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RUNNING HEAD: Tactile Distance on the Foot

Tactile Distance Anisotropy on the Feet

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Abstract

Perception of distance between two touches varies with orientation on the hand, with distances aligned with hand width perceived as larger than those aligned with hand length. Similar anisotropies are found on other body parts (e.g., the face), suggesting they may reflect a general feature of tactile organization, but appear absent on other body parts (e.g., the belly). Here, we investigated tactile distance anisotropy on the foot, a body part structurally and embryologically similar to the hand, but with very different patterns of functional usage in humans. In three experiments, we compared the perceived distance between pairs of touches aligned with the medio-lateral and proximal-distal foot axes. On the hairy skin of the foot dorsum, anisotropy was consistently found, with distances aligned with the medio-lateral foot axis perceived as larger than those in the proximo-distal axis. In contrast, on the glabrous skin of the sole, inconsistent results were found across experiments, with no overall evidence for anisotropy. This shows a pattern of anisotropy on the foot broadly similar to the hand, adding to the list of body parts showing tactile distance anisotropy, and providing further evidence that such biases are a general aspect of tactile spatial organization across the body.

Significance: The perception of tactile distance has been widely used to understand the spatial structure of touch. On the hand, anisotropy of tactile distance perception is well-established, with distances oriented across hand width perceived larger than those oriented along hand length. We investigated tactile distance anisotropy on the feet, a body part structurally, genetically, and developmentally homologous to hands, but with strikingly different patterns of functional usage. We report highly similar patterns of anisotropy on the hairy skin of the hand dorsum and foot dorsum. This suggests that anisotropy arises from the general organization of touch across the body.

Illusions of the perceived distance between touches on the skin have been investigated since the seminal studies of Weber (1834) in the 19th century. Weber found that the perceived distance between the two points of a compass changed as he moved them across his skin, feeling farther apart on regions of relatively high sensitivity than on regions of lower sensitivity. This general pattern has been replicated in subsequent studies (Anema, Wolswijk, Ruis, & Dijkerman, 2008; Cholewiak, 1999; Fitt, 1917; Goudge, 1918; Miller, Longo, & Saygin, 2016; Taylor-Clarke, Jacobsen, & Haggard, 2004), and is now referred to as *Weber's illusion*. Weber's illusion provides an intriguing window into somatosensory organization and suggests a perceptual echo of the homuncular distortions known to characterize primary somatotopic maps (Penfield & Boldrey, 1937; Sur, Merzenich, & Kaas, 1980).

Analogous illusions have also been reported comparing the perceived distance between pairs of touches presented in different orientations on a single skin surface, with several studies reporting anisotropies of tactile distance perception (e.g., Fiori & Longo, 2018; Green, 1982; Longo & Haggard, 2011; Wong, Ho, & Ho, 1974). For example, Longo and Haggard (2011) compared the perceived distance between pairs of touches oriented with the medio-lateral vs. the proximo-distal axes of the hand dorsum using a two-alternative forced-choice paradigm. Touches oriented across the width of the hand were judged as substantially larger than touches oriented along the length of the hand, an effect also observed in several subsequent studies (e.g., Canzoneri et al., 2013; Fiori & Longo, 2018; Longo & Golubova, 2017; Longo & Sadibolova, 2013; Miller, Longo, & Saygin, 2014; Tamè, Bumpus, Linkenauger, & Longo, 2017). Recent studies have increasingly used these illusions as measures of body perception disturbance in conditions such as eating disorders (Engel & Keizer, 2017; Keizer et al., 2011; Keizer,

Smeets, Dijkerman, van Elburg, & Postma, 2012; Spitoni et al., 2015) and obesity (Mölbart et al., 2016; Scarpina, Castelnovo, & Molinari, 2014).

Anisotropy of tactile distance has been observed on a range of skin surfaces, and is not specific to the hands. For example, studies have reported similar anisotropies on the forearm (Green, 1982; Le Cornu Knight, Longo, & Bremner, 2014; Wong et al., 1974), the forehead (Fiori & Longo, 2018; Longo et al., 2020; Longo, Ghosh, & Yahya, 2015), the thigh (Green, 1982; Tosi & Romano, 2020), and the shin (Stone, Keizer, & Dijkerman, 2018). Intriguingly, in each of these cases, the direction of the illusion is similar, with biases to overestimate tactile distances across the width of the body compared to body length or height. This consistency suggests that anisotropy may be a general characteristic of the perceptual representation of the body, perhaps linked to overrepresentation of body width seen in a range of other tasks (e.g., Dolan, Birtchnell, & Lacey, 1987; Dolce, Thompson, Register, & Spana, 1987; Fuentes, Longo, & Haggard, 2013; Fuentes, Runa, Blanco, Orvalho, & Haggard, 2013; Halmi, Goldberg, & Cunningham, 1977; Longo & Haggard, 2010, 2012).

Despite the qualitatively similar anisotropies found on a range of skin regions, there is also evidence that the magnitude of such effects may differ systematically across the body and that anisotropy may not be present at all on some skin areas. There is evidence that anisotropy is larger on the forearm than either the belly (Marks et al., 1982) or the hand dorsum (Le Cornu Knight et al., 2014), and larger on the dorsum than on either the forehead (Longo et al., 2015) or palm (Longo & Haggard, 2011). On the belly, studies have consistently failed to find any evidence for an anisotropy in non-clinical samples (Green, 1982; Longo, Lulciuc, & Sotakova, 2019; Marks et al., 1982), although such a bias may be present in women with anorexia nervosa (Spitoni et al., 2015).

One particularly interesting difference between skin surfaces is between the hairy skin of the hand dorsum and the glabrous skin of the palm. To our knowledge, every study that has investigated the hand dorsum has found clear evidence for an anisotropy in tactile distance, with distances across the hand judged as larger than distances along the hand (e.g., Fiori & Longo, 2018; Longo & Golubova, 2017; Longo & Haggard, 2011). In contrast, results on the palm have been strikingly different. Several studies have failed to find any evidence for anisotropy on the palm (Calzolari, Azañón, Danvers, Vallar, & Longo, 2017; Cholewiak, 1999; Green, 1982; Longo & Golubova, 2017; Longo & Haggard, 2011). Other studies have found evidence for some level of anisotropy, but this has always been substantially smaller than that found on the dorsum (Fiori & Longo, 2018; Le Cornu Knight et al., 2014; Longo et al., 2015). A recent meta-analysis of these studies (Longo, 2020) found evidence that there is an anisotropy on the palm, but substantially smaller in magnitude than on the hand dorsum and with a high level of heterogeneity across studies, the reasons for which are not fully clear.

