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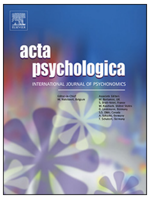

A common representation of fingers and toes

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ABSTRACT

There are many similarities and differences between the human hands and feet. On a psychological level, there is some evidence from clinical disorders and studies of tactile localisation in healthy adults for deep functional connections between the hands and feet. One form these connections may take is in common high-level mental representations of the hands and feet. Previous studies have shown that there are systematic, but distinct patterns of confusion found between both the fingers and toes. Further, there are clear individual differences between people in the exact patterns of mislocalisations. Here, we investigated whether these idiosyncratic differences in tactile localisation are shared between the fingers and toes, which may indicate a shared high-level representation. We obtained confusion matrices showing the pattern of mislocalisation on the hairy skin surfaces of both the fingers and toes. Using a decoding approach, we show that idiosyncratic differences in individuals' pattern of confusions are shared across the fingers and toes, despite different overall patterns of confusions. These results suggest that there is a common representation of the fingers and toes.

1. Introduction

The human hands and feet are serially homologous structures that have co-evolved (Rolian, Lieberman, & Hallgrímsson, 2010), resulting in numerous similarities between the two body parts. They have an identical number of homologous digits (Lewis, 1989), a common overall bone structure (Owen, 1849/2008), and distinct hairy and glabrous skin surfaces on their alternate sides (Lewis, 1989; Mountcastle, 2005). However, there are also obvious and profound differences between the hands and feet in humans. Both body parts have become highly specialised by evolution for distinct functions (McNutt, Zipfel, & DeSilva, 2018; Tocheri, Orr, Jacofsky, & Marzke, 2008), and have gross differences in shape, and distinct representations in the somatosensory cortex in both monkeys (Hashimoto et al., 2013; Merzenich, Kaas, Sur, & Lin, 1978; Nelson, Sur, Felleman, & Kaas, 1980) and humans (Akselrod et al., 2017; Disbrow, Roberts, & Krubitzer, 2000; Fox, Burton, & Raichle, 1987; Hashimoto et al., 2013). Not only are representations of the hands and feet distinct in S1, they vary in their somatotopic organisation – a number of studies have shown that the fingers are ordered along the medio-lateral axis of the postcentral gyrus (Kolasinski et al., 2016; Martuzzi, van der Zwaag, Farthouat, Gruetter, & Blanke, 2014; Schweizer, Voit, & Frahm, 2008), no somatotopy was found for the toes, as well as lower selectivity in responding to each individual toe compared to the individual fingers (Akselrod et al., 2017).

Beyond comparisons of the physical and functional properties of the hands and feet, it is unclear how high-level mental representations of these two body parts are related, although there are hints in the literature towards there being deep functional connections. One line of evidence for this comes from Gerstmann syndrome (Gerstmann, 1939), in which some patients show specific deficits in identifying digits, whether fingers or toes (Mayer et al., 1999; Tucha, Steup, Smely, & Lange, 1997). Another line of evidence comes from recent studies of tactile localisation in healthy adults, which have identified distinct patterns of confusions between the fingers and toes, but with some similarities in mislocalisations (Cicmil, Meyer, & Stein, 2016; Manser-Smith, Tamè, & Longo, 2018; Schweizer, Braun, Fromm, Wilms, & Birbaumer, 2001; Tamè, Wühle, Petri, Pavani, & Braun, 2017). For example, digits of both the hands and feet are more frequently mislocalised to neighbouring than distant digits, however not equally to each neighbouring digit, but more often in the direction of the central digits of the hand or foot (Cicmil et al., 2016; Manser-Smith et al., 2018). These similarities in tactile mislocalisation of the digits indicate that there may be commonalities in mental representations of the hands and feet, despite their divergent physical and functional properties. However, this has not been supported by a direct comparison of the representations of fingers and the toes in the same individuals.

In a recent study (Manser-Smith et al., 2018), we investigated

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whether the patterns of confusion between digits arise from relatively early representations, such as somatotopic maps in primary somatosensory cortex (SI), or from higher-level representations of the body. Given that somatotopic maps have distinct representations of the glabrous and hairy skin surfaces of the hands and feet (Merzenich et al., 1978; Nelson et al., 1980), mislocalisations between digits arising from SI may show different patterns on each skin surface, resulting from idiosyncrasies in somatotopy of S1. In contrast, if digit confusions arise from higher-level representations of the body as a coherent, volumetric whole (wherein each digit is a single unit that happens to contain the two skin surfaces), then similar patterns of mislocalisation should be found on each skin surface. We found that confusion matrices were highly similar on the glabrous and hairy surfaces of both the toes (Experiment 1) and fingers (Experiment 2). Moreover, we used a form a representational similarity analysis (RSA; Kriegeskorte, Mur, & Bandettini, 2008) to investigate whether individual differences between participants are shared across the glabrous and hairy skin surfaces of each limb. We showed that idiosyncratic differences in the pattern of mislocalisation on one skin surface predicted such patterns on the other skin surface, for both the fingers and toes. Together these results suggest that mislocalisations arise at the level of complete digits, not of individual skin surfaces, consistent with their arising from higher-level body representations.

