Tactile distance anisotropy on the palm: A meta-analysis

Matthew R. Longo[1]

Abstract

Illusions of the perceived distance between two touches on the skin have been studied since the classic work of Weber in the 19th century. For example, anisotropies of perceived tactile distance have been consistently found on several body parts, including the hand dorsum, the forearm, and the face. In each case, tactile distances that are oriented across body width are perceived as being larger than those oriented along body length. Several studies have investigated tactile distance anisotropy on the glabrous skin of the palm of the hand, but they have reached inconsistent conclusions—with some studies finding no anisotropy, and others finding an anisotropy analogous to that found on the dorsum. Given these inconsistencies, the aim of this study was to conduct a systematic meta-analysis of the existing data regarding anisotropy on the palm. A total of ten experiments were identified, which overall provided strong evidence for an anisotropy on the palm (Hedges's $g = 0.521$), with distances aligned with hand width being perceived as approximately 10% bigger than distances aligned with hand length. While this anisotropy is analogous to that found on the hand dorsum, it is substantially smaller in magnitude, and the two biases appear to be uncorrelated. The present results show that, despite inconsistent results across studies, the existing data do indicate an anisotropy of tactile distance on the palm of the hand.

Keywords Touch · Spatial cognition

The sense of touch is a rich source of spatial information about the world. Touch has sometimes been claimed to provide more veridical or reliable spatial information than other senses do, as in Bishop Berkeley's (1709) famous claim that touch is used to calibrate vision. Indeed, recent research has shown that in ambiguous situations, people show more confidence in touch than in vision (Fairhurst, Travers, Hayward, & Deroy, 2018). There is, nevertheless, a substantial literature on spatial distortions and illusion in touch. In his classic studies in the 19th century, E. H. Weber (1834) reported that the perceived distance between two points of a compass touching the skin felt farther apart when applied to a highly sensitive region of skin (such as the palm) than when applied to a less sensitive region (such as the forearm). Subsequent work has replicated Weber's observations and documented a systematic relation across the skin surface between tactile acuity and perceived tactile distance, an effect known as *Weber's illusion* (Anema, Wolswijk, Ruis, & Dijkerman, 2008; Cholewiak, 1999; Fitt,

1917; Goudge, 1918; Marks et al., 1982; Miller, Longo, & Saygin, 2016; Taylor-Clarke, Jacobsen, & Haggard, 2004).

Recent research has revealed deep links between the perception of tactile distance and aspects of higher-level body representation. Perceived tactile distance has been found to change systematically as a result of illusions altering perceived body size (de Vignemont, Ehrsson, & Haggard, 2005; Tajadura-Jiménez et al., 2012; Taylor-Clarke et al., 2004), tool use (Canzoneri et al., 2013; Miller, Cawley-Bennett, Longo, & Saygin, 2017; Miller, Longo, & Saygin, 2014, 2017), vision of the body (Longo & Sadibolova, 2013), and categorical segmentation of the body into distinct parts (de Vignemont, Majid, Jola, & Haggard, 2008; Le Cornu Knight, Cowie, & Bremner, 2017; Le Cornu Knight, Longo, & Bremner, 2014). Other studies have found that tactile distance perception is systematically altered in a variety of clinical conditions, including eating disorders (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). Thus, perception of tactile distance appears integrated with various other aspects of perception and cognition and is a valuable research tool for both basic and clinical research on body representation.

✉ Matthew R. Longo
m.longo@bbk.ac.uk

[1] Department of Psychological Sciences, Birkbeck University of London, London, UK

The original tactile distance illusions reported by Weber (1834) involved comparisons of perceived tactile distance on different skin surfaces. Analogous illusions have also been described based on the orientation of stimuli on individual skin surfaces, with many studies reporting anisotropies in which perceived tactile distance differs across orientations. Such anisotropies have been reported on the forearm (Green, 1982; Le Cornu Knight et al., 2014), the hand dorsum (Longo & Golubova, 2017; Longo & Haggard, 2011), the thigh (Green, 1982), the shin (Stone, Keizer, & Dijkerman, 2018), and the face (Fiori & Longo, 2018; Longo, Ghosh, & Yahya, 2015). Notably, in each of the cases the biases reported involve overestimation of distances oriented with the width of the body as compared with distances oriented with the length (or height) of the body. My colleagues and I (Longo, 2017; Longo & Haggard, 2011) have argued that this relates to known anisotropies in the geometry of the receptive fields of tactile neurons in the spinal cord (P. B. Brown, Fuchs, & Tapper, 1975) and primary somatosensory cortex (Alloway, Rosenthal, & Burton, 1989; Brooks, Rudomin, & Slayman, 1961), which are generally elongated along the proximo-distal limb axis.

Although the known anisotropies in tactile distance perception all involve overestimation of distance aligned with body width versus length, anisotropy does vary in magnitude across the skin and does not appear to be present on all body parts. For example, the magnitude of anisotropy has been found to be smaller on the dorsum of the hand than on the forearm (Le Cornu Knight et al., 2014), smaller on the forehead than on the dorsum (Longo et al., 2015), and smaller on the belly than on the forearm (Marks et al., 1982). Indeed, studies have consistently found no evidence for any anisotropy at all on the belly (Green, 1982; Longo, Lulciuc, & Sotakova, 2019; Marks et al., 1982). Thus, despite the qualitative similarities in the direction of tactile distance anisotropies when they are found, there are nevertheless differences across the body in the presence and magnitude of such biases. Understanding these variations across the body and how they relate to other aspects of somatosensory organization or of experience may provide important insight into the mechanisms underlying tactile distance perception.