These differences between the hairy skin of the hand dorsum and the glabrous skin of the palm raise the question of whether similar effects exist on the foot. Like the hand, the foot has hairy skin on its dorsal surface (the foot dorsum) and glabrous skin on its ventral surface (the sole). Hands and feet are serially homologous structures with a common underlying bone structure (Lewis, 1989; Owen, 1849) and arise from similar genetic and developmental programs (Logan, 2003; Shubin, Tabin, & Carroll, 1997). In humans, hands and feet clearly have numerous derived features showing specialization for manipulation and for bipedal locomotion, respectively (Lewis, 1989; McNutt, Zipfel, & DeSilva, 2018; Tocheri, Orr, Jacofsky, & Marzke, 2008; Tuttle, 1981). Nevertheless, there are also intriguing similarities in the nature of the specializations of the hand (Marzke, 1997; Susman, 1979) and foot (Harcourt-Smith & Aiello, 2004; Schultz, 1963),

with large and robust first digits (i.e., thumb and big toe) and short lateral digits. Indeed, individuals born without arms are able to learn to use their feet in ways strikingly similar to hands (Dempsey-Jones, Wesselink, Friedman, & Makin, 2019; Hahamy et al., 2017). Moreover, analyses of skeletal morphology in a range of species show striking patterns of co-variation in the bones of the fingers and toes, indicating a high degree of co-evolution of the hands and feet in human evolution (Rolian, 2009; Rolian, Lieberman, & Hallgrímsson, 2010; Young & Hallgrímsson, 2005).

Beyond their physical similarities, there are also deeper levels of similarity in how the hands and feet are represented in the nervous system. Peripheral microneurographic recordings of afferent signals from the glabrous skin of the palmar hand surface (Johansson & Vallbo, 1979) and of the sole of the foot (Kennedy & Inglis, 2002) reveals qualitative similarities between these surfaces, but also quantitative differences in the ratios of different types of receptors, receptive field size, in the activation thresholds of afferent fibres, and in the level of background activity in the absence of stimulation, differences presumably related to the different functional roles of hands and feet (Kennedy & Inglis, 2002). In the primary somatosensory cortex, single-unit neurophysiological studies of somatotopic maps in monkeys show that both the fingers and toes are similarly represented separately from the rest of the hand or foot (Liao, Qi, Reed, Miller, & Kaas, 2016; Merzenich, Kaas, Sur, & Lin, 1978; Nelson, Sur, Felleman, & Kaas, 1980). Notably, however, while neuroimaging studies in adult humans have found clear evidence for somatotopic organisation of the five fingers (Besle, Sánchez-Panchuelo, Bowtell, Francis, & Schluppeck, 2014; Ejaz, Hamada, & Diedrichsen, 2015; Kolasinski et al., 2016; Mancini, Haggard, Iannetti, Longo, & Sereno, 2012; Sanchez-Panchuelo et al., 2012), no comparable evidence has been found for somatotopic organisation of the toes (Akselrod et al., 2017; Hashimoto et al., 2013).

Intriguingly, however, individuals born without arms who show extreme levels of dexterity in using their foot for manipulative actions do show hand-like patterns of somatotopy for their toes (Dempsey-Jones et al., 2019). This result converges with other results to suggest that the organisation of somatosensory representations is intimately linked to patterns of functional usage (Ejaz et al., 2015; Gindrat, Chytiris, Balerna, Rouiller, & Ghosh, 2015), patterns which obviously differ dramatically between the hands and feet.

There is also some evidence that there may be overlapping mental representations of hands and feet. For example, patients with Gerstmann's syndrome in which finger agnosia is a common symptom also frequently show toe agnosia (Mayer et al., 1999; Tucha, Steup, Smely, & Lange, 1997). There are also similarities in the patterns of mislocalisations between the fingers (Braun et al., 2005; Manser-Smith, Tamè, & Longo, 2018; Schweizer & Braun, 2001) and toes (Cicmil, Meyer, & Stein, 2016; Manser-Smith et al., 2018) in tactile localisation tasks. We recently showed further that there are shared individual differences in the patterns of mislocalisation between the fingers and the toes, suggesting that there is a common representation of digits across the hands and feet (Manser-Smith, Tamè, & Longo, 2019). Finally, Badde and colleagues (Badde, Röder, & Heed, 2019) recently reported intriguing patterns of systematic mislocalisations of tactile stimuli between the left and right sides of the body and between the upper and lower limbs. Thus, a touch applied to the left hand might be perceived as located on the left foot, or vice versa, suggesting that aspects of tactile organisation abstract across the specific skin surface stimulated (Azañón & Longo, 2019).

In this study, we investigated whether there are anisotropies of tactile distance perception on the foot. If the anisotropy found consistently on the hand and other body

parts reflects a basic aspect of somatosensory organization, it should be similar on the hands and feet given their clear structural homology. In contrast, if anisotropy results from specific patterns of functional usage of different skin surfaces, different patterns may arise on the hands and feet given their grossly different roles in everyday behaviour. In three experiments, we measured tactile distance anisotropy on the hairy skin of the foot dorsum and the glabrous skin of the sole, using a two-alternative forced-choice (2AFC) procedure identical to that used previously on the hands (e.g., Longo & Haggard, 2011).

Experiment 1

The first experiment investigated anisotropy of tactile distance perception on the dorsum and sole of the foot using a within-subject design. We hypothesized that there would be an anisotropy on the hairy skin of the foot dorsum with distances oriented across the width of the foot perceived as larger than distances oriented along the length of the foot, analogous to that found on the hand dorsum. We further predicted that this anisotropy would be reduced or eliminated on the glabrous skin of the sole of the foot, again analogous to the pattern seen on the hand. The experimental design, analysis plan, and hypotheses were preregistered on the Open Science Framework (osf.io/dzn65).

