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# Tactile confusions of the fingers and toes

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**Abstract**

Recent research has shown systematic patterns of confusions between digits of the hands and feet. The present study addressed whether such confusions arise from early somatosensory maps or higher-level body representations. As the glabrous and hairy skin of the hands and feet have distinct representations in somatosensory cortex, an effect arising from early somatotopic maps may show distinct patterns on each skin surface. In contrast, if the effect arises from higher-level body representations which represent the digits as volumetric units, similar patterns should be apparent regardless of which side of the digit is touched. We obtained confusion matrices showing the pattern of mislocalisation on the glabrous and hairy skin surfaces of the toes (Experiment 1) and fingers (Experiment 2). Our results replicated the characteristic pattern of mislocalisations found on the glabrous skin reported in previous studies. Critically, these effects were highly similar on the hairy skin surface of both the toes and fingers. Despite the pattern of mislocalisations being highly stereotyped across participants, there were consistent individual differences in the pattern of confusions across the two skin surfaces. These results suggest that mislocalisations occur at the level of individual digits, consistent with their resulting from higher-level body representations.

**Keywords:** body representation, somatosensation, tactile localisation, fingers, toes

**Public Significance Statement**

Patterns of tactile confusions on the fingers and toes are not only highly consistent and stereotyped across individuals, but also over the hairy and glabrous skin surfaces. Despite this, we found consistent individual differences in the pattern of confusions across the two skin

surfaces. These findings provide strong evidence that tactile confusion of the digits arises from higher-level body representations, where the digits are represented as 3-D, volumetric units, as opposed to arising in early somatotopic maps.

## Introduction

The ability to localise tactile stimuli on the skin is a fundamental function of the somatosensory system. Nevertheless, research has shown that there are systematic biases in this ability. For example, on the hand dorsum, consistent distal (i.e., towards the knuckles) and radial (i.e., towards the thumb) biases in localisation have been found (Culter, 1970; Mancini, Longo, Iannetti, & Haggard, 2011). However, a distinct pattern of biases is found when identifying which of the individual fingers was touched, as opposed to localising touch on the continuous skin surface. When using a tactile stimulus near to the sensory threshold, finger mislocalisations on the glabrous skin are biased more towards neighbouring fingers than distant fingers (Braun et al., 2005; Schweizer, Braun, Fromm, Wilms, & Birbaumer, 2001; Schweizer, Maier, Braun, & Birbaumer, 2000). Moreover, mislocalisations are not equally likely onto each neighbouring finger, but more common towards the middle and ring fingers than the outer fingers (Braun et al., 2005, 2011; Schweizer et al., 2001; Tamè, Wühle, Petri, Pavani, & Braun, 2017). It is unsurprising that differences occur in mislocalisation across the continuous skin surface of the hand versus the individual fingers – localising touch to an individual finger may be simpler than localising a point of touch on the palm or dorsum of the hand as the fingers provide an inherent structure and categorical decision, as opposed to the potentially infinite possibilities on the continuous skin. Further to this, the fingers are represented separately both from one another (Besle, Sánchez-Panchuelo, Bowtell, Francis, & Schluppeck, 2014; Martuzzi, van der Zwaag, Farthouat, Gruetter, & Blanke, 2014), and from the rest of the hand (Gálvez-García, De Haan, Lupiañez, & Dijkerman, 2012; Haggard, Kitadono, Press, & Taylor-Clarke, 2006). This is evident in body representation disturbances such as finger agnosia, a symptom of Gerstmann syndrome in which individuals experience the selective loss of ability to recognise, identify,

distinguish or indicate individual fingers, on either the patient's own or another's fingers (Anema et al., 2008; Gerstmann, 1939; Kinsbourne & Warrington, 1962; Mayer et al., 1999). Even in healthy adults, identifying touch to an individual finger is not as straightforward as one might expect (Rusconi et al., 2014; Rusconi, Gonzaga, Adriani, Braun, & Haggard, 2009; Tamè, Dransfield, Quettier, & Longo, 2017).

Not only does the pattern of mislocalisations differ between the individual fingers and the continuous skin surface of the hand, it appears to differ between the hairy and glabrous skin surfaces as well. Distal and radial biases are found in localising points on the hand dorsum, but no overall biases are found when localising points on the palm of the hand (Mancini et al., 2011). The difference in strength of bias on the two skin surfaces of the hand may be attributable to increased sensitivity on the palm (Ackerley, Carlsson, Wester, Olausson, & Backlund Wasling, 2014; Johansson & Vallbo, 1979), however, the direction of biases on the hand dorsum are consistent across tactile (Aβ), thermal (C), and painful (Aδ) fibers, indicating it is unlikely that directional differences in biases arise during low-level processing of different afferent pathways (Mancini et al., 2011). Instead, they likely arise from separate somatotopic maps of the palm and dorsum in the somatosensory cortex. Single cell recordings in old world and owl monkeys show that the somatotopic map in the postcentral parietal cortex is not represented as a continuous, 3-D homunculus, but is represented as separate somatotopic maps of each skin surface (Merzenich, Kaas, Sur, & Lin, 1978; Nelson, Sur, Felleman, & Kaas, 1980). Given the substantial conservation of the overall organisation of somatosensory cortex between human and non-human primates (Kaas, 2008), we assume that the separation of the two skin surface representations was conserved between human and non-human primates. As such, it is likely that differences in the pattern of mislocalisations across the two skin surfaces arises from processing in the primary

somatosensory cortex (S1), but may also involve higher-level processing in parietal areas posterior to S1 (Longo, Azañón, & Haggard, 2010). However, higher-level processing in parietal areas posterior to S1 may also be involved (Longo et al., 2010) – similarities in the observed biases on the two skin surfaces indicate that biases may also occur at a higher level, where the body is represented as a 3-D, volumetric object, as opposed to separate 2-D skin surfaces (Longo, 2014).

As the hands and feet are serially homologous structures that co-evolved in human evolution (Rolian, Lieberman, & Hallgrímsson, 2010), there are many common physical characteristics of the hand and foot, such as the presence of hairy and glabrous skin surfaces (Marieb, 2012). A number of idiosyncrasies in the mental representation of these physical properties also appear to be common to both the hand and the foot. For example, there is evidence that toe agnosia also commonly occurs in Gerstmann syndrome alongside finger agnosia, suggesting that beyond the physical similarities in structure, there is a deeper level of similarity in how the digits are represented in relation to the rest of the hand or foot (Mayer et al., 1999; Tucha, Steup, Smely, & Lange, 1997). Moreover, both the hairy and glabrous skin surfaces of the hands and feet have separate somatotopic maps in owl monkeys (Merzenich et al., 1978). However, there is evidence that processes such as tactile localisation do differ across the hands and feet. For example, tactile localisation of the toes is less precise than on the fingers, especially for the second, third and fourth toes (Cicmil, Meyer, & Stein, 2016; Halnan & Wright, 1960). This may be a result of differences in size and shape of the bones present in both the hands and feet (Rolian et al., 2010; Marieb, 2012), differences in the way the fingers and toes are ordered in the somatosensory cortex (Akselrod et al., 2017; Martuzzi et al., 2014), or differences in usage, as in humans the toes are not used independently and dextrously as the fingers are,

though with the intriguing exception of compensatory use of the feet in congenital one-handers (Hahamy et al., 2017). Differences in mechanoreceptor density and activity may also affect the ability to localise tactile stimuli – for example, mechanoreceptors have much higher activation thresholds on the glabrous skin of the foot than the hand, which may reduce ability to precisely localise touch (Kennedy & Inglis, 2002; Rolian et al., 2010).