Several researchers, myself included, have claimed that there is no anisotropy of tactile distance perception on the glabrous skin of the palm of the hand (Cholewiak, 1999; Green, 1982; Longo & Haggard, 2011), in contrast to the highly robust anisotropy found on the hairy skin of the hand dorsum (e.g., Longo & Golubova, 2017; Longo & Haggard, 2011; Miller et al., 2014). Some other, more recent studies, however, have reported significant anisotropy on the palm (Fiori & Longo, 2018; Le Cornu Knight et al., 2014; Longo et al., 2015), though in each case this has been smaller in magnitude than that found on the dorsum. Thus, it remains uncertain whether there is an anisotropy on the palm. The palm, however, is a particularly interesting part of the skin to investigate in the context of spatial distortions, given its fundamental role in haptic object exploration (Gibson, 1962; Lederman & Klatzky, 1987) in grasping (Napier, 1956), and in skilled action more generally (Jeannerod, 1997). In this study, I therefore conducted a systematic meta-analysis of the existing data measuring tactile distance anisotropy on the palm.

Method

Literature search and study selection

To identify eligible studies, I searched the Pubmed, Scopus, and Web of Science databases on May 20, 2019. Each database was searched using the following search string: "("tactile distance" or ((touch or tactile) and (distance or size) and (palm)))." To try to identify other eligible studies, I searched the reference lists of all eligible studies for potentially relevant studies, and also used Google Scholar to look at studies that cited each of the eligible studies.

Studies were eligible for inclusion in the analysis if (1) they measured an anisotropy in tactile distance perception on the palm (i.e., the glabrous skin of the volar hand surface) of either hand in adult human participants. Studies were considered to measure tactile distance perception if participants were asked to judge the distance (absolute or relative) between two tactile stimuli; studies measuring two-point discrimination thresholds by asking whether participants felt one point or two were therefore excluded, as were studies in which made a different sort of spatial judgment (i.e., whether a second touch was to the left or right of a first touch). Studies that only measured anisotropy on the hand dorsum, and not on the palm, were also excluded. (2) The measured anisotropy compared the proximo-distal and medio-lateral axes of the hand (sometimes called longitudinal and transverse, respectively). (3) The measured anisotropy involved a within-participants comparison. (4) The study reported enough information for calculation or estimation of effect sizes, or if these could be reconstructed from raw data. Despite these four criteria being specified at the outset of the literature search, in fact all studies excluded were based on the first criterion.

Searches of electronic databases produced a total of 291 publications (133 from Scopus, 104 from Web of Science, 54 from Pubmed). Of these, 126 were removed as duplicates. Of the 165 unique publications identified, 80 were excluded on the basis of a review of the title. For the remaining 85 publications, I reviewed the full text, excluding 77 further articles that did not measure anisotropy on the palm. This left eight articles that reported usable data, one of which (Le Cornu Knight et al., 2014) reported two separate usable experiments. In addition, one additional unpublished study from

my lab was also included (Manser-Smith, Tamè, & Longo, 2019). Thus, ten eligible experiments were included in the analysis, with a total of 189 participants. Table 1 provides details about these experiments.

Coding and quantification of results

For each eligible experiment, I coded a number of variables, including the task used, the stimuli applied, the timing between stimuli (i.e., whether each pair of touches was presented simultaneously or sequentially), which hand was tested, the posture of the hand and full body, which other skin surfaces were also tested in the same participants, the number of participants, the mean magnitude of anisotropy, and the standard deviation of this mean. In addition, when the same participants were tested on both the palm and the hand dorsum, the mean magnitude of anisotropy and its standard deviation were also coded.

Of the ten eligible experiments, four involved participants making verbal estimates of the distance between a single pair of touches presented on each trial (Cholewiak, 1999; Fiori & Longo, 2018; Green, 1982; Longo & Golubova, 2017), and the other six used a two-alternative forced choice (2AFC) procedure in which participants judged which of two pairs of touches felt larger. Because of these differences, the magnitude of anisotropy in each experiment was quantified using a standardized effect size. Because the most common measure

of standardized effect size (Cohen's d) introduces a small bias for small samples, the corrected effect size Hedges's g was used (Borenstein, Hedges, Higgins, & Rothstein, 2009).

Of the four experiments involving verbal estimates, the studies of Green (1982) and Cholewiak (1999) asked participants to use an arbitrary magnitude scale, whereas the studies of Longo and Golubova (2017) and of Fiori and Longo (2018) asked participants to make judgments in centimeters. In quantifying the magnitude of anisotropy it is not critical what the exact scale used to judge distance is, so long as the same scale is used for judgments of stimuli in both orientations. Therefore, these four studies were treated collectively.