Methods

Participants

A number of studies have been conducted investigating anisotropies in tactile distance perception on the hairy skin of the hand. To conduct a power analysis to find the appropriate number of participants for the present study, we took effect sizes from 19 studies conducted in our lab investigating tactile distance anisotropy on the hand

dorsum (total N = 394), resulting in a weighted average Cohen's d of 1.50. We conducted a power analysis using G*Power (Faul, Erdfelder, Land, & Buchner, 2007) with this effect size, an alpha value of 0.05 and power of 0.95, which indicated 7 participants would be required for sufficient power. While anisotropy on the foot may be smaller than on the hand, we expect a broadly comparable magnitude of anisotropy.

We recruited 20 participants, though one participant was removed from analyses (see Analysis section). As such, data from 19 participant was analysed (10 female; mean age = 27.1 years; range = 20 - 46). This gave us a power of over 90% to detect an effect of even half the size as that found on the hand. Participants all reported normal or corrected-to-normal vision and normal touch. All 19 participants were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; M : 69.2, range: 38 - 96) and 18 were right-footed as assessed by the Waterloo Footedness Questionnaire (Elias, Bryden, & Bulman-Fleming, 1998; M : 52.1, range: -5 - 100). EHI and WFQ scores were strongly correlated across participants, $r(16) = 0.74$, $p < 0.0001$. All participants gave written informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

Procedures

All procedures were consistent with our pre-registered plans, and closely followed those used in several previous studies from our lab (e.g., Longo, 2017; Longo et al., 2015; Longo & Haggard, 2011; Longo & Morcom, 2016). Tactile stimuli were pairs of wooden posts mounted in foamboard, separated by 20, 30, or 40mm, as in previous studies (Longo et al., 2015; Longo & Haggard, 2011). The ends of the wooden posts were tapered to a point, but not sharp.



Figure 1. Experimental set-up. Participants sat with their left foot rest on a stool, and arms resting on the arm rests of the chair. In Experiment 2, participants sat with their left foot resting on a stool and left hand resting on a table (as shown above). Participants were blindfolded in all experiments.

Participants were evaluated on their hand and foot dominance, though all participants were tested on their left foot, regardless of assessed foot dominance. Participants were seated in a comfortable position with their left foot resting on a stool, as shown in Figure 1, and were asked to remain as still as possible throughout each experimental block. On each trial, participants were touched twice on the hairy skin or glabrous skin of the left foot, once with the posts oriented along the proximodistal axis of the hand (along stimulus), and once oriented along the mediolateral axis (across stimulus). Touch was applied manually, approximately in the center of either surface of the foot, and with moderate pressure. The duration of each touch was approximately one second, with an interstimulus interval of approximately one second. Participants made untimed two-alternative forced choice judgments of whether the first or second stimulus felt larger (i.e. the two points felt farther apart) and responded verbally.

Participants were blindfolded throughout the procedure but were briefly shown the 30mm stimuli only before testing commenced to familiarise themselves with the stimuli.

There were four blocks, two in which the hairy skin surface of the foot was tested, and two in which the glabrous skin surface of the foot were tested. ABBA counterbalancing was used to vary order of presentation, with the first condition counterbalanced across participants. Each block contained 100 trials, resulting in 20 trials per block for each of the five stimulus pairings (across/along): 20/40 mm, 20/30 mm, 30/30 mm, 30/20 mm, and 40/20 mm. Therefore, there was a total of 400 trials, and 80 trials per stimulus pairing. The order of along and across stimuli was counterbalanced within each stimulus pair, and the order of the trials was randomised and shown to the experimenter through a custom MATLAB script.

Analysis

All analyses were consistent with our pre-registered plans. The proportion of trials in which the 'across' stimulus was judged as larger was analysed as a function of the ratio of the length of the along and across stimuli, logarithmically transformed to produce a symmetrical distribution around the point-of-actual-equality (i.e. where the ratio equals 1). Cumulative Gaussian functions were fitted to each participant's data on each skin surface, using maximum-likelihood estimation with the Palamedes toolbox for MATLAB (Prins & Kingdom, 2009). For each curve, we obtained: (1) the *point of subjective equality* (PSE; i.e., the mean of the Gaussian), that is the point at which the psychometric function crosses 50%; (2) the standard deviation of the Gaussian, which is inversely related to the slope of the psychometric function; and (3) the R^2 value, the

proportion of the variance in the mean values across the 5 trial types accounted for by the psychometric function.

Participants with an R^2 value less than 0.5 for either the hairy or glabrous skin surface were excluded from the analysis, as this indicates poor fit of the data. This is the same criterion we have used in several other studies using this paradigm in our lab (Longo, 2017b; Longo et al., 2015; Longo & Morcom, 2016). One participant had R^2 values below 0.5 on both the hairy and glabrous skin surfaces, and was therefore excluded from analyses.

Initially, we investigated whether there are anisotropies in tactile distance perception on the foot. We conducted two one-sample t-tests comparing the PSEs on the hairy skin and glabrous skin of the foot to 1 (i.e. no bias in responding). Note that as the PSEs are ratios, the calculation of means and all statistical tests were conducted on log-transformed values, which were converted back to ratios for reporting. We also investigated similarity of tactile distance perception across the hairy and glabrous skin of the foot, by correlating PSE values for each participant across the two skin surfaces, although it is important to note that our sample size is small for looking at correlations and our considerations of power were not based on correlations. We also carried out a paired-samples t-test between PSE values on the hairy and glabrous skin surfaces.