One recent study reported a consistent pattern of mislocalisations for stimuli on the glabrous skin of the toes (Cicmil et al., 2016). Cicmil and colleagues measured this using a simple task: the experimenter stimulated a toe on each trial, using a suprathreshold stimuli, and asked the participant to identify the toe. As for the fingers, touches on the glabrous skin of the toes were more frequently localised to neighbouring toes than distant toes. Performance was worst for the middle three toes, where incorrect localisations were not equally likely to either neighbouring toe but biased towards one of their neighbours. The second and third toe were more frequently localised towards the outer toes, whereas the fourth toe was more frequently localised towards the big toe. It is possible that these biases arise from processing in S1 such as the results of Mancini et al. (2011). However, Cicmil and colleagues describe these biases as arising from an inaccurate internal body representation used when remapping somatosensory information onto the body in external space. Particularly, they suggest that their results reflect an "equal spatial representation hypothesis" wherein toes are represented as being of equal size, despite their actual size differences. This hypothesis accounts for the directional bias observed for each toe, including the mostly veridical identification of the big toe and small toe, as the perceived location in the body representation and actual location in external space are misaligned most significantly for the middle three toes.

Other studies support the hypothesis that tactile localisation occurs in primary somatosensory cortex and higher cortical areas. Localising touch on the body should be seen as a two-step process – first, touch is localised on the somatotopic map, then second, the somatotopic location is mapped onto the body representation (Longo et al., 2010). There is evidence that tactile biases occur in early somatosensory processing (when touch is localised on the somatotopic map), from differences in tactile biases across the two skin surfaces of the hand (Mancini et al., 2011), which are represented separately in the somatosensory cortex of old world and owl monkeys (Merzenich et al., 1978; Nelson et al., 1980). As well as the hand dorsum and palm being represented separately, so are the two surfaces of the fingers (Nelson et al., 1980). In contrast, behavioural studies in humans have found that the conscious body image represents the hands as complete, volumetric units (Longo, 2014). Such differences suggest that different processing stages represent the body either in terms of a collection of 2-D skin sheets (e.g., somatotopic maps) or as a coherent 3-D object (e.g., the body image) (Longo, 2015). If biases in tactile localisation arise in early somatosensory processing, using distinct hairy and glabrous skin representations in the somatosensory cortex, there may be a distinct pattern of mislocalisations for each skin surface of the fingers. In contrast, if biases arise in higher-level processing involving the three-dimensional representation of the fingers, the same pattern of mislocalisation across the fingers could be expected on both the hairy and glabrous skin. In the present study we therefore compared patterns of mislocalisation of touch on both the glabrous and hairy skin surfaces of the toes (Experiment 1) and the fingers (Experiment 2).

## Experiment 1

This study aims to investigate whether tactile mislocalisation of touch to the toes arises from early somatosensory maps or from higher-level body representations. By using a method closely modelled on the study of Cicmil et al. (2016), we aimed to: (1) replicate the pattern of results they found on the glabrous surface of the toes; (2) investigate whether the same pattern of results is found on the hairy surface of the toes; and (3) determine whether individual differences in patterns of mislocalisation are shared across the two surfaces.

*Methods*

*Participants*. Twenty individuals participated (10 female; mean age = 30 years; range = 19 – 58). Participants all reported normal or corrected-to-normal vision and normal touch. Eighteen participants were right-handed and two left-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean = 63, range = -92 – 100). The same 18 participants were right-foot dominant, and two left-foot dominant as assessed by the Waterloo Footedness Questionnaire (Elias, Bryden, & Bulman-Fleming, 1998; mean = 44, range = -40 – 100). EHI and WFQ scores were strongly correlated across participants ($r = 0.74$, $p < 0.001$). All participants gave written informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

The mislocalisations reported by Cicmil et al. (2016) were strikingly strong. The directionality indices (DIs) for toes 2 and 3 (which are the two most characteristic mislocalisations reported) showed Cohen's *d*'s of 1.81 and 1.04, respectively. We conducted a power analysis using G*Power 3.1 (Faul, Erdfelder, Buchner, & Lang, 2007) taking the smaller of these two effect sizes, an alpha value of 0.05 and power of 0.95, which indicated that 12 participants were required. Thus, with 20 participants our experiment has appropriate statistical

power to replicate the results of Cicmil and colleagues and to extend their results to the top of the toes.

*Apparatus and stimuli*. The experimental setup is shown in Figure 1. Participants were asked to sit with their leg outstretched and bare foot resting on a stool (height: 40cm), with toes pointing upwards so that both the top and bottom surfaces of the foot were easily accessible to the experimenter. A piece of black cardboard attached to a post was used as a partition to occlude the participant's sight of their toes. Information about the current trial was presented to the experimenter on a monitor by a custom MATLAB script (Mathworks, Natick, MA), but was not visible to the participant. Participants gave their responses verbally, which were manually entered into MATLAB by the experimenter.

*Figure 1*. Experimental set-up for Experiment 1. Participants sat on a chair with their left foot resting on a stool, giving the experimenter access to both sides of the toes. A black cardboard partition was used to occlude participant's sight of their toes.

*Procedure*

On arriving to complete the experiment, participants were evaluated on their hand and foot dominance using the Edinburgh Handedness Inventory and the Waterloo Footedness Questionnaire.

The procedures were closely modelled on those used by Cicmil and colleagues (2016). Cicmil and colleagues reported that while the pattern of bias was consistent across the dominant and non-dominant foot, biases were stronger on the non-dominant foot. As we expected the majority of participants to be right-foot dominant, we chose to test all participants on their left foot, regardless of assessed foot dominance, for consistency. Once participants were seated with their foot in a comfortable position on the stool, they were instructed to fixate on a yellow sticker on the partition to keep their gaze position constant (Medina, Tamè, & Longo, 2017). They were also instructed to keep their feet as still as possible throughout each experimental block. The experimenter used the tip of her finger to apply tactile stimulation to the section of the participant's toe between the metatarsophalangeal joint (at the base of the toe) and the interphalangeal joint (in the middle of the toe), for around 500 ms. Stimulation was well above detection threshold (estimated 15 to 20 g of force), but indentation of the skin was the only visible motion caused by the stimulation. One toe was stimulated per trial. Participants were asked to respond as quickly and accurately as possible, by verbally identifying which toe they felt had been stimulated. Toes were identified by numbers from 1 to 5: the big toe corresponded to number 1, through to the little toe which corresponded to number 5. Participants generally responded within 1 to 3 seconds after stimulation, so that overall stimulation was applied at a rate of roughly 20 trials per minute. Individual response times were not recorded.

There were four experimental blocks, two in which the hairy skin of the toes was stimulated and two in which the glabrous skin of the toes was stimulated. ABBA counterbalancing was used to vary order of presentation, with the first condition counterbalanced across participants. Each block contained 125 trials, 25 for each of the 5 toes. Each surface of each toe was therefore stimulated a total of 50 times. The order of digit stimulation was pseudo-randomised within each block of trials, so that there was an approximately equal number of each type of preceding trial. Between each block, participants were allowed a short break.

*Data Analysis*

Our main analyses closely followed those of Cicmil and colleagues (2016). A directionality index (DI) was calculated in order to give a single value to indicate both direction and magnitude of bias in toe selection. For each toe, the mean of the responses given to identify which toe was stimulated was calculated, minus the actual digit number of the stimulated toe:

DI = (mean of response toe numbers - stimulated toe number)

A positive DI indicates a lateral bias (towards toe 5), with greater values indicating stronger bias i.e. if the participant responded toe 5 was stimulated when it was toe 3, DI = 5 – 3 = 2. A negative DI indicates a medial bias (towards toe 1), again where greater values indicate stronger bias, i.e. response of toe 2 when toe 3 stimulated, DI = 2 – 3 = -1. DI scores of zero indicate no directional bias in responding, but may occur in two different scenarios. Firstly, if responses to stimulation of toe 3 were entirely accurate, i.e. DI = 3 – 3 = 0. Secondly, if participants had responded equally to neighbouring toes (2 and 4), i.e. DI = 3 – 3 = 0. As such accuracy was also used as a measure of performance on the task.