Both Green (1982) and Cholewiak (1999) stated that there was no statistically significant anisotropy on the palm in their respective studies, but neither reported the actual test statistic. Green quantified anisotropy by comparing the slope of regression lines regressing perceived distance (using an arbitrary numerical scale calibrated in a practice period to visual distances) on actual distance. Statistically significant differences between these slopes in the medio-lateral and proximo-distal axes were reported for both the forearm and the thigh. No such differences were reported for the palm or the stomach, but statistical tests are not reported for these skin surfaces. The slope in each orientation was, however, reported. I therefore estimated the standard deviation of the difference between the slopes in the two orientations for the two skin surfaces (the forearm and thigh) for which means and t tests are reported

Table 1 Experiments included in the meta-analysis

Study	Experiment	Method	N	Stimulus	Timing	Hand Tested	Other Skin Surfaces Tested	Conditions
Green (1982)	1	Verbal estimate (arbitrary units)	15	Brass rods	Simultaneous	Right	R Forearm, R Thigh, Belly	
Cholewiak (1999)	1	Verbal estimate (arbitrary units)	15	Vibrations	Sequential	Left	L Thigh	
Longo & Haggard (2011)	2	2AFC	10	Wooden sticks	Simultaneous	Left	L Dorsum	
Le Cornu Knight et al. (2014)	1	2AFC	14	Wooden sticks	Simultaneous	Left	L Volar Forearm, L Volar Wrist	
Le Cornu Knight et al. (2014)	2	2AFC	15	Wooden sticks	Simultaneous	Left	L Dorsum, L Dorsal Forearm, L Volar Forearm, L Dorsal Wrist, L Volar Wrist	
Longo et al. (2015)	1	2AFC	35	Wooden sticks	Simultaneous	Both	L/R Dorsum, Forehead	
Calzolari et al. (2017)	8	2AFC	19	Wooden sticks	Simultaneous	Left	L Dorsum	Only pre-adaptation baseline condition used
Longo & Golubova (2017)	2	Verbal estimate (cm)	21	von Frey Hair	Sequential	Left	L Dorsum	
Fiori & Longo (2018)	2	Verbal estimate (cm)	25	Wooden sticks	Simultaneous	Left	L Dorsum	
Manser-Smith et al. (2019)	1	2AFC	20	Wooden sticks	Simultaneous	Left	L Dorsum, L Foot Top, L Foot Bottom	

and imputed the mean of these two estimates for the palm for the present analysis.

Cholewiak (1999) quantified anisotropy by comparing the mean distance estimate (using an arbitrary magnitude scale) for distances in the proximo-distal and medio-lateral orientations using a factorial analysis of variance (ANOVA). He stated that the main effect of orientation was not significant, but he did not report the F statistic. He did, however, show the mean results in a figure broken down by actual size, orientation, and the interstimulus interval (ISI) between the two touches, which I coded manually. Because F statistics for the significant main effects of actual size and ISI were reported for both orientations, I estimated the within-cell variance from these values and the means coded from the figure. The mean of these estimates was imputed to estimate the test statistics for the comparison of the two orientations. As is described below, given that estimates of the variance were used for the studies of Green (1982) and Cholewiak (1999), a sensitivity analysis was performed to determine whether the exact values imputed for these studies had an important influence on the conclusions drawn.

In the study of Longo and Golubova (2017), multidimensional scaling (MDS) was used to reconstruct a perceptual map of a 4-by-4 grid of tactile locations on the hand palm and dorsum. Anisotropy in these maps was quantified by finding the extent to which a rectangular grid needed to be stretched or compressed in the medio-lateral axis to maximize its similarity to each perceptual map. The value used here is the logarithm of these stretch parameters. In the study of Fiori and Longo (2018), participants made verbal size estimates (in centimeters) of distances presented in eight orientations on the palm and dorsum. Anisotropy was quantified as the logarithm of the ratio of judged distance for stimuli aligned with the medio-lateral axis and the proximo-distal axis.

The other six experiments used a 2AFC procedure in which participants judged which of two tactile distances felt bigger (Calzolari, Azañón, Danvers, Vallar, & Longo, 2017; Le Cornu Knight et al., 2014, Exps. 1 and 2; Longo et al., 2015; Longo & Haggard, 2011). In each case, psychometric functions were expressed in terms of the proportion of trials on which the stimulus in the medio-lateral axis was judged as bigger as a function of the logarithm of the ratio between the distance in the medio-lateral and proximo-distal axes. The point of subjective equality (PSE) was calculated for each participant as the ratio between the two stimuli for which the participant was equally likely to judge stimuli in each of the two orientations as bigger. Anisotropy was quantified as the logarithm of this ratio.

Regarding posture, there was not sufficient variability across studies to conduct any formal analysis. Green (1982) had participants lay supine on a mattress during testing, but does provides no further information about the exact posture of the hand. Cholewiak (1999) had participants sit with their palm face down on the array of stimulators, but does not specify anything further about hand orientation. All of the other studies (each of which I was personally involved in) used a posture in which the participant sat at a table with the stimulated skin surface facing upward and the fingers pointing directly away from the torso.

