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A common representation of the left and right fingers

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Abstract

The left and right hands, beyond being physically identical structures, have a number of functional connections. Their representations are both morphologically similar and highly integrated, in primary somatosensory cortex as well as higher cortical areas. Previous studies have shown that there is a highly consistent pattern of tactile confusions made between fingers of the left and right hand, but none have directly compared the patterns on the two hands. Here, we investigated the similarity of patterns of confusions across the fingers of the left and right hands. We also investigated whether there are individual differences in response patterns that are shared across the two hands. We obtained confusions matrices showing the pattern of tactile mislocalisations on the hairy skin surfaces of the fingers of the left and right hands, and show that these patterns are similar. Using a decoding approach, we show that there are idiosyncratic differences in individual participants' patterns of confusions that are shared across the fingers of both hands, despite the overall patterns of confusions being highly consistent across participants. These results demonstrate that there is a common high-level representation of the hands that does not distinguish body-side, as has been suggested in previous studies.

Keywords: body representation, somatosensation, tactile localisation, fingers, body side

Introduction

The left and right hands are mirror images of each other, and each is predominantly controlled by the contralateral cerebral hemisphere for both motor and sensory functions (Longo 2025). For example, stimulation of sensorimotor cortex in one hemisphere elicits movements and sensations on the contralateral side of the body (Penfield and Boldrey 1937; Flesher et al. 2016), while hemiparesis and hemianaesthesia on the contralateral side result from damage to one hemisphere (Sterzi et al. 1993; Louis 1994) or by temporary inactivation of one hemisphere in the so-called the 'Wada test' (Wada and Rasmussen 1960). At the same time, a variety of lines of evidence suggest that there are interactions between the representations of the two hands. In the motor system, this is shown by single neurons which respond to movements of either hand (Mountcastle et al. 1975; Aizawa et al. 1990), contralateral transfer of motor training (Scripture et al. 1894; Calvert and Carson 2022), and phenomena like mirror movements (Schott and Wyke 1981; Armatas et al. 1994) and mirror writing (Allen 1896; Schott 1999).

In the somatosensory system, there is also evidence for links between tactile representations of the two hands (Tamè et al. 2016). For example, neurophysiological studies in monkeys have reported individual neurons in primary somatosensory cortex (S1) and posterior parietal cortex with mirror symmetric receptive fields on both hands (Iwamura et al. 1994; Iwamura 2000). Evidence for similar representations in humans comes from studies using functional magnetic resonance imaging (Tamè et al. 2012) and magnetoencephalography (Tamè et al. 2015). Other evidence comes from the clinical phenomenon of tactile extinction, in which touch on one hand is not experienced when paired with a simultaneous touch on the other hand (Bender et al. 1949; Vallar et al. 1994).

Thus, while tactile information from each hand is processed primarily by the contralateral cerebral hemisphere, there are also numerous functional links between tactile

representations of the two hands. One potentially interesting window in these links comes from tactile mislocalisations. For example, when participants have to judge which finger was touched, they tend to mislocalise to neighbouring fingers, and generally in the direction of the middle of the hand (Schweizer et al. 2000, 2001; Braun et al. 2005, 2011; Manser-Smith et al. 2018). While these biases are qualitatively similar across people, there is also evidence for reliable individual differences in the specific pattern of mislocalisations between fingers (Manser-Smith et al. 2018).

In recent studies, we have exploited these individual differences to investigate shared representations of different skin surfaces using the logic of representational similarity analysis (RSA; Kriegeskorte et al. 2008). Although RSA was originally developed to analyse neuroimaging data, we applied a similar logic to confusion matrices generated from behavioural judgments. By showing that idiosyncratic differences between people in localisation are correlated across different regions, we have provided evidence for common representations of the hairy and glabrous surfaces of the hand (Manser-Smith et al. 2018) and of the fingers and the toes (Manser-Smith et al. 2019).

In this study, we applied the same logic to investigate whether there is a common representation of the fingers of the left and right hands. On each trial, the participant was touched on one finger and judged which finger had been touched. This allowed us to construct confusion matrices for each hand which we then compared using RSA. If there is a common representation of the left and right fingers, then individual differences in the pattern of confusions between fingers should be correlated between the confusion matrices of the two hands.

Methods

All procedures, including sample size, exclusion criteria, and analysis plans were pre-registered on the Open Science Framework (http://osf.io/msb6d). There were no deviations from our preregistered design and analysis.