Where we found important null results we carried out Bayesian statistical tests in order to assess whether the null hypothesis ($H_0$) should be accepted over the alternative hypothesis ($H_1$). In these cases, we reported $BF_{01}$, which expresses the likelihood of $H_0$ relative to $H_1$ given the current data. Bayesian repeated-measures ANOVAs were conducted using JASP 0.8.2.0 (Wetzels, Grasman, & Wagenmakers, 2012).

*Results and Discussion*

*Accuracy and directional biases.* Figure 2 shows confusion matrices for tactile toe localization on the glabrous skin of the bottom of the toes (left panel) and the hairy skin of the top of the toes (right panel). The pattern on the glabrous skin was very similar to that reported by Cicmil and colleagues (2016). Localisation accuracy was highest for toes 1 and 5 (0.98 and 0.89 respectively), but poorer for toes 2, 3, and 4, where the majority of mislocalisations were made onto neighbouring toes (see Figure 3, right panel). This pattern replicates the findings of Cicmil and colleagues, as does our finding that middle toe identification errors were not random but biased towards the lateral toes for toes 2 and 3. The left panel of Figure 3 shows DI values. DI values were significantly different from zero for toe 2 (*M*: 0.37, SD: 0.30), $t(19) = 5.45$, $p < 0.001$, $d = 1.23$, and toe 3 (*M*: 0.18, SD: 0.17), $t(19) = 3.18$, $p < 0.01$, $d = 1.06$, indicating a bias towards the lateral side of the foot. For toe 4, in contrast, there was a significant medial bias (*M*: -0.19, SD: 0.17), $t(19) = -4.84$, $p < 0.001$, $d = 1.12$. These results provide a direct replication of the main findings of Cicmil et al. (2016) that there are consistent directional biases for tactile toe localization in response to stimulation of the bottom of the toes.

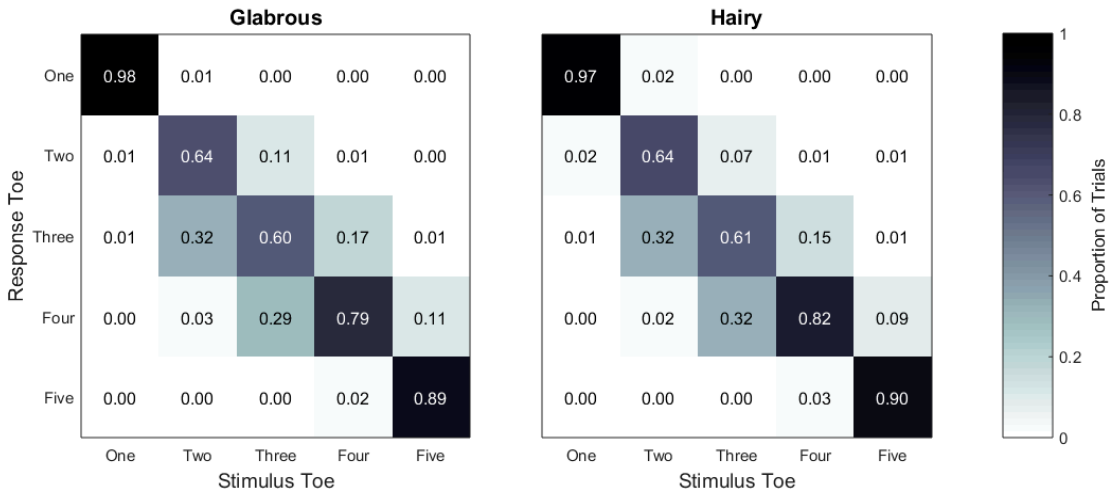


*Figure 2.* Confusion matrices from Experiment 1 showing the proportion of stimuli judged as located on each of the five toes as a function of which toe was actually stimulated. Toes were identified by numbers one (the big toe) through five (the small toe). Data from the glabrous skin of the bottom of the toes is shown in the left panel and data from the hairy skin of the top of the toes is shown on the right panel. The proportion of correct responses for each toe is shown along the diagonal from the top-left to the bottom-right. By definition, each column adds up to exactly 1. Highly similar patterns of mislocalisations were observed for the two sides of the toes.

The novel question in this study was whether similar results would also be found for the hairy skin on the top of the toes. As can be seen in Figure 2, the confusion matrices on the two sides of the foot were extremely similar. As on the glabrous surface, localization accuracy on the hairy surface of the toes was highest for toes 1 and 5 (0.97 and 0.90 respectively), but poorer for toes 2, 3, and 4. DI values indicated significant lateral biases for the tops of toe 2 (*M*: 0.35, SD: 0.24), $t(19) = 6.46$, $p < 0.001$, $d = 1.46$, and toe 3 (*M*: 0.24, SD: 0.22), $t(19) = 4.83$, $p < 0.001$, $d = 1.09$, but a significant medial bias for toe 4 (*M*: -0.13, SD: 0.26), $t(19) = -3.79$, $p < 0.01$, $d = 0.87$ (Figure 3, left panel). To directly compare the similarity of the pattern of mislocalisations on the two surfaces of the toes, we calculated the correlation between the two grand average response matrices (as shown in Figure 2), excluding the diagonals (i.e., the correct responses). This correlation was essentially perfect, $r(18) = 0.99$, $p < 0.01$, showing that the overall mislocalisation pattern was highly similar on the two sides of the foot. Thus, these results show

that the pattern of mislocalisations which Cicmil and colleagues reported following stimulation of the glabrous skin of the bottom of the toes appears in a very similar way following stimulation of the hairy skin of the tops of the toes.

To further investigate the similarities of performance on both skin surfaces of each toe, repeated-measures ANOVAs were performed with two factors: Stimulated Toe (1 to 5) and Skin Surface (hairy/glabrous). DI and accuracy were tested separately as dependent variables. The results of the first ANOVA showed that performance was significantly different across the toes ($F(4,76) = 36.17$, $p < 0.01$, $\eta_p^2 = 0.66$). Post-hoc comparisons confirmed that all toes were significantly different from each other, apart from toes 4 and 5 (all $p < 0.05$, Bonferroni corrected for multiple comparisons). As shown in Figure 3a, while toes 4 and 5 show comparable medial bias, lateral bias for toe 2 was significantly stronger than for toe 3. This is consistent with Cicmil and colleagues' equal spatial representation hypothesis (toes are represented of being of equal size, despite differing in actual size), in which toes 2 and 3 are the most displaced from their actual spatial location. The ANOVA also confirmed that DI was not significantly different between the two skin surfaces of the foot ($F(1,19) = 0.76$, $p > 0.05$, $\eta_p^2 = 0.04$), and there was no difference in DI of each toe depending on which skin surface was stimulated ($F(4,76) = 1.48$, $p > 0.05$, $\eta_p^2 = 0.07$). A Bayesian repeated-measures ANOVA provided moderate evidence in support of the null hypothesis, that there was no difference in DI on the two skin surfaces ($BF_{01} = 5.70$), and strong evidence against there being an interaction of toe and surface ($BF_{01} = 13.48$).