Analysis

In all cases, standardized measures of effect size (i.e., Cohen's d or d_z, depending on the details of the experiment) were calculated on the basis of the statistical comparison that most directly quantified anisotropy. For the subset of eligible experiments that also tested the same participants on the dorsum of the hand, corresponding effect sizes were coded for (1) anisotropy on the dorsum, (2) the difference in anisotropy between the dorsum and palm, and (3) the correlation coefficient (Pearson's r) between anisotropy on the two surfaces. Because of the small bias introduced by Cohen's d in meta-analyses (Borenstein et al., 2009), Hedges's (1981) correction was applied using the "escalc" function in the metafor package for R (Viechtbauer, 2010) resulting in all effects being expressed as Hedges's g. Effect sizes were coded such that positive values indicate bias for distances aligned with the medio-lateral hand axis to be overestimated relative to the proximo-distal axis, and negative values indicate the converse bias.

All meta-analyses reported here were conducted using the random-effects model in the metafor package. Separate meta-analyses were conducted to investigate (1) the overall evidence for tactile distance anisotropy on the palm, (2) differences in the magnitude of anisotropy on the palm and dorsum, (3) the correlation between anisotropy on the two skin surfaces, and (4) the magnitude of anisotropy on the palm in absolute (i.e., nonstandardized units).

Finally, for studies in which the individual participant data were available (i.e., all except those of Green, 1982, and Cholewiak, 1999), I used linear mixed-effect models (Baayen, Davidson, & Bates, 2008) to investigate the effects of method (2AFC vs. verbal estimation), sex, and age on both the magnitude of anisotropy on the palm and the difference in anisotropy on the palm and dorsum. Mixed-effects models were calculated using the lme4 toolbox for R (Bates, Mächler, Bolker, & Walker, 2015). Each of the two dependent variables was modeled using method, sex, and age as fixed effects and study as a random effect, including random intercepts for studies and by-study random slopes for the effects of sex and age. The significance of fixed effects was assessed using model comparison (Barr, Levy, Scheepers, & Tily, 2013).

Results

Overall anisotropy on the palm

Figure 1 shows a forest plot of tactile distance anisotropy on the palm across the ten experiments. Overall, there was clear evidence for anisotropy, with an overall meta-analytic mean estimated effect size of Hedge's $g = 0.521$, 95% CI = [0.221, 0.821], $z = 3.41$, $p < .001$. There was also evidence of heterogeneity across studies, $Q(9) = 32.99$, $p < .0001$, indicating that the differences between studies were larger than would be expected given the within-study variability. The I^2 statistic indicated that 71.44% of the variability across studies was due to heterogeneity.

Subgroup analyses revealed significant evidence for anisotropy in studies using 2AFC methods (Hedges's $g = 0.655$, 95% CI = [0.238, 1.073]), $z = 3.07$, $p < .005$, but no significant effect in studies using verbal estimates (Hedge's $g = 0.333$, 95% CI = [– 0.076, 0.742]), $z = 1.60$, $p = .110$. However, an analysis treating method as a moderator variable found no evidence for a reliable difference between the two tasks, $z = 1.01$, $p = .310$.

Because the standard deviations for the studies of Green (1982) and Cholewiak (1999) had to be estimated, I conducted a sensitivity analysis in which the standard deviations from these two studies were either

multiplied or divided by a factor of 5. These analyses were run adjusting the values from each study individually and both collectively. In every case, the change had no substantive effect on the results reported in the previous two paragraphs. This shows that the conclusions of this analysis do not depend on specific assumptions made about how to estimate missing data from these studies.