Results and Discussion

The results are shown in Figure 2. Overall, there was good fit of the psychometric functions to the data, with mean R^2 values of 0.949 (SD = 0.061, range: 0.778 – 0.999) on the foot dorsum and 0.963 (SD = 0.049, range: 0.833 – 0.999) on the sole. To investigate whether there is anisotropy on each skin surface, we conducted one-sample t-tests comparing the mean PSE on each surface to 1. (Note that since the PSE is a ratio, all

statistics are conducted on log-transformed values, which have been converted back to a ratio for reporting of means.) On the foot dorsum, there was a clear anisotropy (mean PSE = 0.832), $t(18) = -4.22$, $p < 0.0005$, $d = 0.969$. This indicates a bias to judge stimuli oriented across the width of the foot as farther apart than stimuli oriented along the length of the foot, consistent with findings from the hand dorsum (e.g., Longo & Golubova, 2017; Longo & Haggard, 2011). On the sole of the foot, there was a similar anisotropy (mean PSE = 0.817), $t(18) = -6.64$, $p < 0.0001$, $d = 1.523$. There was no evidence for a difference in the magnitude of anisotropy on the two sides of the foot, $t(18) = 0.635$, $p = 0.533$, $d_z = 0.146$, which were significantly correlated across participants, $r(17) = 0.723$, $p < 0.0005$.

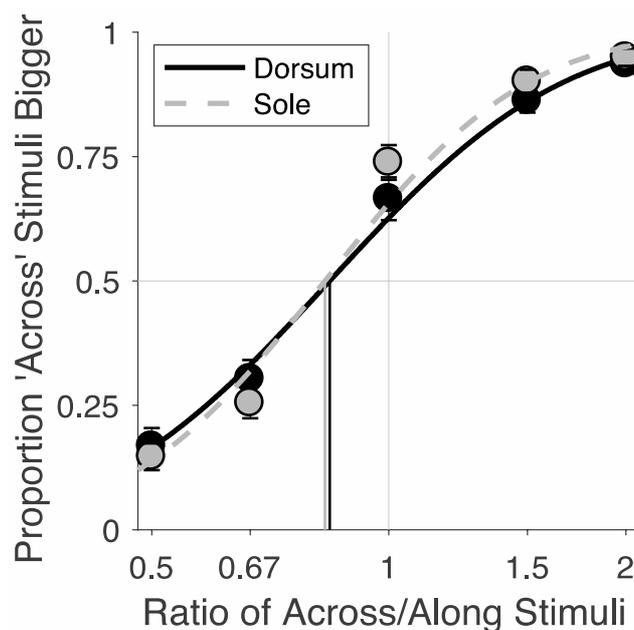


Figure 2. Results from Experiment 1. The curves are cumulative Gaussian functions fit with maximum-likelihood estimation. Error bars represent the standard error of the mean. The solid vertical line crossing 1 on the x-axis represents the point of subjective equality if there was no anisotropy (i.e., where 50% of stimuli are judged as larger). The black and grey vertical lines represent the grand average PSE for both the dorsum and sole of the foot.

These results show that biases in tactile distance perception are also evident on the hairy skin surface of the foot – like the hairy skin surface of the hand, the foot was

perceived as wider than it is. Intriguingly, we also found anisotropies in tactile distance perception on the glabrous skin surface of the foot of the same magnitude as on the hairy skin of the foot. These findings suggest that anisotropies in tactile distance perception are a general characteristic of the limbs, as we find similar results on the hairy skin of the hands and both skin surfaces of the feet. That anisotropies in tactile distance perception are reduced or non-existent on the palm of the hands indicates that this skin surface is in some way special – the palm of the hand is of fundamental importance for goal directed actions, such as skilled instrumental action and haptic object manipulation (Gibson, 1962; Lederman & Klatzky, 1987). As such, anisotropies may be reduced on the glabrous skin of the palm in order to carry out these actions with higher precision.

Experiment 2

The aim of this study is to replicate the anisotropies in tactile distance perception found on both skin surfaces of the foot in Experiment 1, and to directly compare tactile distance perception on the hairy and glabrous skin of both the hands and feet in the same participants. We did this using testing and analysis methods similar to Experiment 1. The experimental design, analysis plan, and hypotheses were pre-registered on the OSF (osf.io/npkhc).

Methods

Participants

The results of Experiment 1 showed Cohen's d values of 0.969 and 1.523 on the hairy and glabrous skin surfaces of the foot, respectively. We conducted a power analysis using G*Power (Faul et al., 2007) with the smallest effect size from Experiment 1, an alpha value of 0.05 and power of 0.95, which indicated 13 participants would be

required for sufficient power. We aimed to recruit 20 participants, as participants completed fewer trials per skin surface than in our previous experiment.

We recruited 20 participants (12 female; mean age = 27.0 years; range = 18 - 46). This gave us a power of over 90% to detect an effect of even half the size as that found on the hand. Participants all reported normal or corrected-to-normal vision and normal touch. Participants were mostly right-handed as assessed with the EHI (mean = 62.5, range = -90 - 100) and right-footed as assessed with the WFQ (mean = 52.8, range = -75 - 100). EHI and WFQ scores were strongly correlated across participants, $r(18) = 0.67, p < 0.001$.

Procedures

The procedures closely followed those used in Experiment 1. All participants were tested on their left hand and foot, regardless of assessed hand and foot dominance. Participants were seated in a comfortable position with their left foot resting on a stool, and their left hand resting on a table (Figure 1).

There were eight blocks, two on each of the four skin surfaces. Latin-square counterbalancing was used to vary order of presentation for the first four blocks, and this order reversed for the next four blocks. Each block contained 50 trials, resulting in 10 trials per block for each of the five stimulus pairings (across/along): 20/40 mm, 20/30 mm, 30/30 mm, 30/20 mm, and 40/20 mm. Therefore, there was a total of 400 trials, and 20 trials per stimulus pairing on each skin surface. The order of along and across stimuli was counterbalanced within each stimulus pair, and the order of the trials was randomised and shown the experimenter through a custom MATLAB script.

Analysis

Analyses closely followed Experiment 1, and with one exception (see below) were consistent with our pre-registered analysis plans. No participants were excluded due to poor model fit. However, there was one participant whose PSE for the sole of the foot (i.e., 2.687) was substantially outside of the range of values tested (i.e., 0.5 – 2). While exclusion on this basis was not part of the pre-registered analysis plan, we nevertheless decided to exclude this participant from analyses given the lack of confidence we have in a PSE extrapolated that far out of the range of stimuli we applied. There were no substantial changes in the results of the analysis depending on whether this participant was included or excluded.