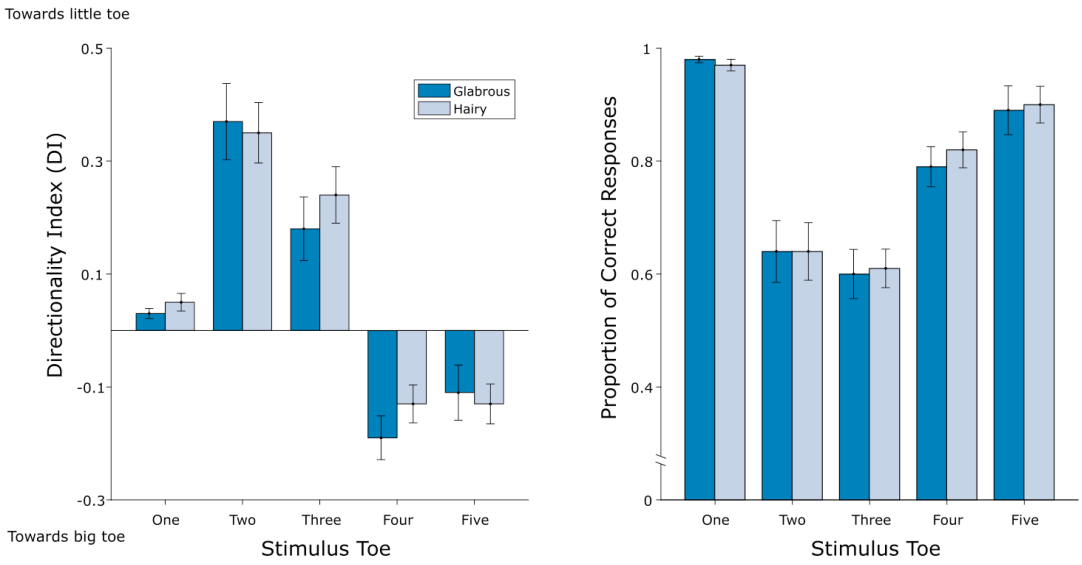


*Figure 3.* Results from Experiment 1. The left panel shows the grand average DI scores for each toe, on the glabrous skin on the bottom of the foot, and hairy skin on the top. The right panel shows the grand average percentage of correct responses made to each toe, on the glabrous skin on the bottom of the foot, and hairy skin on the top. Toes were identified by numbers one (the big toe) through five (the small toe). Error bars represent the standard error of the mean. Highly similar patterns of results were found for the two sides of the toes for both DI and accuracy.

The second ANOVA again indicated that accuracy was significantly different depending on which toe was stimulated ($F(4, 76) = 27.59$, $p < 0.01$, $\eta_p^2 = 0.59$), with post-hoc comparisons revealing that all toes apart from toes 2 and 3 showed significant differences in accuracy of responses (see Figure 3b). This finding again lends itself to Cicmil and colleagues' equal spatial representation hypothesis. The ANOVA also confirmed that overall accuracy was also not different depending on which skin surface was stimulated ($F(1,19) = 0.35$, $p > 0.05$, $\eta_p^2 = 0.02$), and did not differ depending on which surface of each toe was stimulated ($F(4,76) = 0.32$, $p > 0.05$, $\eta_p^2 = 0.02$). A Bayesian repeated-measures ANOVA provided moderate evidence in support of the null hypothesis that there was no difference in accuracy on the two skin surfaces ($BF_{01} = 6.40$), and strong evidence that there were no differences in accuracy for each toe, depending on which skin surface was stimulated ($BF_{01} = 20.15$).

*Shared individual differences across the two sides of the toes.* If the patterns of mislocalisation we have described arise from higher-level body representations in which the different skin surfaces of the toes are integrated into a volumetric, 3-D representation of the whole toe, then person-to-person differences in the pattern of mislocalisation should be shared across the two surfaces. The results above show that there are highly similar patterns of mislocalisations on the two surfaces of the toes at the level of grand averages. We also investigated whether idiosyncratic differences across participants are also common to the two sides of the toes. To isolate individual differences in each participant we used a *leave-one-participant-out* procedure in which we regressed the 20 off-diagonal cells (i.e., the localisation errors) of each participant's confusion matrix on the grand average confusion matrix for the other 19 participants. The resulting residuals quantify the way in which a given participant's confusion matrix differs idiosyncratically from the pattern shown by the other participants. Critically, this procedure eliminates differences between participants in overall levels of accuracy, isolating the *pattern* of confusions between fingers, rather than overall performance. For example, two individuals may produce the same DI for toe 5 (their overall performance), but have different *patterns* of performance. Such as if the first person continually identified toe 5 as toe 3, whereas the second person responded an equal number of times that toe 5 it was toe 2, 3 or 4. In these two cases, the first person would show a relatively strong bias for toe 3, and weak biases for toes 2 and 4, whereas the second person would show moderate biases for toes 2, 3 and 4. Moreover, individuals may even show biases in the opposite direction to those reported in the analysis of overall bias. These residuals were calculated separately for the confusion matrices on the top and bottom of the toes, resulting in two sets of residuals per participant.

If there are shared individual differences on the two sides of the toes, the two sets of residuals for a given participant should be similar. That is, a participant who differs idiosyncratically from other people on the bottom of the toes should also differ in the same way on the top of the toes. For example, if a person showed strong biases for toe 3, but weak biases for toes 2 and 4 on both skin surfaces, this may reflect idiosyncratic differences in performance. In contrast, if a person showed strong biases for toe 3 and weak biases for toes 2 and 4 on the glabrous skin, but moderate biases for toes 2, 3 and 4 on the hairy skin (same DI, different pattern of results), this may reflect that there are not idiosyncratic differences in performance. To assess this, we used a cross-correlation classification procedure. For each participant, we calculated the correlation between the two patterns of residuals, the within-participant cross-correlation. Then we calculated the 38 cross-correlations comparing each of that participant's two patterns to the opposite pattern of each of the other 19 participants. Classification accuracy was calculated for each participant as the percentage of those 38 between-participant correlations which were smaller than the within-participant cross-correlation.

On average, classification accuracy was 82.37%, significantly higher than chance (i.e., 50%), $t(19) = 7.89$, $p < 0.001$, $d = 1.76$. Across participants, classification accuracy ranged from 18.42% to 97.37%, but exceeded 50% in 19 of 20 participants. This provides strong evidence for shared individual differences in mislocalisation patterns on the two surfaces of the toes. Although the pattern of mislocalisations appears to be highly consistent across participants, as shown by Cicmil et al. and the current replication, there are nevertheless idiosyncratic differences between people in mislocalisations, that are consistent across the two skin surfaces. This adds support to our novel finding that participants show consistent patterns in mislocalisation across the two skin surfaces at the group level.

These results replicate the highly stereotyped pattern of mislocalisations found by Cicmil et al. (2016) on the toes, and showed that similar patterns of mislocalisation are found on both the hairy and glabrous skin. Moreover, we showed that although the pattern is highly consistent across participants, there are individual differences in task performance that are consistent across the two skin surfaces. This result indicates that mislocalisations arise at a level of somatosensory processing in which the toes are represented as complete, volumetric units, and supported that directional disturbances in localisation arise from higher-order representations of the body.

*Effect of previously stimulated toe on current toe identification.* To fully replicate the analyses carried out by Cicmil and colleagues, we investigated the effect of identity of the previously stimulated toe on the directionality of identification errors. Cicmil and colleagues investigated this for toes 2 and 3, as responses to these toes were significantly biased in their analysis. As responses to toe 4 also showed significant biases in our analysis, we included it our analyses. Toes 1 and 5 were compared in the analysis as 'previously stimulated toes', as accuracy rates for these toes were high and they are separated by the greatest distance (Cicmil et al., 2016). Response data for the two surfaces of the foot was grouped according to which toe had been stimulated on the immediately preceding trial and DI and accuracy were calculated.