Participants

In our previous study (Manser-Smith et al. 2018), the t-test assessing individual differences found between the two surfaces of the fingers had a Cohen's *d* of 1.04. We based our calculations on a one-tailed t-test, as we have a clear directional prediction that classification accuracy should be greater than chance levels, rather than lower than chance. As such, we conducted a power analysis using G*Power 3.1 (Faul et al. 2007) an effect size of 1.04, an alpha value of 0.05, and power of 0.90, which indicated that 10 participants were required.

To remain consistent with previous experiments, we recruited 20 participants (11 female; mean age = 29.4 years, SD = 11.0). All 20 participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield 1971); mean = 64.5, range = 10 – 100). All participants gave written informed consent before participating in the study, which was approved by the Birkbeck School of Psychological Sciences Research Ethics Committee.

Stimuli

As in our previous experiment, tactile stimuli were applied to the fingers using a von Frey hair. As the fingers have a small point localisation threshold and pressure sensitivity threshold (Schweizer et al. 2000), individuals can very accurately localise touch to the individual fingers when using an above-threshold stimulus (Cicmil et al. 2016). As such, we used a procedure adapted from our previous studies at the beginning of each experiment, to determine the weakest strength von Frey hair that the participant could consistently detect while still making mistakes (mislocalisations) for us to measure. The results of our previous

study (Manser-Smith et al. 2018) and other studies (Sathian and Zangaladze 1996; Vega-Bermudez and Johnson 2001; Duncan and Boynton 2007) showed that tactile sensitivity decreases from the thumb to the little finger. As such, we only tested the little finger in this procedure, as the weakest strength of von Frey hair detectable by the little finger should also be detectable on the other fingers. We carried out this procedure on both hands, as previous research suggests that tactile sensitivity may differ across the two hands (Weinstein and Sersen 1961). If the detection threshold is different across the two hands, the weaker von Frey hair was used on both hands.

Five strengths of von Frey hair were tested, from 0.008g (1.65) to 0.16g (3.22). Participants received tactile stimulation on the hairy skin of the little finger of the left or right hand, by each strength von Frey hair, starting from the weakest strength. Once the little finger was tested with the strongest von Frey hair the procedure was reversed, reducing the strength of the von Frey hair to the weakest again. This staircase was carried out twice, and the average number of correct responses was calculated for each strength of von Frey hair. The weakest strength von Frey hair used by which participants could correctly localise above 70% of touches was chosen for use in the experiment. This threshold was chosen as it is greater than chance performance, but still provides mislocalisations for us to measure. The mean strength von Frey hair used was 2.34 (range = 1.65 – 2.44). The measured threshold did not differ between the left little finger (*M*: 2.37, *SD*: 0.20) and the right little finger (*M*: 2.38, *SD*: 0.20), $t(19) = 0.36$, $p = 0.72$, $d_z = 0.08$.

Task

The procedures closely followed those used in our previous experiments (Manser-Smith et al. 2018, 2019) and did not deviate from our preregistered plans. Participants were seated in a comfortable position with their left and right hands resting palm-down on a table in their

respective hemispaces at equal distances from the body midline. A screen blocked them from seeing their hands (see Figure 1). This posture was kept consistent regardless of whether the left or right hand was being tested, and they were instructed to remain as still as possible throughout each experimental block. The experimenter used a von Frey hair to apply tactile stimulation to the medial phalanx of the dorsal surface of the participant's finger for around 500ms. One finger was stimulated per trial. Participants were asked to respond by verbally identifying which digit they felt had been stimulated. Digits are identified by numbers 1 to 5: the thumb corresponding to number 1, to the little finger corresponding to number 5.

There were four experimental blocks, two in which the fingers of the left hand were stimulated, and two in which the fingers of the right hand were stimulated. Stimulation was only applied to the hairy skin, and not the glabrous skin. The hairy skin was chosen because in our previous experiment (Manser-Smith et al. 2018) participants reported it to be more comfortable to sit in the position where the hairy skin can be tested, and because tactile sensitivity thresholds were more consistent over the hairy skin of the fingers, meaning it was easier to select an appropriate von Frey hair. ABBA counterbalancing was used to vary order of presentation, with the first condition counterbalanced across participants. Each block contained 100 trials, 20 for each of the 5 digits. 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.



Figure 1: Experimental set-up. The participant sat in a chair with both their hands resting palm-down on a table in front of them. Vision of the hands was obscured using a piece of black cardboard.