For both the hand and the foot, we investigated whether there are anisotropies in tactile distance perception on both the hairy and glabrous skin. First, we conducted four one-sample t-tests comparing the PSEs on the hairy skin and glabrous skin of the hand and foot to 1 (i.e. no bias in responding). We investigated similarity of tactile distance perception across the hairy and glabrous skin of the hand and foot, first by correlating PSE values across the two skin surfaces of each body part independently, then by correlating PSE values across the hand and foot, for each skin surface separately. We also compared similarity of tactile distance perception across the hairy and glabrous skin of the hand and foot by running four paired-samples t-tests, firstly comparing PSE values across the two skin surfaces of each body part independently, then comparing PSE values across the hand and foot, for each skin surface separately. Finally, to compare PSE across both body parts and skin surfaces, we conducted a repeated-measures ANOVA with two factors: SKIN SURFACE (hairy/glabrous) and BODY PART (hand/foot), with PSE as the dependent variable.

Results and Discussion

The results are shown in Figure 3 for the dorsum and palm of the hand (left panel) and the dorsum and sole of the foot (right panel). There was good model fit overall, with mean R^2 values of 0.958 (SD: 0.039) on the hand dorsum, 0.979 (SD: 0.025) on the palm, 0.941 (SD: 0.093) on the foot dorsum, and 0.932 (SD: 0.077) on the sole. On the hand, there was a clear anisotropy on the dorsum (mean PSE = 0.836), $t(18) = -6.98$, $p < 0.0001$, $d = 1.602$, and a smaller anisotropy in the same direction on the palm (mean PSE = 0.935), $t(18) = -3.27$, $p < 0.005$, $d = 0.749$. The magnitude of anisotropy differed significantly between the two skin surfaces, $t(18) = -3.96$, $p < 0.001$, $d_z = 0.909$. There was no significant correlation between the magnitude of anisotropy on the hand dorsum and palm, $r(17) = 0.375$, $p = 0.114$. These effects are consistent with previous results.

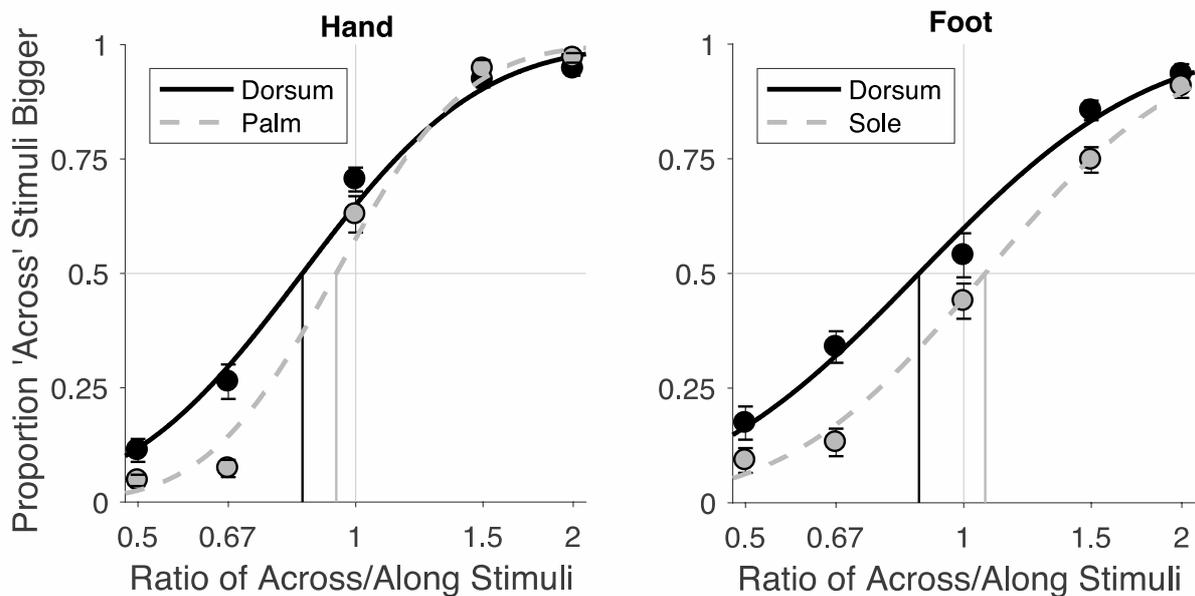


Figure 3. Results from Experiment 2 on the two surfaces of the hand (left panel) and foot (right panel). The curves are cumulative Gaussian functions fit with maximum-likelihood estimation. Error bars represent one standard error. The vertical lines represent the grand average PSE for each skin surface.

On the foot, there was again a clear anisotropy on the dorsum (mean PSE = 0.855), $t(18) = -2.92$, $p < 0.01$, $d = 0.671$. On the sole, however, there was a significant anisotropy in the opposite direction as found in Experiment 1 (mean PSE = 1.074), $t(18)$

= 2.41, $p < 0.05$, $d = 0.552$. Also unlike the first experiment, there was a significant difference in the magnitude of anisotropy between the two skin surfaces, $t(18) = 4.51$, $p < 0.005$, $d_z = 1.035$. There was no significant correlation between the magnitude of anisotropy on the foot dorsum and sole, $r(17) = 0.275$, $p = 0.255$.

We also compared the magnitude of anisotropy on the hand and foot, separately for the hairy and glabrous skin surfaces. On the hairy skin, there was no difference the magnitude of anisotropy between the hand and foot, $t(18) = 0.40$, $p = 0.693$, $d_z = 0.092$, which were not correlated, $r(17) = 0.170$, $p = 0.486$. On the glabrous skin, there was a difference between the hand and foot, $t(18) = 3.78$, $p < 0.002$, $d_z = 0.867$, which were not correlated, $r(17) = 0.232$, $p = 0.341$.