Comparison of the magnitude of anisotropy on the palm and dorsum

Figure 2 shows a forest plot of the difference in the magnitude of anisotropy on the dorsal and palmar hand surfaces for the subset of experiments that tested both surfaces. Overall, there was clear evidence for a larger anisotropy on the dorsum than on the palm, Hedges's $g = 0.683$, 95% CI = [0.423, 0.821], $z = 5.16$, $p < .0001$. I observed a modest trend toward evidence of heterogeneity, $Q(6) = 11.62$, $p = .071$, with the I^2 statistic indicating that 47.33% of the variability across studies was due to heterogeneity. Thus, whereas the previous analysis demonstrated the existence of a clear anisotropy in tactile distance perception on the palm, this analysis showed that the magnitude of this bias is nevertheless substantially smaller than that on the dorsum.
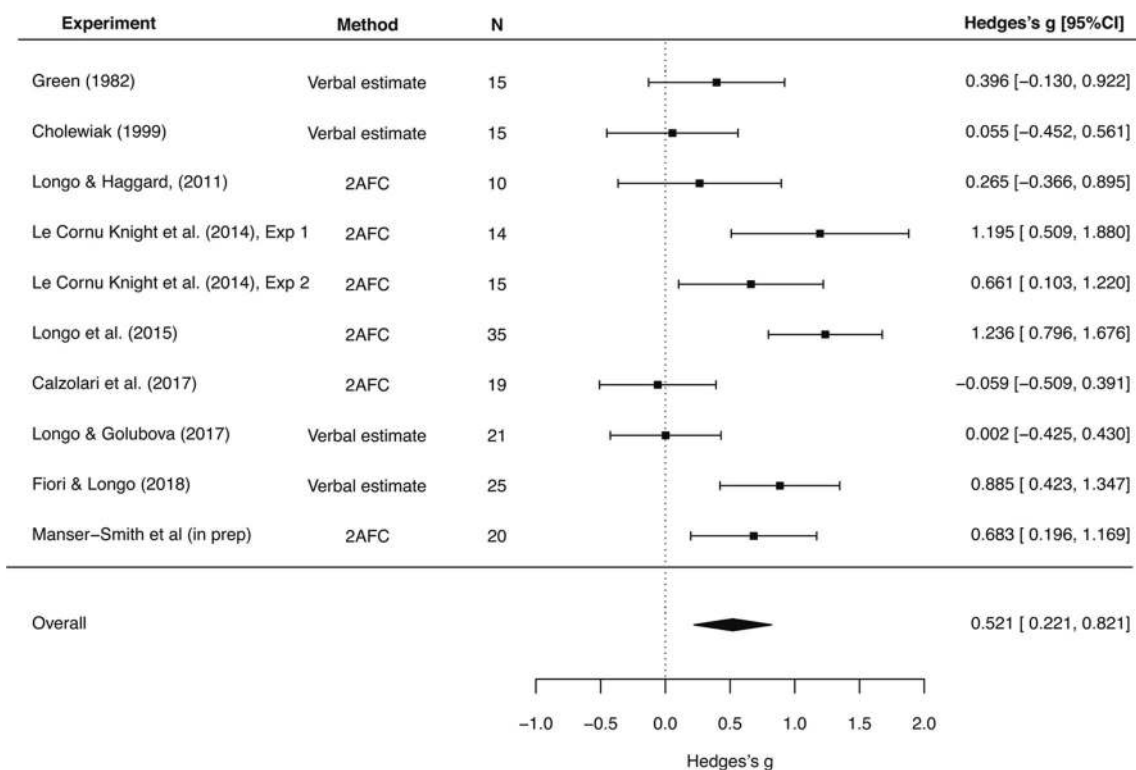

Experiment	Method	N	Hedges's g [95%CI]
Green (1982)	Verbal estimate	15	0.396 [–0.130, 0.922]
Cholewiak (1999)	Verbal estimate	15	0.055 [–0.452, 0.561]
Longo & Haggard, (2011)	2AFC	10	0.265 [–0.366, 0.895]
Le Cornu Knight et al. (2014), Exp 1	2AFC	14	1.195 [0.509, 1.880]
Le Cornu Knight et al. (2014), Exp 2	2AFC	15	0.661 [0.103, 1.220]
Longo et al. (2015)	2AFC	35	1.236 [0.796, 1.676]
Calzolari et al. (2017)	2AFC	19	–0.059 [–0.509, 0.391]
Longo & Golubova (2017)	Verbal estimate	21	0.002 [–0.425, 0.430]
Fiori & Longo (2018)	Verbal estimate	25	0.885 [0.423, 1.347]
Manser–Smith et al (in prep)	2AFC	20	0.683 [0.196, 1.169]
Overall			0.521 [0.221, 0.821]

Fig. 1 Forest plot showing overall results for tactile distance anisotropy on the palm. Positive values of Hedges's g indicate a bias to overestimate distances oriented with the medio-lateral hand axis; negative values indicate a bias to overestimation distances oriented with the proximo-distal axis.
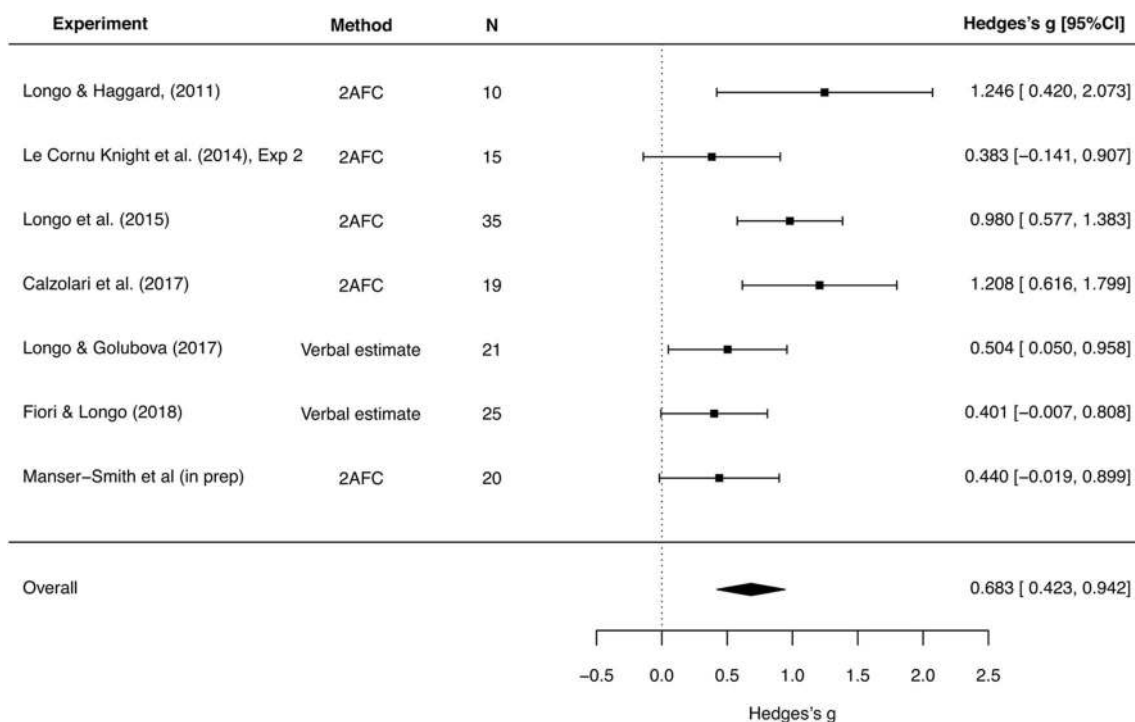
Fig. 2 Forest plot showing comparisons of anisotropy on the glabrous skin of the palm and the hairy skin of the dorsum. Positive values of Hedges's *g* indicate larger anisotropy on the dorsum; negative values indicate larger anisotropy on the palm.