Analysis

The analyses closely followed our previous studies and our preregistered plans. Two confusion matrices were obtained per participant, one showing the pattern of mislocalisations on the hairy skin of the fingers of the left hand, and the other showing the pattern of mislocalisations on the right hand. Each confusion matrix is a 5x5 grid where each column represents stimuli applied to one digit, and each row represents the proportion of trials on which the participant judged that one digit was touched. As such, the confusion matrix nicely shows the proportion of correct localisations, as well as the direction and magnitude of bias for mislocalisations.

A directionality index (DI) was calculated in order to give a single value to indicate both direction and magnitude of bias in finger selection, as in our previous studies (Manser-Smith et al. 2018, 2019) and that of Cicmil et al. (2016). For each finger, the mean of the responses given to identify which finger was stimulated was calculated, minus the actual digit number of the stimulated finger:

DI = (mean of response finger numbers - stimulated finger number).

Thus, positive values of the DI indicate a bias in the direction of the little finger, while negative numbers indicate a bias in the direction of the thumb.

We first attempted to replicate the pattern of directional biases found on the hairy skin of the fingers in our previous study. To do this we carried out one-sample t-tests comparing the DI score of the central three digits of the left and right hand to zero. We also carried out a repeated-measures ANOVA with two factors: Stimulated Digit (1 to 5) and Hand (left/right), and percent accuracy as the dependent variable. A Bayesian repeated-measures ANOVA (Wetzels et al. 2012) using the default parameters in JASP 0.95.4 was also carried out with the same factors and dependent variable, in order to assess whether the null hypothesis (H_0) should be accepted over the alternative hypothesis (H_1).

The central question of this experiment concerns whether there are shared individual differences in the pattern of mislocalisation on the two hands. To address this we used representational similarity analysis (RSA) (Kriegeskorte et al. 2008) to assess the overall pattern of the confusion matrices on the two hands, analogous to the procedure we used in our previous studies to compare the two sides of the feet and hands (Manser-Smith et al. 2018) and the fingers to the toes (Manser-Smith et al. 2019). The logic of this analysis is to identify the specific way in which each participant differs idiosyncratically from the group mean, separately for each hand. Then we can ask whether these idiosyncrasies are similar for the left hand and the right hand.

Specifically, 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. We thus conducted 40 separate least-squares regression analyses, one for each participant for each of the two hands.

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 isolates the pattern of confusions between digits, rather than overall performance. These residuals were calculated separately for the confusion matrices on the left and right hand, resulting in two sets of residuals per participant.

If there are shared individual differences between the fingers of the left and right hand, the two sets of residuals for a given participant should be similar. That is, a participant who differs idiosyncratically from other people on the fingers of the left hand should also differ in the same way on the right hand. 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 pattern from the opposite hand 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. A one-sample t-test was used to assess whether classification accuracy is significantly greater than a chance result (i.e. 50%). We used a one-tailed test given that we have a clear directional prediction that classification accuracy will be above chance. We also carried out a Bayesian one-sample t-test using the default parameters in JASP 0.95.4, in order to assess whether the null hypothesis (H_0) should be accepted over the alternative hypothesis (H_1).

The raw data from this study are available on the Open Science Framework (https://osf.io/fhm9r/).

Results

Directional Bias for Localisation of the Fingers

Figure 2 (left panel) shows the confusion matrix for tactile localisation on the fingers of the left hand. The overall pattern of confusions was highly similar for the two hands. The correlation between the two confusion matrices was $r(18) = .994$. When the diagonal was excluded, the correlation remained very high, $r(18) = .857$. As in our previous study, finger identification errors were not randomly distributed, but biased towards the centre of the hand. DIs are plotted in the left panel of Figure 3. On the left hand, the DI results showed that the index finger was biased towards the little finger (M: 0.27, SD: 0.17), $t(19) = 6.93$, $p < 0.0001$, $d = 1.55$; the middle finger showed no overall bias, (M: 0.00, SD: 0.12), $t(19) = 0.05$, $p = 0.96$, $d = 0.01$; and the ring finger was biased towards the thumb (M: -0.33, SD: 0.21), $t(19) = -7.06$, $p < 0.0001$, $d = 1.58$.