Finally, we conducted a ANOVA on PSE values, which revealed significant main effects of body part, $F(1, 18) = 4.97$, $p < 0.05$, $\eta_p^2 = 0.216$, and of skin surface, $F(1, 18) = 30.71$, $p < 0.0001$, $\eta_p^2 = 0.630$, which were modulated by a significant interaction, $F(1, 18) = 4.63$, $p < 0.05$, $\eta_p^2 = 0.205$.

Experiment 2 again showed that tactile distances were perceived as farther apart when oriented across the hairy skin surface of the hand, as opposed to along. On the glabrous skin surface of the hand we found the same pattern of anisotropies but significantly reduced in magnitude, consistent with previous studies (Fiori & Longo, 2018; Longo et al., 2015). On the hairy skin of the foot dorsum, we replicated our finding of anisotropy from Experiment 1. However, on the glabrous skin of the sole we found results directly contrary to those of Experiment 1 – tactile distances were perceived as father apart when going along the foot than across. Thus, Experiments 1 and 2 reached exactly opposite conclusions about the presence of anisotropy on the sole of the foot.

One possible explanation of these contradictory findings on the glabrous skin of the foot in our two experiments is that there were carryover effects between the different skin surfaces we tested. In both Experiments 1 and 2 all skin surfaces were tested in the same participants, and different skin surface blocks were interleaved. ANOVAs on the results from Experiments 1 and 2 including counterbalance group as a between-subjects factor did not reveal any effects of block order, nor any interaction of block order and skin surface. Nevertheless, given that the only systematic difference between the two experiments was whether participants were tested only on the foot (Exp 1) or on both the hand and foot (Exp 2), we decided to run a third experiment in which participants were only tested on a single body part to avoid any possibility of carryover effects.

Experiment 3

The aim of the Experiment 3 is to investigate whether there are anisotropies on both the hairy and glabrous skins surfaces of the foot, independent of any potential carryover effects between conditions. We did this using testing and analysis methods very similar to Experiments 1 and 2, but with independent groups of participants tested on the hairy and glabrous skin surfaces. Because each participant was only tested on a single skin surface, the possibility of carry-over effects between skin surfaces is removed. The experimental design, analysis plan, and hypotheses were pre-registered on the OSF (osf.io/npkhc).

Methods

Participants

For this experiment, we relied on the same power analysis as in Experiment 2. We aimed to recruit 20 participants per group (testing either the hairy or glabrous skin surface), resulting in a total of 40 participants.

We recruited 40 participants, 20 tested on the foot dorsum (14 female; mean age = 29.7 years, range = 18 – 58), and 20 on the sole (12 female; mean age = 28.9 years, range = 20 – 50). Participants were predominantly right-handed as assessed by the EHI (mean = 69.4, range = -50 – 100) and right-footed as assessed by the WFQ (mean = 46.4, range = -95 – 100). EHI and WFQ scores were strongly correlated across participants, $r(38) = 0.705, p < 0.001$.

Procedures

The procedures closely followed those used in Experiment 1 and Experiment 2. Participants were evaluated on their hand and foot dominance, though all participants were tested on their left foot, regardless of assessed foot dominance. Participants were seated in a comfortable position with their left foot resting on a stool (Fig. 1), and were asked to remain as still as possible throughout each experimental block. On each trial, participants were touched twice on the hairy skin or glabrous skin of the left foot, once with the posts oriented along the proximodistal axis of the hand (along stimulus), and once oriented along the mediolateral axis (across stimulus). Stimuli used were the same as in Experiment 1 and 2.

Participants were randomly assigned to one of two groups, testing either the hairy or glabrous skin surface of the foot. Participants completed two blocks of 100 trials each, resulting in a total of 200 trials, and 40 trials for each of the five stimulus pairings (across/along): 20/40 mm, 20/30 mm, 30/30 mm, 30/20 mm, and 40/20 mm. This is the same number of trials as completed for one skin surface in Experiment 1. The

order of along and across stimuli were counterbalanced within each stimulus pair, and order of trials randomised and shown the experimenter through a custom MATLAB script.

Analysis

All analyses were as described in our pre-registered analysis plan. Analyses closely followed Experiment 1 and 2. We initially investigated whether there are anisotropies in tactile distance perception on the two skin surfaces of the foot. We conducted two one-sample t-tests comparing the PSEs on the hairy skin and glabrous skin of the foot to 1 (i.e. no bias in responding). We also investigated similarity of tactile distance perception across the hairy and glabrous skin of the foot, first by correlating PSE values across the two skin surfaces. We also carried out an independent-samples t-test between PSE values on the hairy and glabrous skin surfaces.

Results and Discussion

Results from Experiment 3 are shown in Figure 4. Overall, there was good fit of the psychometric functions to the data, with mean R^2 values of 0.976 (SD: 0.022) on the foot dorsum and 0.965 (SD: 0.041) on the sole. Consistent with the results of Experiments 1 and 2, there was clear anisotropy on the dorsum (mean PSE = 0.858), $t(19) = -4.51$, $p < 0.0001$, $d = 1.008$. On the sole, there was a non-significant trend in the same direction (mean PSE = 0.934), $t(19) = -1.92$, $p = 0.071$, $d = 0.429$. There was a non-significant trend for anisotropy to be larger on the dorsum than on the sole, $t(38) = 1.73$, $p = 0.093$, $d = 0.545$.

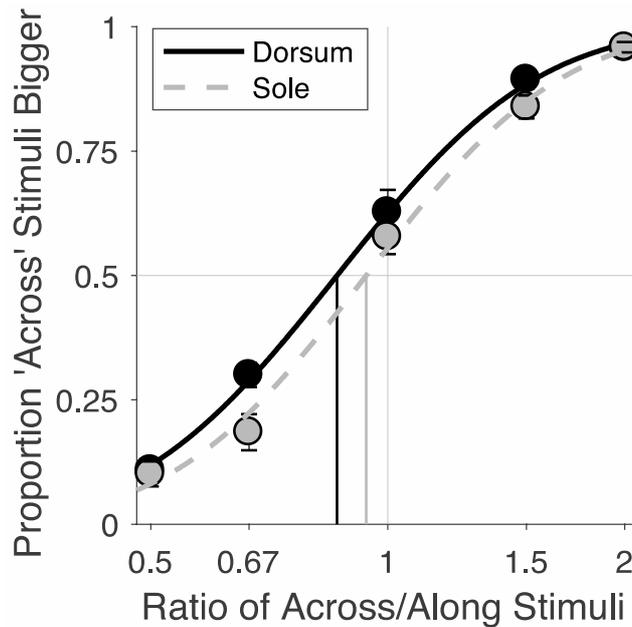


Figure 4. Results from Experiment 3. The curves are cumulative Gaussian functions fit with maximum-likelihood estimation. Error bars represent the standard error of the mean. The solid vertical line that crosses the x-axis at one represents the point of subjective equality (i.e., where the curve crosses 50%). The dashed vertical line represents the grand average PSE for both the hairy and glabrous skin surfaces.