In this study we investigated whether there are individual differences in patterns of tactile localisation that are shared between the fingers and toes, applying the logic of our previous study. That is, we used RSA to determine whether idiosyncratic person-to-person differences in the pattern of confusions between fingers predict such differences in the confusions between toes, and vice versa. As the identification of shared individual differences between the two skin surfaces of the fingers and toes suggested that mislocalisations arise from a high-level representation of the digits as single units (incorporating both skin surfaces), individual differences shared between the fingers and toes would suggest that there are shared high-level representations of the hands and feet. All procedures, including sample size, exclusion criteria, and analysis plans were pre-registered on the Open Science Framework (OSF; osf.io/4kdte).

2. Methods

2.1. Participants

In our previous study (Manser-Smith et al., 2018), the individual differences found between the two surfaces of the fingers and toes using our decoding approach showed Cohen's *d*'s of 1.76 and 1.04, respectively. As we reduced the number of trials completed by each participant in the present experiment (due to time constraints during testing), and we expected a weaker effect than in our previous study because we were comparing two different body parts, we conducted a power analysis using an effect size of half the smaller value found in our previous study. 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, Erdfelder, Buchner, & Lang, 2007), a Cohen's *d* of 0.52, an alpha value of 0.05, and power of 0.90, which indicated that 34 participants were required.

To use a round number, we recruited 40 participants (22 female; mean age = 27.2 years; SD = 8.27). Thirty-nine participants were right-handed, and one left-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean = 60.8, range = −13–100). Of the 39 right-handed participants, 38 were right-foot dominant and one participant was not dominant for either foot. The one left-handed participant was also left-foot dominant, as assessed by the Waterloo Footedness Questionnaire (Elias, Bryden, & Bulman-Fleming, 1998; mean = 38.0, range = −75–100). EHI and WFQ scores were strongly correlated across participants, $r = 0.66$, $p < 0.001$. All participants gave written informed consent before participating in the study, which was approved by the Birkbeck Department of Psychological Sciences ethics committee.

2.2. Stimuli

In our previous study, two different types of tactile stimuli were used to stimulate the fingers and toes. The tip of the experimenter's finger was used for the toes, and a von Frey hair for the fingers. As the fingers have low pressure sensitivity thresholds in comparison to the toes, a near-threshold stimulus is needed to give a clear pattern of mislocalisations (Schweizer, Maier, Braun, & Birbaumer, 2000) and avoid ceiling effects such as encountered by Cicmil et al. (2016). However, given the aims of the present study, it was critical to use a consistent type of tactile stimulation across the fingers and toes. As such, tactile stimuli were delivered to both the fingers and toes using von Frey hairs. The strength of von Frey hairs to be used was determined at the beginning of the experiment using the same procedure as in Experiment 2 of our previous study (Manser-Smith et al., 2018). Five strengths of von Frey hair were tested, from 0.008 g to 0.16 g for the hand. For the foot, five strengths of von Frey hair from 0.04 g to 0.6 g were used, as during pilot testing most participants could not localise above chance (i.e., 50%) of touches using the same stimuli that were used on the fingers. We stated in our pre-registered plan that if the participant was not performing well enough using the five von Frey hairs stipulated previously, progressively stronger von Frey hairs were tested until they were performing at the required level (70% correct responses). However, this issue did not arise with any participants. The mean strength von Frey hair used on the hands was 0.018 g (range = 0.008 g–0.04 g), and on the feet was 0.19 g (range = 0.04 g–0.6 g).

During the stimulus identification procedure, participants received tactile stimulation on the top of every digit of the left hand or foot in a random order, by each von Frey hair, starting from the weakest strength. Once the digits had been 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 percentage of correct responses was calculated for each strength of von Frey hair across all digits. The weakest strength von Frey hairs that participants could correctly localise above 70% of touches were used in the experiment. This threshold was chosen as it was greater than chance performance, but still provides a sufficient number of mislocalisations for us to measure. As the fingers and toes have quite different sensitivity thresholds (Mancini et al., 2014; Weinstein, 1968), the strength of von Frey hair used was determined separately for the fingers and toes. Moreover, although tactile acuity differs significantly across the fingers (Duncan & Boynton, 2007; Sathian & Zangaladze, 1996) and toes (Manser-Smith et al., 2018), for ease of testing and consistency with our previous study, one strength of von Frey hair was used across all five fingers/toes.