On both skin surfaces, when toe 1 was immediately preceding, mean DI values for toes 2 (hairy: 0.19, glabrous: 0.16) and 3 (hairy: 0.03, glabrous: 0.08) were close to zero, indicating little directional bias in responding. DI score for toe 4 was greater than in the original analysis on both skin surfaces when preceded by toe 1 (hairy: -0.21, glabrous: -0.42), indicating a stronger bias towards toe 1. When toe 5 was immediately preceding, mean DI values for toes 2 (hairy: 0.37, glabrous: 0.42) and 3 (hairy: 0.38, glabrous: 0.24) were greater than in our original

analysis, indicating a stronger bias towards toe 5. DI score for toe 4 were closer to zero then in our original analysis when preceded by toe 5 (hairy: -0.14, glabrous: -0.27), indicating little bias in responding. Our findings replicate those reported by Cicmil and colleagues, showing that identification of the current toe is biased in the direction of the immediately preceding toe. DI was significantly different depending on whether toe 1 or toe 5 was previously stimulated, on both surfaces of the second toe (paired t-tests, glabrous: $t(19) = -3.30$, $p < .01$, $d = 1.27$; hairy: $t(19) = -3.17$, $p < .01$, $d = 0.70$), and the hairy skin of the third toe (paired t-test, $t(19) = -5.52$, $p < .01$, $d = 1.23$).

Error rates also differed depending on which toe was stimulated on the immediately preceding trial. On both skin surfaces, error rates were greatest for toe 2 following stimulation of toe 4, and for toes 3 and 4 following toe 5. This corroborated the findings of Cicmil and colleagues, that error rate increases the further the currently stimulated toe is from the preceding toe. Number of errors was significantly different depending on whether toe 1 or 5 was previously stimulated for the glabrous skin of the second toe (paired t-test, $t(19) = 2.95$, $p < 0.01$, $d = 0.75$) and hairy skin of the third toe (paired t-test, $t(19) = 3.21$, $p < .01$, $d = 0.89$).

In addition to the analyses carried out by Cicmil and colleagues, we investigated whether DI was significantly different on the two skin surfaces of each toe, depending on the previously stimulated toe. Repeated-measures ANOVAs were performed with two factors: Previously Stimulated Toe (1 to 5) and Skin Surface (hairy/glabrous). Each of the currently stimulated toes (2, 3 and 4) were tested separately as dependent variables. Each toe showed a significant effect of Previously Stimulated Toe, (toe 2: $F(4, 76) = 10.06$, $p < 0.001$, $\eta_p^2 = 0.72$, toe 3: $F(4, 76) = 13.40$, $p < 0.001$, $\eta_p^2 = 0.77$, toe 4: $F(4, 76) = 3.22$, $p = 0.04$, $\eta_p^2 = 0.45$), showing again that previously stimulated toe biases current toe identification. For two of the toes there was no

significant effect of Skin Surface, (toe 2: $F(1, 19) = 0.56$, $p = 0.82$, $\eta_p^2 = 0.003$, toe 3: $F(1, 19) = 0.32$, $p = 0.58$, $\eta_p^2 = 0.02$), indicating DI was not significantly different on the hairy and glabrous skin. However, there was a significant effect of Skin Surface for toe 4 ($F(1, 19) = 11.79$, $p < 0.01$, $\eta_p^2 = 0.38$). There was a trend for stronger bias towards toe 5 on the glabrous skin than on the hairy skin, although post-hoc comparisons showed that strength of bias was only significantly different on the two skin surfaces when the immediately preceding stimulation was to the big toe, $t(19) = 2.87$, $p = 0.01$, $d = 0.70$. None of the three interactions were significant (toe 2: $F(4, 76) = 92$, $p = 0.46$, $\eta_p^2 = 0.05$, toe 3: $F(4, 76) = 2.09$, $p = 0.09$, $\eta_p^2 = 0.10$, toe 4: $F(4, 76) = 2.31$, $p = 0.07$, $\eta_p^2 = 0.11$). This supports the findings of our original analysis, that the characteristic pattern of mislocalisations of the toes is consistent across the hairy and glabrous skin surfaces.

## Experiment 2

In the second experiment, we used the same method (adapted for the hands) to investigate whether the pattern on the toes is congruent with localisation on the hairy and glabrous surface of the fingers.

### *Methods*

*Subjects.* Twenty participants took part in the experiment (11 female; mean age = 30 years; range = 18-46). Participants all reported normal or corrected-to-normal vision and normal touch. Eighteen participants were right-handed and two left-handed, as assessed by the Edinburgh Handedness Inventory (mean = 55 years, range = -83 – 100). The same 18 participants were right-foot dominant, and two left-foot dominant as assessed by the Waterloo Footedness Questionnaire (mean = 43, range = -20 – 100). EHI and WFQ scores were strongly correlated across participants ($r = 0.70$, $p < 0.001$). All participants gave written informed

consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

*Procedure*. The protocol was kept as close to Experiment 1 as possible, although we altered our method of applying the stimuli to avoid problems such as were encountered by Cicmil et al. (2016). In their experiment, the same strength stimuli were used across the fingers and toes, resulting in ceiling effects in localisation of the fingers (i.e., literally no mislocalisations were reported on the fingers for any of their participants). As the fingers have a small point localisation threshold and pressure sensitivity threshold in comparison to the toes a near-threshold stimulus is needed to give a clear pattern of mislocalisations (Schweizer et al., 2000). Therefore, stimulation was applied using von Frey hairs. This allowed the experimenter to present weaker and more precise force to the fingers than manual stimulation. The strength of von Frey hair used was determined at the beginning of the experiment by finding the threshold stimuli for each participant where they scored roughly 70% correct across all fingers. Threshold testing was done separately for both sides of the hand, although the most frequently used strength was the same for both skin surfaces (mean strength glabrous = 2.30g, range = 1.65g – 2.83g; mean strength hairy = 2.28g, range = 1.65g – 2.83g). Tactile stimulation was applied to the medial phalanx of the finger or proximal phalanx of the thumb for on average 500ms.

Participants were always tested on the left hand to remain consistent with Experiment 1, where the left foot was tested. Participants sat on a chair with their arm resting on a desk. The hand was kept in a neutral posture, with the fingers slightly apart. The hand was either flat with the palm against the desk or with the back of the hand against the desk, depending on the condition. Participants wore an eye mask to prevent vision of their hand. Fingers were identified

by numbers from 1 to 5: the thumb corresponded to number 1, through to the little finger which corresponded to number 5.

*Results and Discussion*

*Accuracy and directional biases.* Confusion matrices for Experiment 2 are shown in Figure 4. The left panel of Figure 4 shows the proportion of correct localisations were again highest for the thumb than for other fingers on the glabrous skin of the hand (0.89). In contrast to the findings on the toes, the little finger had the least correct localisations (0.52). Tactile identification was again less accurate for the index, middle and ring finger with accuracy decreasing from the index to the ring finger. As for the toes, finger identification errors were not random but biased towards the little finger for the index finger (*M*: 0.20, SD: 0.17), $t(19) = 5.27$, $p < 0.001$, $d = 1.18$, and towards the thumb for the ring finger (*M*: -0.40, SD: 0.24), $t(19) = -7.44$, $p < 0.001$, $d = 1.67$. In contrast to the toes, however, there was no selection bias for the middle finger on either skin surface, suggesting that lateral or medial fingers were chosen interchangeably (*M*: -0.04, SD: 0.01), $t(19) = -1.77$, $p > 0.05$, $d = -0.40$.