Correlation between anisotropy on the palm and dorsum

Figure 3 shows a forest plot of the correlation across participants between the magnitudes of anisotropy on the palm and dorsum. No significant correlation was apparent, with an overall meta-analytic estimate of *r* of .113, 95% CI = [– .053, – .279], *z* = 1.33, *p* = .18. There was no evidence for heterogeneity, *Q*(6) = 5.66, *p* = .46, with the I^2 statistic indicating that 7.61% of the variability across studies was due to heterogeneity.

The magnitude of anisotropy on the palm in absolute units

The preceding analyses compared the magnitude of anisotropy across studies using standardized units (i.e., Hedges's *g*). It is also of interest, however, to quantify anisotropy in absolute units—that is, at what ratio are stimuli in the medio-lateral and proximo-distal hand axes perceived as equal? Studies in which participants judge tactile distance using magnitude comparison in arbitrary units (e.g., Cholewiak, 1999; Green, 1982) do not allow for direct comparisons of distance in meaningful absolute distances. Studies in which participants make verbal distance judgments in absolute units such as cm (e.g., Fiori & Longo, 2018; Longo & Golubova,

2017) could conceivably allow for this sort of inference, but this is complicated by potential biases in numerical estimation, such as preferential use of round numbers or logarithmic compression of the mental number line (e.g., Gallistel & Gelman, 1992; Longo & Lourenco, 2007). I therefore excluded studies using verbal estimation methods from this analysis and focused on studies using 2AFC comparisons of stimuli in the medio-lateral versus proximo-distal orientations. The PSE estimated in such experiments represents the ratio between the stimuli in the two orientations that are perceived as being the same size by the participant.

Figure 4 shows a forest plot of the PSEs from studies that quantified anisotropy using 2AFC methods, reporting effect sizes in raw units, rather than standardized units as in the previous analyses. Note that all analyses were conducted on PSEs, represented as the logarithm of the ratio between the two orientations, which were converted back to raw ratios for reporting. There was clear evidence for an overall anisotropy with a meta-analytic mean PSE of 1.096, 95% CI = [1.033, 1.146], *z* = 3.29, *p* < .001, indicating that, on average, tactile distances oriented with the medio-lateral axis of the palm are perceived as being about 10% larger than distances oriented with the proximo-distal axis. There was also evidence for heterogeneity, *Q*(5) = 25.28, *p* < .001, with the I^2 statistic indicating that 80.11% of the variability across studies was due to heterogeneity.
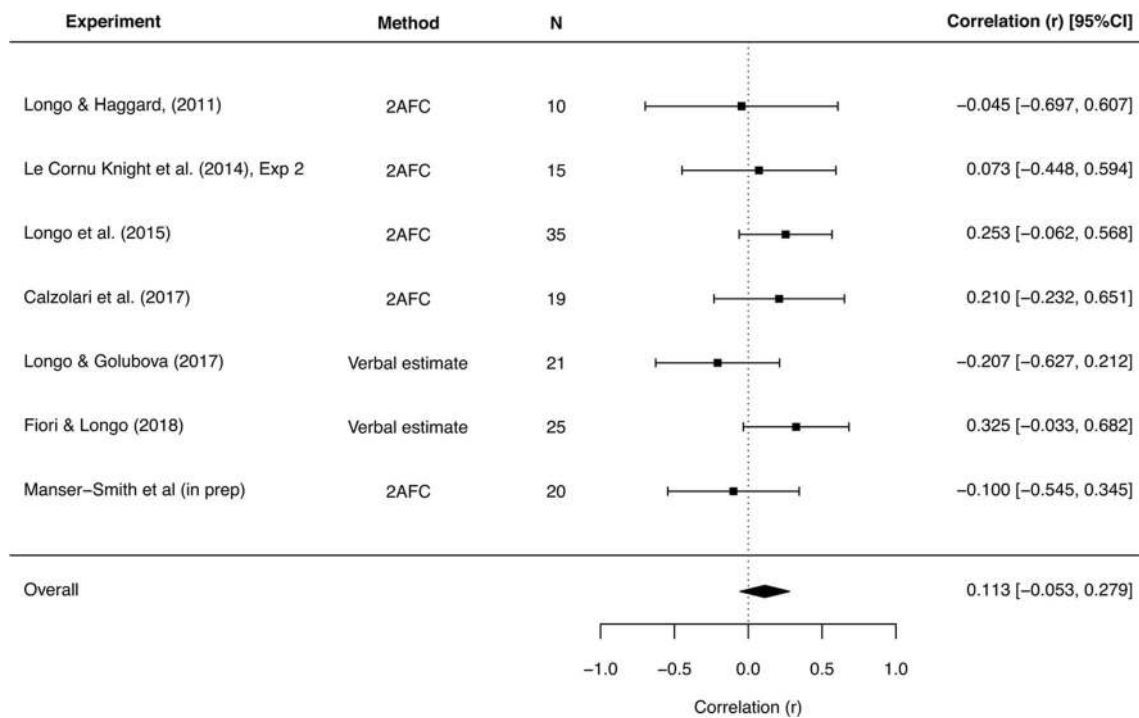
Fig. 3 Forest plot showing correlation across participants between the magnitudes of anisotropy on the palm and dorsum. There was no evidence for correlation between anisotropy on the two skin surfaces.