2.3. Task

The testing procedure closely resembled that used in our previous study (Manser-Smith et al., 2018). All participants were tested on their left hand and foot, regardless of assessed hand and foot dominance. Fig. 1 shows participant's posture during testing: they were seated in a comfortable position with their left foot resting on a stool, and their left hand resting palm-down on a table. This posture was kept consistent regardless of whether the hand or foot 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 dorsal surface 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), or the medial phalanx of the finger or proximal phalanx of the thumb, for about 500 ms. One finger or toe was

Fig. 1. Experimental set-up. Participants sat in a chair with their left foot resting on a foot rest, and their left hand resting on a table. This posture gave the experimenter easy access to both the fingers and toes. Vision was prevented using a blindfold.

stimulated per trial. Participants responded by verbally identifying which digit they felt had been touched. Digits were identified by numbers 1 to 5: the big toe or thumb corresponding to number 1, to the little toe or finger corresponding to number 5. Touch was only applied to the hairy skin, and not the glabrous skin. The hairy skin was chosen because we found in our previous study that participants find it to be more comfortable to sit in the position where the hairy skin can be tested. Vision was prevented throughout the experiment using a blindfold.

The experiment consisted of four blocks, two in which the fingers were stimulated and two in which the toes were stimulated. 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, resulting in 400 total trials completed by the participant. 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.

2.4. Analysis

The analyses carried out closely resembled those of our previous study, and were exactly as described in the pre-registration document. Two confusion matrices were obtained per participant, one showing the pattern of mislocalisations on the hairy skin of the fingers, and the other showing the pattern of mislocalisations on the hairy skin of the toes. Each confusion matrix is a 5 × 5 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 pattern of mislocalisations between digits.

In order to obtain a single value which indicates both direction and magnitude of bias in toe selection we used the directionality index (DI) developed by Cicmil et al. (2016), as in our previous study. For each digit the mean of the responses given to identify which digit was stimulated was calculated, minus the actual digit number of the stimulated toe, as shown in Eq. (1):

$$\text{DI} = (\text{mean of response digit numbers} - \text{stimulated digit number}) \tag{1}$$

One-sample *t*-tests were carried out to assess whether DI scores of the central three digits of the hand and foot were significantly different from zero. Response accuracy was also analysed as DI scores of zero (no bias in responding) may occur in two different scenarios. Firstly, if responses to stimulation of a toe were entirely accurate. Secondly, if participants had responded equally to neighbouring toes, for example toes 2 and 4 when toe 3 was stimulated. As such accuracy was also used as a measure of performance on the task. The analysis of response accuracy can be found in Supplementary material.

The key novel question of this study was whether idiosyncratic person-to-person differences in the pattern of confusions between digits are shared between the fingers and toes. To isolate individual differences in each participant we used a leave-one-participant-out procedure, identical to that was used previously to show that confusions arise from a common representation of the two sides of the hand/foot (Manser-Smith et al., 2018). We regressed the 20 off-diagonal cells (i.e., the localisation errors) of each participant's confusion matrix (C_i) on the grand average confusion matrix for the other 39 participants (C_{GA}), as in Eq. (2).

$$\widehat{C_i} = \beta_1 C_{GA} + \beta_0 \tag{2}$$

The regression parameters (β_1 and β_0) were calculated using standard least-squares methods as the values that minimised the sum of squares of the residual values that is the difference between the fitted values and the actual values, as in Eq. (3).

$$residuals_i = \widehat{C_i} - C_i \tag{3}$$

These 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 and toes, rather than overall performance. These residuals were calculated separately for the confusion matrices on the fingers and the toes, resulting in two sets of residuals per participant.

If there are shared individual differences between the fingers and 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 fingers should also differ in the same way on the toes. 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 78 cross-correlations comparing each of that participant's two patterns to the opposite pattern of each of the other 39 participants. Classification accuracy was calculated for each participant as the percentage of those 78 between-participant correlations which were smaller than the within-participant cross-correlation. High classification accuracy indicated that there were fewer incidences when participants were more like others' scores than their own scores, and low classification accuracy indicated that there were more incidences when participants were more like others' scores than their own scores. Our preregistered analysis plan specified a one-sample *t*-test to assess whether classification accuracy was significantly greater than chance (i.e. 50%). We used a one-tailed test given that we had a clear directional prediction for greater than chance classification (indicating individual differences were stronger within- than between-participants). We also carried out a Bayesian one-sample t-test to assess whether the null hypothesis (H_0) should be accepted over the alternative hypothesis (H_1). This was done using the default parameters in JASP 0.8.2.0 (Wagenmakers et al., 2018).