Meta-Analysis of Experiments

Given the inconsistency we found on the sole of the foot across our experiments, we conducted a mini meta-analysis of our three studies (Goh, Hall, & Rosenthal, 2016). We aimed to identify whether our experiments collectively provided evidence for anisotropy on the foot dorsum and sole separately and also for a difference in the magnitude of anisotropy across the two surfaces.

Analysis

The analysis was similar to our recent meta-analysis of data from the same paradigm on the palm of the hand (Longo, 2020). We conducted separate meta-analyses on PSE values on the foot dorsum and sole across our three experiments. For each skin

surface we conducted a random-effects meta-analysis (Borenstein, Hedges, Higgins, & Rothstein, 2009) using the *metafor* package (Viechtbauer, 2010) for R (version 3.4.3). Because the dependent variable and units were identical across experiments, we conducted the meta-analysis on raw mean PSE values rather than standardized values (e.g., Cohen's *d*, Hedges's *g*).

We were also interested in the difference in PSE values between the foot dorsum and sole. Because this comparison was within-subject in Experiments 1 and 2, but between-subject in Experiment 3, it is difficult to model using standard meta-analytic methods. Because we have the individual-subject data, we therefore conducted a linear mixed-effects model (Baayen, Davidson, & Bates, 2008) using the *lme4* toolbox (Bates, Mächler, Bolker, & Walker, 2015) for R (version 3.4.3). We modeled PSE as a dependent variable with skin surface (foot dorsum, sole) as a fixed effect and study as a random effect, including random intercepts for studies and by-study random slopes for the effect of skin surface. The statistical significance of the effect of surface was assessed using model comparison (Barr, Levy, Scheepers, & Tily, 2013).

Results and Discussion

Figure 5 shows a forest plot of the results on both the foot dorsum and sole across the three experiments. On the dorsum, the results were consistent across experiments and there was clear evidence for anisotropy (mean PSE = 0.850, 95% CI: [0.811 – 0.890]), $z = -6.81$, $p < 0.0001$. There was no evidence for heterogeneity across studies, $Q(2) = 0.331$, $p = 0.847$, with the I^2 statistic indicating that 0% of the between-experiment variability was due to heterogeneity. That is, the variability across experiments was no larger than would be expected given the participant-to-participant variance within each experiment.

In contrast, on the sole there was no overall evidence for anisotropy (mean PSE = 0.936, 95% CI: [0.801 – 1.094]), $z = -0.832$, $p = 0.405$. There was clear evidence for heterogeneity across studies, $Q(2) = 41.44$, $p < 0.0001$, with the I^2 statistic indicating that 94.7% of the between-experiment variability was due to heterogeneity. Thus, the experiments differed substantially more than would be expected given the variability within each experiment.

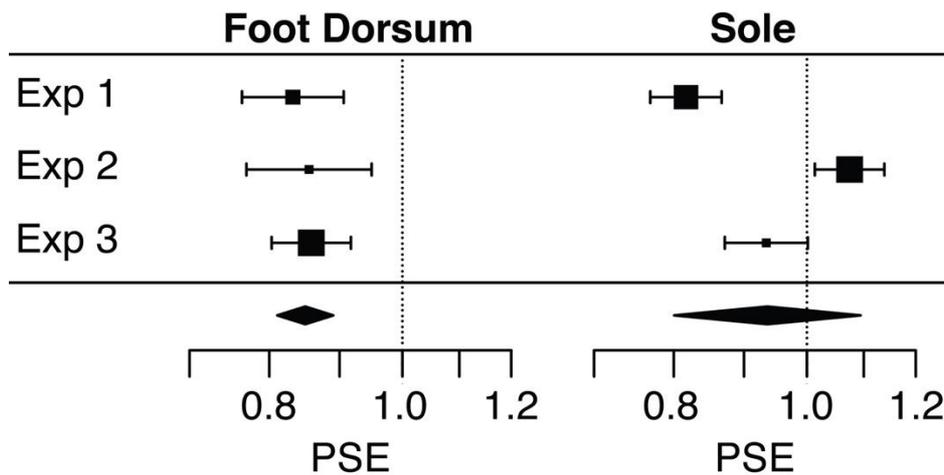


Figure 5: Forest plot showing the results from the meta-analysis of the three experiments. Overall, there was clear evidence for an anisotropy on the foot dorsum, but not on the sole.

Finally, our linear mixed-model analysis found no significant effect of skin surface, $\chi^2(1) = 1.62$, $p = 0.204$. On average, PSEs on the sole of the foot had a PSE 0.042 \log_{10} units higher than on the dorsum.

General Discussion

Across three experiments, clear tactile distance anisotropy was found on the hairy skin of the foot dorsum. Tactile distances were judged as substantially farther apart when oriented across the width of the foot than along its length, mirroring the pattern found consistently on the hairy skin of the hand dorsum in previous research (e.g., Longo & Golubova, 2017; Longo & Haggard, 2011) as well as on other sites on the lower

limb such as the thigh (Green, 1982) and shin (Stone et al., 2018). In contrast, results on the glabrous skin of the sole of the foot were less consistent, with no overall evidence for an anisotropy.