Individual participant data

Because the data from individual participants were available for all studies except those of Green (1982) and Cholewiak

(1999), I investigated the effects of method, sex, and age using linear mixed-effect models. Method (i.e., 2AFC vs. verbal estimation), sex, and age were modeled as fixed effects, including random intercepts for studies and by-study random
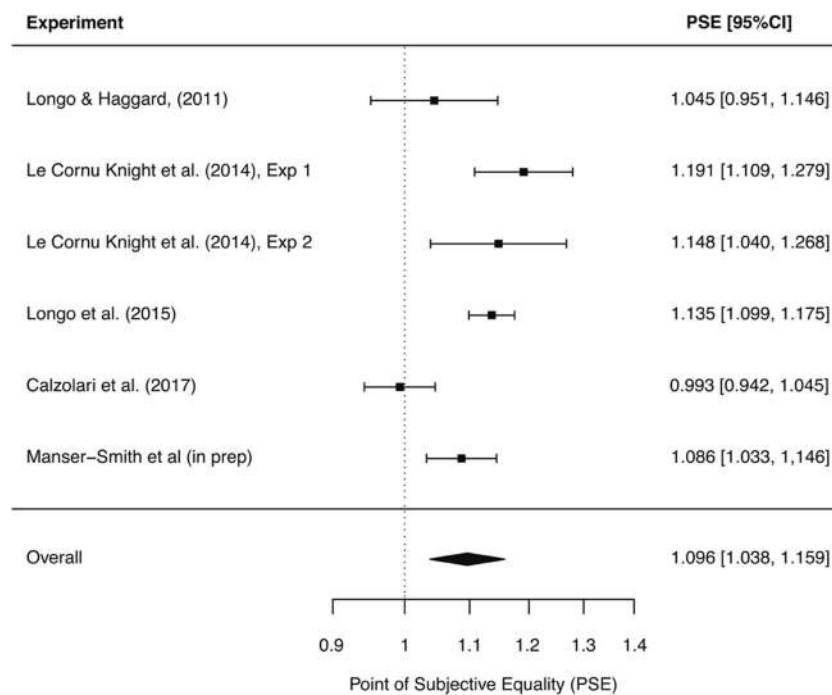
Fig. 4 Forest plot showing anisotropy on the palm in raw point of subjective equality (PSE) units, representing the ratio between stimuli oriented with the proximo-distal and medio-lateral hand axes. A PSE of 1 indicates no anisotropy; values bigger than 1 indicate a bias to perceive stimuli in the medio-lateral axis as larger than stimuli in the proximo-distal axis; and values less than 1 indicate the converse.

slopes for the effects of sex and age. This analysis revealed no significant effects of method ($\beta = 0.00895$ log$_{10}$ units), $\chi^2(1) = 0.181$, $p = .670$, sex ($\beta = -0.00930$ log$_{10}$ units), $\chi^2(1) = 0.650$, $p = .42$, or age ($\beta = 0.00001$ log$_{10}$ units), $\chi^2(1) = 0.001$, $p = .982$.

A similar analysis on the difference in the magnitude of anisotropy on the palm and dorsum revealed a significant effect of method ($\beta = -0.0917$ log$_{10}$ units), $\chi^2(1) = 5.10$, $p = .024$, with a greater difference between skin surfaces using 2AFC than verbal estimation methods. There were no significant effects of sex ($\beta = 0.00037$ log$_{10}$ units), $\chi^2(1) = 0.0003$, $p = .986$, or of age ($\beta = -0.00191$ log$_{10}$ units), $\chi^2(1) = 1.13$, $p = .288$.

Discussion

The results of this meta-analysis provide evidence for the existence of anisotropy of tactile distance on the glabrous skin of the palm. As on the hand dorsum, and several other body parts, tactile distances on the palm are perceived as larger when oriented with the medio-lateral hand axis than when oriented with the proximo-distal axis. On the palm, distances across the hand are perceived as about 10% larger than distances along the hand, an effect qualitatively similar to, but smaller in magnitude than, that found on the dorsum. Although individual studies have come to different conclusions about anisotropy on the palm, with some studies reporting such an effect (Fiori & Longo, 2018; Le Cornu Knight et al., 2014; Longo et al., 2015) and others failing to do so (e.g., Calzolari et al., 2017; Green, 1982; Longo & Haggard, 2011), this meta-analysis shows that treating this literature collectively, there is strong evidence for such anisotropy.