2.5. Data availability

The data associated with this research are available through the OSF

Fig. 2. 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 (the big toe/thumb) through five (the little toe/finger). Data from the foot is shown on the left panel, and data from the hand is shown 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 digits.

(osf.io/mh9xs).

3. Results

3.1. Directional bias for localisation of the toes

Fig. 2 (left panel) shows the confusion matrix for tactile toe localisation on the hairy skin of the toes. As in our previous study, the majority of mislocalisations were made onto neighbouring toes. Toe identification errors were not randomly distributed across toes but biased towards the lateral side of the foot for toe 2 (M: 0.37, SD: 0.21), $t(39) = 11.00$, $p < 0.0001$, $d = 1.76$, and toe 3 (M: 0.20, SD: 0.20), $t(39) = 6.35$, $p < 0.0001$, $d = 1.00$. For toe 4, there was a significant medial bias (M: -0.16, SD: 0.14), $t(39) = -7.45$, $p < 0.0001$, $d = -1.14$. These results provide a direct replication of the results of our previous study and of Cicmil et al. (2016), corroborating the presence of directional biases for tactile toe localisation in response to stimulation of the hairy skin of the toes.

3.2. Directional bias for localisation of the fingers

Fig. 2 (right panel) shows the confusion matrix for tactile finger localisation on the hairy skin of the fingers. Finger identification errors were not randomly distributed, but biased towards the little finger for the index finger (M: 0.11, SD: 0.17), $t(39) = 3.92$, $p < 0.0001$, $d = 0.65$, and towards the thumb for the ring finger (M: 0.03, SD: 0.10), $t(39) = -7.56$, $p < 0.0001$, $d = 0.30$. There was no selection bias for the middle finger (M: -0.13, SD: 0.11), $t(39) = 1.94$, $p = 0.06$, $d = -1.18$, suggesting that lateral or medial fingers were chosen interchangeably. Once again, these results provide a direct replication of the results of our previous study, that there are consistent directional biases for tactile finger localisation in response to stimulation of the hairy skin of the fingers.

3.3. Shared individual differences between the fingers and the toes

The key question was whether person-to-person differences in the pattern of mislocations are shared between the fingers and toes. On average, classification accuracy was 59.25%, which was significantly above chance (i.e., 50%), $t(39) = 2.29$, $p = 0.01$, $d = 0.36$. A Bayesian one-sample t-test provided moderate evidence in support of the alternative hypothesis against the null hypothesis, $BF_{10} = 3.56$. Across participants, classification accuracy ranged from 0% to 95%, but exceeded 50% in 26 out of 40 participants. As classification accuracy was only marginally above chance on average, and was not above chance in 14 of 40 participants, we performed an additional analysis to those described in the preregistration of this study. We calculated the bootstrapped 95% confidence intervals (CIs), resampling 10,000 times with replacement, to estimate the likelihood of replicating our present results of above chance classification accuracy. The lower and upper bounds of the bootstrapped CIs were 51.38% and 67.00%, respectively. This result provides evidence for shared individual differences between the fingers and toes in how people mislocalise touch on the digits. These idiosyncratic differences between people are apparent despite there being distinct patterns of mislocalisation bias found on the fingers and toes.

4. Discussion

These results provide evidence for a common representation of fingers and toes. We investigated whether there are shared individual differences in patterns of confusion for localisation of tactile stimuli on the fingers and the toes. We found that idiosyncratic differences in participants' performance were shared between the fingers and toes, despite the overall different patterns of localisation bias found on these two body parts, suggesting that idiosyncratic differences arise from a single representation of the digits, as opposed to separate representations. As such, this result suggests that there is a shared representation of the fingers and toes, despite their differences in form (i.e., morphological structure) and use (i.e., motor function). Moreover, we replicated the distinct patterns of tactile confusion found on the digits of the hand and the foot found in previous studies (Cicmil et al., 2016; Manser-Smith et al., 2018; Schweizer et al., 2001).In a recent study (Manser-Smith et al., 2018) we found that there are idiosyncratic differences in patterns of tactile confusions that are shared between the two skin surfaces of the fingers and toes. From this finding we concluded that individual differences in mislocalisations may arise from higher-level representations of the body as a single, volumetric whole, as opposed to arising from distinct somatotopic maps of the two skin surfaces. In the present study we also identified individual differences in performance that are shared between the fingers and toes. Following the logic of our previous study, we suggest that there is a single high-level representation of the fingers and toes from which mislocalisations arise. Such a shared representation indicates that deep functional connections between the hands and feet are preserved from their co-development in humans (Rolian et al., 2010), despite their present differences in shape and use, as evidenced by clinical cases such as both finger and toe agnosia occurring in Gerstmann syndrome (Mayer et al., 1999; Tucha et al., 1997).