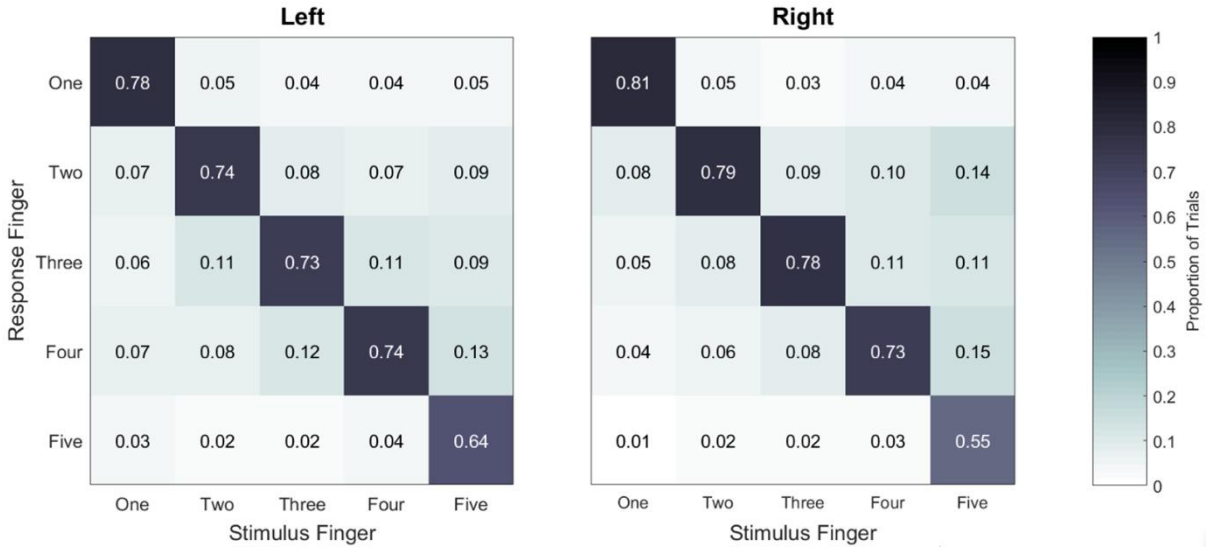

Figure 2: Grand average confusion matrices showing the proportion of stimuli judged as located on each of the five digits as a function of which digit was actually stimulated. Digits were identified by numbers one (thumb) through five (little finger). Data from the left hand is shown in the left panel, and from the right hand in the right panel. The proportion of correct responses for each digit is shown along the diagonal from the top-left to the bottom-right. The off-diagonal cells represent mislocalisations between the digits.

Figure 2 (right panel) shows the confusion matrix for tactile localisation on the fingers of the right hand. As for the left hand, finger identification was biased towards the centre of the hand. Similarly, on the right hand, the index finger was biased towards the little finger

(*M*: 0.22, SD: 0.20), $t(19) = 5.09$, $p < 0.0001$, $d = 1.14$; the middle finger showed no overall bias, (*M*: -0.02, SD: 0.14), $t(19) = -0.53$, $p = 0.60$, $d = 0.12$; and the ring finger was biased towards the thumb (*M*: -0.37, SD: 0.24), $t(19) = -7.06$, $p < 0.0001$, $d = 1.58$. While correction for multiple comparisons in these tests was not part of our pre-registered analysis plans, we note that all the significant effects we report on DIs survive Holm-Bonferroni correction. These results provide a direct replication of the results of our previous studies (Manser-Smith et al. 2018, 2019), that there are consistent directional biases in tactile fingers localisation in response to stimulation of the hairy skin of the fingers.