Despite the clear meta-analytic evidence for the presence of anisotropy on the glabrous skin of the palm, the magnitude of this bias was substantially smaller than that found on the hairy skin of the hand dorsum, a consistent finding in every study that tested both skin surfaces in the same participants. This fits with previous findings (described in the introduction) that the magnitude of anisotropy differs across the body (Green, 1982; Le Cornu Knight et al., 2014; Longo et al., 2015; Longo et al., 2019; Marks et al., 1982). Nevertheless, it is striking that in every case in which anisotropy has been reported, the bias has been to overestimate tactile distances aligned with body width as compared to those aligned with body length or height.

I have argued that such effects can be interpreted in terms of the geometry of the receptive fields (RFs) of somatosensory neurons. In the "pixel model" my colleagues I put forward (Longo, 2017; Longo & Haggard, 2011), the distance between two touches is calculated by counting the number of unstimulated RFs between the two activation foci. Because the size of RFs across skin surfaces is directly related to the

sensitivity of those surfaces and the overlap between the RFs of adjacent neurons is a constant proportion of RF width (Sur, Merzenich, & Kaas, 1980), a single tactile distance will feel larger on sensitive skin surfaces than on less sensitive surfaces, because there are a larger number of unstimulated RFs between the activation foci. Thus, the pixel model can explain the classic form of Weber's illusion (Taylor-Clarke et al., 2004; Weber, 1834). Analogously, because the RFs of neurons on the hairy skin of the limbs tend to be oval-shaped and elongated along the proximo-distal limb axis (Alloway et al., 1989; Brooks et al., 1961; P. B. Brown et al., 1975), RFs are smaller in the medio-lateral than in the proximo-distal axis. A single tactile distance will thus feel larger when it is aligned with the medio-lateral axis, since there will again be a larger number of unstimulated RFs between the activation foci.

Little work, to my knowledge, has quantitatively compared the degree of elongation of RFs on the hairy and glabrous skin of the hands, and none in humans. In monkeys, there is some evidence that RFs of neurons in somatosensory cortex on the palm are both smaller and more circular than those on the dorsum and also that when they are elongated they long-axis doesn't tend to have a preferred orientation (DiCarlo & Johnson, 2002; DiCarlo, Johnson, & Hsiao, 1998). It is not clear whether on average there is elongation of the RFs of somatosensory neurons on the palm in the proximo-distal axis that could account for the anisotropy in tactile distance described in this article. It is also possible that the perceptual bias seen on the palm could reflect some form of transfer from the representation of the dorsum. Findings that tactile distance perception are modulated by high-level aspects of body representation, such as body image illusions (de Vignemont et al., 2005; Tajadura-Jiménez et al., 2012; Taylor-Clarke et al., 2004) raise the possibility that perceptual anisotropies may result, at least in part, from body representations outside of primary somatosensory cortex in which the dorsal and palmar skin surfaces are integrated into a common 3-D representation of the whole hand (cf. Longo, 2015; Manser-Smith, Tamè, & Longo, 2018).

One possibility is that the glabrous skin of the palm is less susceptible to distortions than the hairy skin of the dorsum generally. The smaller anisotropy on the palm than the dorsum described in this article mirrors the reduction or absence of other perceptual biases on the palm, including perceptual maps based on proprioceptive localization of hand landmarks (Longo & Haggard, 2012) and tactile localization (Mancini, Longo, Iannetti, & Haggard, 2011). L. E. Brown, Morrissey, and Goodale (2009), similarly, showed that pointing movements to visual targets are more accurate (as well as more precise) when visual stimuli appear on the palm than on the dorsum, although no such advantage was found in a subsequent study that investigated simple visual detection (Kao & Goodale, 2009). Unsurprisingly, basic tactile acuity is also higher on the palm than on the dorsum (Mancini et al.,

2014). Thus, the greater sensitivity of the palm appears to be associated with reduced perceptual bias, though these two factors are logically independent. Both of these factors may be related to the key role of the palm and the palmar surface of the fingers in skilled haptic behavior (Gibson, 1962; Lederman & Klatzky, 1987).

Although the results of the present meta-analysis provide strong evidence for anisotropy on the palm, they also reveal substantial heterogeneity across studies. This finding is consistent with the observation that motivated this meta-analysis in the first place, that different studies (even from my own lab) have reached opposite conclusions about whether or not there is anisotropy on the palm. The existence of this heterogeneity suggests that some factors modulate the strength of anisotropy, but it is not clear exactly what these factors are. Although several different methods have been used to measure anisotropy, there was no significant moderating effect of task type, and heterogeneity was still apparent in the final analysis, which included only studies using 2AFC comparisons. Similarly, substantial heterogeneity was apparent even within studies conducted within my own lab.

Open Practices Statement The raw data on which this meta-analysis is based are available on request from the author.

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