomical landmarks, which are absent in the belly. However, even if landmarks

502 such as joints or facial features may affect tactile distance perception in general, it
503 seems implausible that their use could produce the same type of anisotropies in body
504 parts with very different type of landmarks, such as limbs and faces. Furthermore,
505 there is empirical evidence that the magnitude of anisotropy is not necessarily
506 correlated with the presence or absence of landmarks. For example, anisotropy is
507 substantially smaller (or even absent) on the glabrous skin of the palm compared to
508 the hairy skin of the hand dorsum (Longo, 2019; Longo et al., 2015; Longo &
509 Haggard, 2011), despite the number and location of landmarks being similar on both
510 sides of the hand. Similarly, the magnitude of anisotropy is bigger on the forearm than
511 on the hand dorsum (Le Cornu Knight et al., 2014), though there are more landmarks
512 on the hand.

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

527 al., 2013; Miller et al., 2014; Miller, Longo, & Saygin, 2017) produce corresponding
528 modulations in tactile distance perception.

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

540

541 **Open Practices Statement**

542

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

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