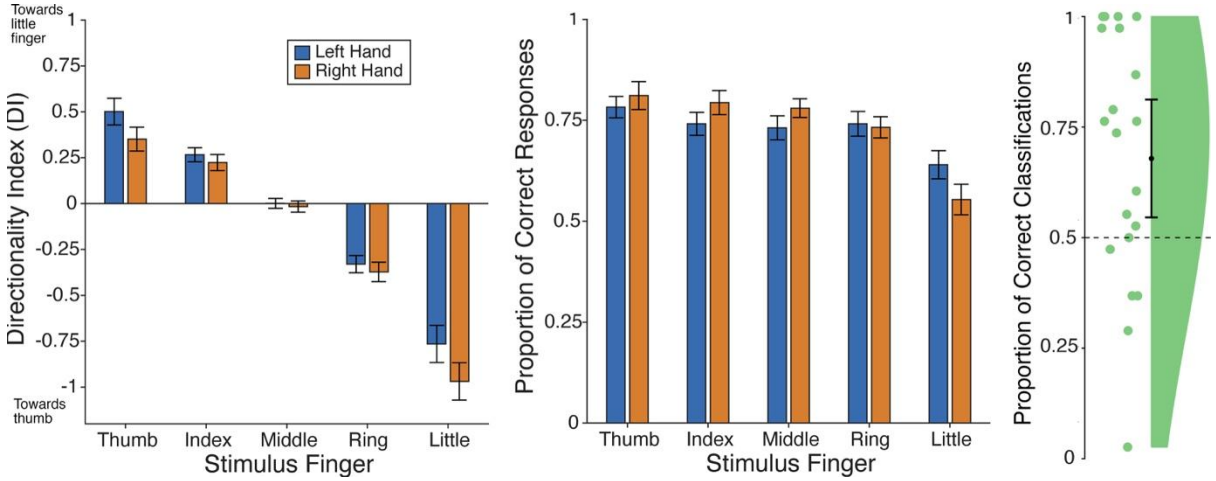

Figure 3: The left panel shows the grand average directionality index (DI) scores for each finger, on the left and right hands. The centre panel shows the grand average percentage of correct responses made to each finger, on both hands. Error bars represent the standard error of the mean. Similar patterns of results were found for the two hands, for both DI and accuracy. The right panel shows classification accuracy in the RSA analysis, shown using a raincloud plot (Allen et al. 2021). Points show data from individual participants. The dashed line indicates chance classification performance (i.e., 50%). The black circle and error bar indicate the mean and 95% confidence interval. Classification accuracy was significantly above chance levels, indicating shared individual differences in patterns of confusion between the two hands.

Response Accuracy for Localisation of the Fingers

The previous analyses concerned directional biases in finger identification. We next investigated differences in accuracy between the fingers (i.e., the proportion of correct responses), irrespective of the nature of the errors made on incorrect trials. Accuracy on each

finger is plotted in the centre panel of Figure 3. The results of the repeated-measures ANOVA indicated that accuracy was significantly different depending on which digit was stimulated, $F(4,76) = 13.89$, $p < 0.001$, $\eta_p^2 = 0.42$. There was, however, no significant difference between the two hands, $F(1,19) = 0.23$, $p = 0.64$, $\eta_p^2 = 0.01$, nor a significant interaction, $F(4,76) = 2.08$, $p = 0.09$, $\eta_p^2 = 0.10$. A Bayesian repeated-measures ANOVA provided extreme evidence for an effect of finger, $BF_{10} = 3.2 \times 10^5$, moderate evidence against an effect of laterality, $BF_{10} = 0.41$, and inconclusive evidence regarding the interaction, $BF_{10} = 1.33$.

Shared Individual Differences Between the Fingers of the Left and Right Hands

The critical question of this study is whether individual differences in the pattern of mislocalisations is shared between the fingers of the left and right hands. Classification accuracy is shown in the right panel of Figure 3. On average, classification accuracy was 67.9%, which was significantly above chance (i.e. 50%), $t(19) = 2.81$, $p < 0.01$, $d = 0.63$, 95% bootstrap confidence interval: [55.5% - 78.8%]. Classification accuracy was above chance in 14 of 20 participants. A Bayesian one-sample t-test provided moderate evidence in support of the alternative hypothesis against the null hypothesis, $BF_{>0} = 9.27$. This above-chance classification indicates that the pattern of mislocalisations between digits constitutes a stable individual 'signature' that generalises across hands.

Discussion

In this study we investigated the patterns of confusions for localisation of tactile stimuli across the fingers of the left and right hands. We replicated the highly consistent patterns of confusions found across the fingers in previous studies (Schweizer et al. 2000, 2001; Braun et al. 2005, 2011; Manser-Smith et al. 2018), and demonstrated that individual differences in

this pattern of tactile confusions are highly consistent across the left and right hands. We also found that despite this highly consistent pattern, there are idiosyncratic differences in participants' performance that were shared between the left and right hands. This result indicates that there is a common high-level representation of the hands that is not specific to body-side.

Although previous studies have tested tactile mislocalisations of both the left and right hands, we are not aware of any studies that directly compare the patterns across the two hands in the same study. In the present study we show that tactile mislocalisations are very similar across the two hands, both in bias direction (towards the middle finger), and magnitude for each finger. This finding is consistent with the fact that the fingers are highly similar in both their physical structure and their representational structure in S1 (Sörös et al. 1999). While classification accuracy was significantly above chance levels, the effect size was smaller than that we had predicted and used for our power analysis. Replication of this result using a larger sample size would thus strengthen confidence in the findings.