These results add the foot dorsum to the list of body parts on which tactile distance anisotropy has been found, a list which now includes the hand dorsum (Longo & Golubova, 2017; Longo & Haggard, 2011), the palm (Fiori & Longo, 2018; Longo, 2020), the forearm (Green, 1982; Le Cornu Knight et al., 2014), the forehead (Fiori & Longo, 2018; Longo et al., 2015), the thigh (Green, 1982), and the shin (Stone et al., 2018). Despite variability in the *magnitude* of these effects across the body, it is notable that in each of these cases the *direction* of anisotropy is the same, for distances oriented across the width of the body to be overestimated relative to distance oriented along the length (or height) of the body. Other studies show analogous biases for tactile time perception, with the interval between touches oriented across hand width overestimated relative to that for touches oriented along hand length (Hidaka, Tamè, Zafarana, & Longo, 2020). Thus, anisotropy appears to be a quite general principle of tactile organization.

Indeed, there are reasons to think that such distortions may generalise beyond touch entirely. Overestimation of body width has been reported in tasks involving proprioceptive localization of landmarks on the hand (e.g., Coelho, Zaninelli, & Gonzalez, 2017; Ganea & Longo, 2017; Longo & Haggard, 2010) and face (e.g., Longo & Holmes, 2020; Mora, Cowie, Banissy, & Cocchini, 2018), visual comparison judgments of hand size (e.g., Longo & Haggard, 2012; Tamè et al., 2017), localization of body landmarks on a screen (e.g., Fuentes, Longo, et al., 2013; Fuentes, Pazzaglia, Longo, Scivoletto, & Haggard, 2013; Fuentes, Runa, et al., 2013), and a range of body size estimation tasks from the eating disorders literature, such as the moving caliper method (e.g., Dolan et

al., 1987; Halmi et al., 1977; Hundleby & Bourgooin, 1993), the adjustable light beam apparatus (e.g., Dolce et al., 1987; Thompson et al., 1986), kinesthetic judgments (e.g., Kreidler & Chemerinski, 1990), and the image marking procedure (e.g., Gorham & Hundleby, 1988; Thomas & Freeman, 1991). Some recent authors have suggested that analogous distortions may affect non-body objects (Peviani, Magnani, Bottini, & Melloni, 2021; Salvato, Romano, Maio, & Bottini, 2020; Saulton, Dodds, Bülthoff, & de la Rosa, 2014; Saulton, Longo, Wong, Bülthoff, & de la Rosa, 2016). These biases have a certain family resemblance to visual effects, such as the classic horizontal-vertical illusion (Avery & Day, 1969; Howe & Purves, 2002; Mamassian & de Montalembert, 2010), although in a recent paper we argued that they can be explained by a geometrically-simple stretch of tactile space in a way that the visual horizontal-vertical illusion cannot (Fiori & Longo, 2018). It will be important in future research to understand the ways in which anisotropy arises from tactile-specific processes versus more general aspects of perception and cognition.

We have previously suggested that such anisotropies may result from the geometry of tactile receptive fields (RFs) in the somatosensory cortex (Longo, 2017a; Longo & Haggard, 2011; Tamè, Azañón, & Longo, 2019). Neurophysiological studies in cats and monkeys have found that tactile receptive fields are generally oval-shaped, rather than circular, with the long-axis of the RF parallel to the long axis of the limb at several places in the nervous system, including peripheral nerves (Burgess, Petit, & Warren, 1968; Gardner & Spencer, 1972), the spinal cord (Brown, Fuchs, & Tapper, 1975; Wall, 1960), subcortical nuclei (Perl, Whitlock, & Gentry, 1962; Winter, 1965), and the primary somatosensory cortex (Alloway, Rosenthal, & Burton, 1989; Brooks, Rudomin, & Slayman, 1961). Because the spacing between neurons in a somatotopic map is known to be a constant proportion of RF size (Sur et al., 1980), two touches

oriented across the width of the limb will be separated by a larger number of unstimulated RFs than the same two touches oriented along the length of the limb. If tactile distance is calculated by essentially counting the number of unstimulated neurons between two activation peaks within a somatotopic map, this could potentially account for the anisotropy (Longo, 2017a; Longo & Haggard, 2011). Moreover, in a recent functional magnetic resonance study in humans we were able to reconstruct the shape of the skin surface in the primary somatosensory cortex that was distorted in a way that matches the perceptual shape of tactile space (Tamè, Tucciarelli, Sadibolova, Sereno, & Longo, 2021).

While anisotropy was found consistently on the foot dorsum in all three experiments, the results on the sole of the foot were strikingly inconsistent across experiments. In Experiment 1, highly similar anisotropies were found on both the dorsum and sole, whereas in Experiment 2 anisotropy on the sole went in exactly the opposite direction. In Experiment 3, a non-significant trend towards an anisotropy was found. The reasons for these differences across experiments are not clear. Experiment 2 was run by a different experimenter than Experiments 1 and 3, although it is not clear what aspects of the experimenter's conduct could lead to opposite anisotropy specifically on the sole. It is also possible that carry-over effects from block-to-block could have some influence, although it is not obvious what the nature of these effects might be. There is some evidence that RFs on the glabrous skin of the sole of the foot are larger and more randomly distributed than on the glabrous skin of the palm of the hand (Kennedy & Inglis, 2002). This might produce greater variability across trials, or across participants, although it is less clear why it would produce variability across experiments. It is also worth noting that whereas anisotropy on the hairy skin of the hand dorsum has been very consistently found across studies, results on the glabrous

skin of the palm have been more mixed, with some studies finding anisotropy (Fiori & Longo, 2018; Le Cornu Knight et al., 2014; Longo et al., 2015) and other not finding any (Cholewiak, 1999; Green, 1982; Longo & Golubova, 2017; Longo & Haggard, 2011). A recent meta-analysis of this literature (Longo, 2020) found overall evidence for an anisotropy on the palm, but also substantial heterogeneity across studies. In this sense, the inconsistency across studies on the sole of the foot is quite similar to what has been found across studies on the palm of the hand.

Open Practices Statement

All three experiments were preregistered and raw data is available as supplemental material.

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Open Practices Statement

All experiments were pre-registered and raw data is available as online supplementary material.