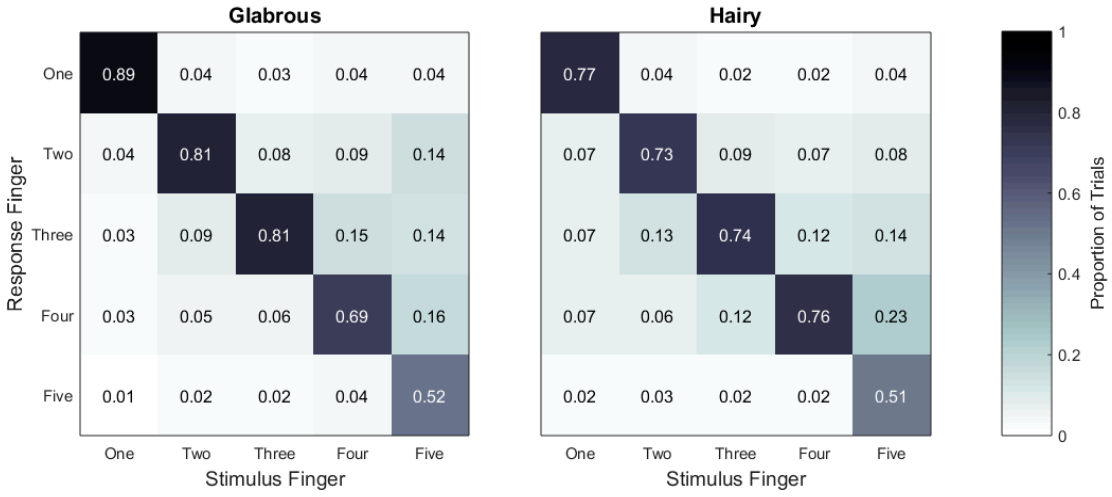

*Figure 4.* Confusion matrices from Experiment 2 showing the proportion of stimuli judged as located on each of the five fingers as a function of which finger was actually stimulated. Fingers were identified by numbers one (the thumb) through five (the little finger). Data from the glabrous skin of the bottom of the fingers is shown in the left panel and data from the hairy skin of the top of the fingers is shown on the right panel. Highly similar patterns of mislocalisations were observed for the two sides of each finger, except for the thumb.

The right panel of Figure 4 shows the results from the hairy skin of the back of the fingers. Consistent with the glabrous skin of the hand, finger identification decreased in accuracy from the thumb (0.77) to the little finger (0.51). The bias in identification errors for the hairy skin was consistent from the glabrous skin, as opposed to those on the hairy skin of the feet. DI values were biased towards the little finger for the index finger ($t(19) = 7.82$, $p < 0.001$, $d = 1.82$) and towards the thumb for the ring finger ($t(19) = -7.47$, $p < 0.01$, $d = -1.63$). Again, there was no significant bias for the middle finger ($t(19) = 0.98$, $p > 0.05$, $d = 0.22$). To directly compare similarity of participants' performance on the two surfaces of the hands, the grand average responses to stimulation on the top and bottom of the hand (see Figure 4) were again correlated. Biases in mislocalisation were highly consistent across the two surfaces ($r = 0.82$, $p < 0.01$).

As opposed to the findings on the toes, this directional bias found in the fingers suggests a 'midline' of the hand towards which participants were biased. The equal spatial representation hypothesis proposed by Cicmil and colleagues to explain their results on the toes seems not to explain this bias towards the mid-line of the hand. As the fingers are in reality of roughly equal size, an equal spatial representation hypothesis would not predict any bias in localisation. This is, however, the result we would expect when using suprathreshold tactile stimuli – such as Cicmil and colleagues reported, localisation of the fingers is extremely accurate when using above-threshold tactile stimuli, which could support an equal spatial representation hypothesis.

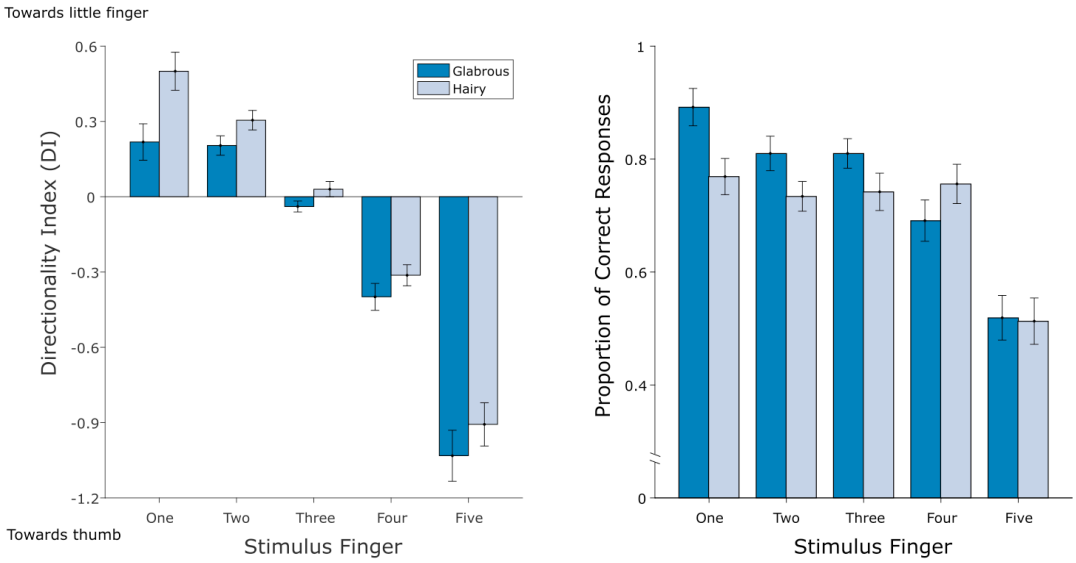


*Figure 5.* Results from Experiment 2. The left panel shows the grand average DI scores for each finger, on the glabrous skin on the bottom of the hand, and hairy skin on the top. The right panel shows the grand average percentage of correct responses made to each finger, on the glabrous skin on the bottom of the hand, and hairy skin on the top. Fingers were identified by numbers one (the thumb) through five (the little finger). Error bars represent the standard error of the mean. Similar patterns of results were found for the two sides of the fingers, for both DI and accuracy.

To further investigate similarities in performance on both skin surfaces, repeated-measures ANOVAs were again performed with two factors: Finger (1 to 5) and Skin Surface (hairy/glabrous). DI and accuracy were tested separately as dependent variables. The first ANOVA indicated that DI was significantly different between the two surfaces of the hand ($F(1,19) = 10.78$, $p < 0.01$, $\eta_p^2 = 0.36$), in contrast to the findings of the correlation. DI was significantly lower for all fingers on the glabrous skin of the hand ($p < 0.05$). However, paired comparisons t-tests between the two skin surfaces for each finger indicated that the difference between the two skin surfaces was driven by a large effect for the thumb ($t(19) = 3.45$, $p < 0.01$, $d = 0.77$), as other t-tests didn't reach significance when corrected for multiple comparisons ($p > 0.01$). There was again a difference in DI between the five fingers ($F(4,76) = 130.89$, $p < 0.01$, $\eta_p^2 = 0.87$), but no difference in DI depending on which skin surface of each finger was

stimulated ($F(4,76) = 1.79$, $p > 0.05$, $\eta_p^2 = 0.09$). As shown in the left panel of Figure 5, DI was biased towards the middle finger of the hand, with bias increasing more towards lateral fingers (1 and 5), except for the glabrous surface of the thumb (all $p < 0.05$). A Bayesian repeated-measures ANOVA provided moderate evidence in support of the null hypothesis, that there were no differences in DI for each finger, depending on which skin surface was stimulated ($BF_{01} = 5.97$).