However, as we have shown in previous studies that biases in tactile localisation of the digits arises in higher-order representations of the body (Manser-Smith et al. 2018), this finding also suggests that there is a common high-level representation of the left and right fingers. Previous neuroimaging research has suggested that the representations of the two hands are strongly integrated (Rusconi et al. 2014), even suggesting that there is a common representation of the hands that does not distinguish between body side (Tamè et al. 2011, 2013). This hypothesis is further supported by our finding that idiosyncratic differences in individuals' responses are shared across the left and right hands, as it is unlikely that these similarities would arise from separate representational structures of the two hands. It is natural to hypothesise that the common representation that we have identified from behavioural judgments is linked to these neural effects described in other work. This link

remains indirect, however, and it will be interesting in future research to draw more direct links between patterns of representational dissimilarity at the behavioural and neural levels.

While our results demonstrate shared individual differences between the two hands, they provide little insight into the precise nature of these differences. In part, this is because the individual differences are intrinsically idiosyncratic and not systematic. It also possible that part of the observed decoding performance could relate to individual differences between participants in decision strategies or response tendencies unrelated to tactile finger representations. It will be interesting in future research to try to determine what drives these individual differences and how they relate to corresponding differences in somatotopic finger maps in the brain.

From the present experiment, and our previous two studies using this paradigm (Manser-Smith et al. 2018, 2019), it seems that reliance on a common representation of two body parts may differ depending on the similarity between them. Although these studies were run separately and used different participants and different sample sizes, they used the same basic paradigm and identical analysis methods. The ‘strongest’ common representation is between the two skin surfaces of the toes (82.37%; Manser-Smith et al. 2018), as being on alternate sides of the same body part that has little flexibility in movement (Hashimoto et al. 2013) they are most likely to be consistent in the same posture. The next strongest is between the two skin surfaces of the fingers (74.61%; Manser-Smith et al. 2018) – although they are also on alternate sides of the same body part, there is greater flexibility of movement between the fingers than the toes (Hashimoto et al. 2013). Next is between the left and right hands in this study (67.9%), as although these structures are physically identical, they can vary widely in their concurrently held postures. The ‘weakest’ common representation is between the hands and feet (Manser-Smith et al. 2019). Although fingers and toes are similar in several ways, they also have the most differences in terms of both physical shape and concurrent use.

These patterns of shared representational structure between skin surfaces are consistent with recent evidence that mislocalisations can even be found between the hands and feet and between the left and right sides of the body (Badde et al. 2019).

In this study we also show that localisation accuracy did not differ between the fingers of the left and right hands. This is somewhat inconsistent from some previous studies that have shown the left hand has greater response accuracy than the right (Schweizer et al. 2000). The lack of difference between the two hands is consistent with a recent meta-analysis which found no evidence for lateral asymmetries in basic tactile sensitivity (Longo and Tucciarelli 2026). On the other hand, there were robust differences between the fingers, with accuracy decreasing broadly from the thumb to the little finger. This pattern is consistent with other studies which have measure tactile spatial acuity directly, finding a radial-ulnar gradient of decreasing tactile acuity (Sathian and Zangaladze 1996; Vega-Bermudez and Johnson 2001; Duncan and Boynton 2007). This gradient is consistent with neural data measuring cortical magnification of each digit (Duncan and Boynton 2007) and the size of population receptive fields (Schellekens et al. 2021). Notably, it is also consistent with evidence about perceived finger length, both from studies measuring proprioceptive hand maps (Longo and Haggard 2010; Ganea and Longo 2017) and explicit judgments of finger size (Longo and Haggard 2012; Longo et al. 2015; Tamè et al. 2017).

In the present experiment we showed that patterns of tactile confusions are highly consistent across the left and right hands. Although this pattern is highly consistent across the two hands, and across participants, we can identify individual differences in response patterns that are shared across the fingers of the left and right hands. This finding supports the hypothesis put forward previously, that there is a common representation of the hands indistinct from body side.

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Author Contributions

K.M.-S., L.T. and M.R.L. conceived and designed the experiment. K.M.-S. analysed the data and drafted the manuscript. K.M.-S., L.T. and M.R.L. edited and revised the manuscript.

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