The second ANOVA confirmed overall accuracy again differed depending on which finger was stimulated ($F(4,76) = 30.97$, $p < 0.01$, $\eta_p^2 = 0.62$), but was not different depending on which skin surface was stimulated ($F(1,19) = 3.06$, $p > 0.05$, $\eta_p^2 = 0.14$). A Bayesian repeated-measures ANOVA provided only weak evidence in support of the null hypothesis, that there was no difference in accuracy on the two skin surfaces ($BF_{01} = 1.73$). There was also a significant interaction ($F(4,76) = 3.93$, $p < 0.01$, $\eta_p^2 = 0.17$), indicating that the pattern across fingers differed on the two skin surfaces. Considering the skin surfaces independently, accuracy was not significantly different between the thumb, index and middle finger on the glabrous skin of the hand (all $p > 0.01$), but was between these fingers and the ring and little finger (all $p < 0.01$). In contrast to the hairy surface of the hand, accuracy was consistent for all fingers from the thumb to the ring finger (all $p > 0.01$), and only different to the little finger (all $p < 0.01$). Paired samples t-tests, however, confirmed that differences in accuracy were only significant between the hairy and glabrous skin of the thumb ($t(19) = 3.72$, $p < 0.01$, $d = 0.83$).

These results suggest that, as for the toes, tactile localisation of the fingers is biased as a result of inaccuracies in high-order body representation used during tactile-spatial remapping, as shown by consistent biases towards the middle finger of the hand. The results of this study are also consistent with previous studies investigating tactile acuity across the fingers, which showed

that sensitivity decreases from the thumb to the little finger (Duncan & Boynton, 2007; Sathian & Zangaladze, 1996; Vega-Bermudez & Johnson, 2001). This occurred as a result of decreasing cortical magnification (the proportion of cortical area given the skin area on the body) across representations in S1 from the thumb to the little finger, similar to macaques (Duncan & Boynton, 2007; Sutherling, Levesque, & Baumgartner, 1992). However, our results indicate that this pattern is only consistent across the two skin surfaces of the four fingers, not including the thumb. There were less localisation errors on the glabrous skin than on the hairy skin of the thumb, which reduced the strength of bias (as it is the outermost finger) and increased accuracy (as is shown in our results).

*Shared individual differences across the two sides of the fingers*. The results above show that there are similar patterns of mislocalisations on the two surfaces of the fingers at the level of grand averages, as well as the toes. We also investigated whether idiosyncratic differences across participants are also common to the two sides of the fingers, using the same method described in Experiment 1.

On average, classification accuracy was 74.61%, significantly higher than chance performance, $t(19) = 4.63$, $p < 0.001$, $d = 1.04$. Across participants, classification accuracy ranged from 13.16% to 100%, but exceeded 50% in 19 of 20 participants. This provides strong evidence for shared individual differences in mislocalisation patterns on the two surfaces of the fingers, as well as the toes. Although the pattern of mislocalisations appears to be consistent on the fingers (if not the thumb), there are again individual differences in mislocalisations that are consistent across the two skin surfaces for each participant. This supports our novel finding that participants show consistent patterns in mislocalisation across the two skin surfaces at the group level also.

*Effect of previously stimulated finger on current finger identification.* We again investigated the effect of identity of the previously stimulated toe on directionality index scores for fingers 2, 3 and 4. Finger 1 and 5 were again used as "previously stimulated fingers" to remain consistent across our analyses, despite accuracy for finger 5 being poorer than the other fingers (0.52 and 0.51 respectively). Response data for the two surfaces of the hand was grouped according to which finger has been stimulated on the immediately preceding trial, and DI and accuracy were calculated.

On both skin surfaces, when the immediately preceding touch was on finger 1, mean DI values for finger 2 were close to zero (hairy: 0.04, glabrous: 0.08), there was little bias in participant's responses. DI scores for fingers 3 (hairy: -0.15, glabrous: -0.15) and 4 (hairy: -0.45, glabrous: -0.76) when preceded by finger 1 were greater than in our original analysis, indicating a stronger bias in responding towards finger 1. When the immediately preceding touch was on finger 5, mean DI scores for fingers 2 (hairy: 0.44, glabrous: 0.29) and 3 (hairy: 0.1, glabrous: 0.01) were marginally greater than in our original analyses, indicating a bias in responding towards finger 5. Mean DI scores for toe 4 when immediately preceded by toe 5 were only marginally weaker than in our original analysis (hairy: -0.29, glabrous: -0.4), showing a slight bias in responding towards toe 5. DI was significantly different depending on whether finger 1 or 5 was previously stimulated on the hairy skin of fingers 2 (paired t-test, $t(19) = -3.46$, $p < .01$, $d = 0.85$) and 3 (paired t-test, $t(19) = -4.86$, $p < .01$, $d = 0.39$). Compared to finger 1, finger 5 may have had a weaker biasing effect when it was the previously stimulated finger as accuracy in localising this finger was poor – if participants did not correctly localise finger 5, it would not bias responses on the next trial.

Error rates again differed depending on which finger was stimulated on the immediately preceding trial. On both skin surfaces error rates were greatest for finger 2 following stimulation of finger 5, for finger 3 following finger 1 or 5, and for finger 4 following finger 1. Number of errors was not significantly different depending on whether finger 1 or 5 was previously stimulated for any fingers (paired t-tests: $p > .01$ in all cases). As for the toes, this pattern of results indicates that touches farther from the preceding toe result in a greater number of erroneous responses. This finding also corroborates our earlier assertion that participants' responses are biased towards the midline of the hand, as identification of finger 3 was equally disrupted by touches to either finger 1 or 5.

We again investigated whether DI was significantly different on the two skin surfaces of the fingers depending on the previously stimulated fingers. Repeated-measures ANOVAs were performed with two factors: Previously Stimulated Finger (1 to 5) and Skin Surface (hairy/glabrous). Each of the currently stimulated fingers (2, 3 and 4) were tested separately as dependent variables. Each finger showed a significant effect of Previously Stimulated Finger, (finger 2: $F(4, 76) = 8.94$, $p = 0.001$, $\eta_p^2 = 0.69$, finger 3: $F(4, 76) = 4.20$, $p = 0.02$, $\eta_p^2 = 0.51$, finger 4: $F(4, 76) = 3.59$ $p = 0.03$, $\eta_p^2 = 0.47$), in line with our previous results. None of the fingers were significantly different depending on which skin surface was stimulated (finger 2: $F(1, 19) = 3.82$, $p = 0.07$, $\eta_p^2 = 0.17$, finger 3: $F(1, 19) = 2.10$, $p = 0.16$, $\eta_p^2 = 0.10$, finger 4: $F(1, 19) = 3.16$, $p = 0.09$, $\eta_p^2 = 0.14$), and none of the interactions were significant (finger 2: $F(4, 76) = 9.32$, $p = 0.45$, $\eta_p^2 = 0.05$, finger 3: $F(4, 76) = 0.87$, $p = 0.48$, $\eta_p^2 = 0.04$, finger 4: $F(4, 76) = 2.41$, $p = 0.06$, $\eta_p^2 = 0.11$). This provides further evidence that characteristic patterns of mislocalisation are highly consistent across the hairy and glabrous skin surfaces of the fingers.

## General Discussion

We investigated patterns of confusion for localisation of tactile stimuli on glabrous and hairy skin surfaces of the toes (Experiment 1) and fingers (Experiment 2). This study yielded three main findings: (1) We replicated the distinct patterns of mislocalisations on the glabrous skin of the fingers and toes; (2) We found that the respective patterns are consistent on the hairy skin of the fingers and toes; and (3) We showed that despite these patterns being very consistent across participants, there are idiosyncratic differences in participant's performance that can predict performance across the two skin surfaces. In addition, we replicated the finding that localisation is biased towards the previously stimulated toe (Cicmil et al., 2016). We showed that this bias is consistent over the glabrous and hairy skin of both the fingers and toes. To our knowledge, this is the first quantitative comparison of tactile mislocalisation over the two skin surfaces of the fingers or toes. The similar patterns on each surface of the digits indicate that biases in tactile mislocalisation occur at the level of complete digits, as opposed to individual skin surfaces. As such, they likely arise in higher-order representations of the body, where the body is represented as a fully-3D, volumetric object (Longo, 2014). This supports conclusions from previous studies, that disturbances in tactile localisation arises from distortions of high-level representations of the body structure (Anema et al., 2008; Cicmil et al., 2016).

Cicmil et al. (2016) describe the directional distortions when localising the toes as arising from inaccuracies in the underlying body image. They suggest that the toes are represented as being of equal sizes, although in reality the big toe is much larger than the remaining toes in order to support bipedal walking (Napier, 1967). From this hypothesis we would predict a high number of mislocalisations, and directional bias of these mislocalisations, exactly as found in this study: the second and third toes are biased towards the little toe, and the fourth towards the

big toe. In support of this account, macaques have roughly equal spacing of the toes and show directional mislocalisation of touch similar to the human hands, i.e. towards the middle digit (Vierck, Favorov, & Whitsel, 1988). This perhaps reflects that primates use their feet both for locomotion, as in humans, and for grasping, as the human hand is used (Holowka, O'Neill, Thompson, & Demes, 2017).

When using a near-threshold stimulus, the stereotypical pattern of mislocalisations found over the fingers still differs from that on the toes: mislocalisation of the fingers is always biased towards the middle finger. This bias is even evident when the additional bias towards the previously stimulated finger is considered. As the distribution of digit size across the hand is more symmetrical than the foot, this pattern of results may be expected if hand representation was distorted to give equal size weighting to each finger. Interestingly, our results indicate that the thumb is included in the hand schema, as it is biased towards the middle finger in the same way as the other fingers. Previous research has indicated that the index finger, rather than the thumb, is perceived as analogous to the big toe (Singh, 1990), indicating that the thumb is perceived differently, in some way, to the rest of the fingers. In the present study, the hairy skin of the thumb showed significantly weaker biases towards the midline of the hand, perhaps indicating a less robust representation of the thumb in relation to the other fingers. This pattern of results may also reflect a bias in selecting points towards the midline of the hand, like the bias in selecting points towards the midline of the torso (Ho & Spence, 2007). As for the fingers, bias towards the midline of the body increases the farther from the midline the tactile stimulus is applied. This effect persists even when the bias towards the previously stimulated finger is accounted for: our results show that even if the previously stimulated finger is away from the midline of the hand, biases continue to be in the direction of the midline (although the strength of

bias is attenuated by the immediately preceding touch). Yet it cannot be determined from these results whether the bias towards the hand or body midline is a product of distortions of the underlying body image, or a bias in decision-making for uncertain cases.

Critically, our findings do not reflect the pattern of results that may arise if performance was based solely on differences in tactile acuity across the fingers. A number of studies have shown that tactile acuity of the glabrous skin of the fingers decreases from the thumb to the little finger, as a result of decreasing cortical magnification across representations in S1 from the thumb to the little finger (Duncan & Boynton, 2007; Sathian & Zangaladze, 1996; Sutherling et al., 1992; Vega-Bermudez & Johnson, 2001). While we do not measure tactile acuity directly, we do have a measure of localisation accuracy. Our second experiment extends previous results, showing a similar pattern on localisation accuracy as spatial acuity across the fingers, and moreover confirming that this pattern is the same over the hairy skin and glabrous skin, apart from on the thumb. Sensitivity of the toes is different: localisation accuracy is high for the big and little toes, but consistently low on the glabrous skin of the middle three toes (Cicmil et al., 2016). Our own accuracy results corroborate these findings on the toes, and suggest that accuracy is similar across the glabrous and hairy surfaces. Importantly, these results differ from the patterns of bias found on the fingers and toes, confirming that the bias found relates to distortions in higher-order representations of the body, not low-level sensory processing.

Previous studies, however, have shown different patterns of mislocalisation bias on the two skin surfaces of the hand. Mancini et al. (2011) found consistent distal and radial biases in localisation (towards the knuckles and the thumb). Weaker proximal biases (towards the central point of the palm) are found on the palm of the hand. Mancini and colleagues suggest that both high- and low-level processes are involved – the greater magnitude of distortions on the dorsum

is attributable simply to lower spatial resolution of the receptive fields, comparable to the palm (Ackerley et al., 2014; Johansson & Vallbo, 1979; Mancini et al., 2011), whereas the differences in direction of the bias is attributed to differences in the underlying 2-D representations of the individual skin surfaces (Longo, Mancini, & Haggard, 2015; Mancini et al., 2011). However, these findings do not necessarily conflict with our results. While localisation on the palm and dorsum of the hand relies solely on the fragmented implicit representation of the hand, finger localisation also relies on proprioceptive information about the variable position of the fingers. For example, recent research has shown that finger posture alters our structural body representation to account for changing position (Tamè, Dransfield, et al., 2017). Moreover, localising touch in external space uses a distorted body representation common to the underlying position sense, as opposed to tactile localisation (Longo et al., 2015). This body representation underlying position sense and tactile spatial remapping necessarily is a fully 3-D representation of the body as it appears in external space (Longo & Haggard, 2012). As such, the fingers may be represented as fully 3-D objects when localising tactile stimuli as we also need to account for their position when localising touch.

This reliance on position sense when localising touch may also account for the subtle differences found across the hairy and glabrous skin of the fingers, as posture was altered when testing the two skin surfaces. We found that DI was marginally lower on the glabrous skin than the hairy skin of all the fingers, indicating biases towards the thumb on the glabrous skin, and towards the little finger on the hairy skin. We also found this slight difference in direction bias on the two skin surfaces while evaluating the effect of previously stimulated finger on current finger identification. When the middle finger was stimulated twice in a row, identification of the finger was biased in opposite directions for the two skin surfaces – towards the thumb on the

glabrous skin, and the little finger on the hairy skin. Although this difference was not significant, it shows a trend in the same direction as our original analysis. Despite these slight differences, we show that the pattern of biases across the fingers is highly consistent on the two skin surfaces. Moreover, due to the changing position of the hand, the differences in DI on the two skin surfaces described above result in biases in the same direction in external space – directed away from the body midline on both the hairy and glabrous skin. This provides further support to our conclusion that we rely on a 3-D representation of the body positioned in external space when localizing touch on the fingers specifically, as we find biases of the same direction in external space, as well as of the same pattern of the two skin surfaces, regardless of hand posture.

We obtained confusion matrices showing the pattern of mislocalisation between toes and fingers on both the glabrous and hairy surface of the foot and hand. This showed that the distinct patterns of mislocalisation biases are highly consistent over the hairy and glabrous skin of the fingers and toes. Although this pattern was highly stereotyped, we found individual differences in each participants' performance, which supports a 3D representation of the individual fingers and that these distortions arise in high-level body representation, rather than low-level somatosensory processing.

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