A shared high-level mental representation of the hands and feet may have developed to be beneficial to our primate ancestors, and would still beneficial to primates that retain similar structure and functional use of the hands and feet, to facilitate co-ordinated use. For example, chimpanzees (our closest primate relatives) retain relatively mobile ankle joints compared to humans, and fully abducted Mt1 (the big toe) similar to the thumb (McNutt et al., 2018). For arboreal and terrestrial quadrupedal monkeys such as chimpanzees, the hands and feet share many functions such as grasping and propulsion during locomotion (Rolian, 2009; Schmitt, Zeininger, & Granatosky, 2016; Szalay & Dagosto, 1988), although there is evidence for divergent use occurring during reaching tasks (Hunt, 1994). In contrast, although humans may co-ordinate use both the hands and feet to perform an action (Dietz, 2002), they do not share the same functional role in reaching the desired outcome. As such, although a shared mental representation of the hands and feet would have been evolutionarily beneficial to non-human primates to facilitate co-ordinated actions it may not be as advantageous to modern humans.

This may be reflected in the relatively weaker classification performance in the present study comparing fingers and toes (59.3%) than that found in our previous study (Manser-Smith et al., 2018) comparing the hairy and glabrous surfaces of the toes (82.4%) and fingers (74.6%). In our previous study we found strong idiosyncratic differences in the tactile localisation task comparing performance on the two skin surfaces of the hand or foot, providing strong evidence that there is a shared mental representation of the two skin surfaces of the hands and feet (such as a volumetric 3-D model of the body part). The individual differences found in the present study are significant but relatively weaker than in our previous study, perhaps indicating the diminished benefit of having a shared representation of the hand and the foot when form and use are as different as they are in humans. This suggests that, despite overlap, the representations of the fingers and toes are at least partly distinct, reflecting the divergent structure and function of the hands and feet in modern-day humans.

One important point to note is that the common representation of the hands and feet is not necessarily a common representation of both body sides. In the present study only the left hand and foot was tested, therefore we can only suggest that there is a common representation for the single body side. However, it is possible that a shared representation of the hands and feet may also be shared across both sides of the body. A number of studies have shown that tactile stimuli applied to one hand can interfere with touch localisation on the other hand (Braun, Hess, Burkhardt, Wühle, & Preissl, 2005; Tamè, Braun, Holmes, Farnè, & Pavani, 2016; Tamè, Farnè, & Pavani, 2011), possibly resulting from bilateral hand representation in postcentral somatosensory cortex (Iwamura, 2000; Iwamura, Iriki, & Tanaka, 1994), or another representational stage at which the differentiation between the two hands is less clearly defined (Tamè et al., 2011). While we are not aware of any studies that show either that there is bilateral foot representation, or interference in tactile localisation between the two feet, these findings for the hands suggest that there could be a common representation of the hands and feet that also does not distinguish between body side.

One possible explanation of our results is that shared idiosyncratic differences in localisation are a result of systematic biases for the perception of space in general, instead of for specific body parts. There are numerous studies that show how the body's position in external space can influence ability to perceive tactile stimuli on the body, for example crossing the hands (Yamamoto & Kitazawa, 2001), feet (Schicke & Röder, 2006), and fingers (de Haan, Anema, & Dijkerman, 2012) reduces our efficiency in localising touch on these body parts. These findings demonstrate how the representation of the body as a 3-dimensional object is intrinsically linked to our perception of it in relation to the external space that it inhabits. In the present experiment, we suggest that idiosyncratic biases in localisation may arise from higher-level representations of the limbs as 3-D objects such as this. To attempt to disentangle how the body representation itself and the body's position in external space contribute to localisation biases, future experiments may focus on manipulating posture of the fingers and toes relative to one another, or relative to the gaze-direction, for example. However, it seems unlikely that biases in the perception of space in general would produce such specific patterns of confusions between the fingers and toes as we have found in this and previous studies.

It is also possible that the biases we describe may arise from post-perceptual decision-making processes, as opposed to tactile perception per se. From the results of this experiment and others we have suggested that patterns of tactile confusions may arise from high-level body representations, which likely originate in the posterior parietal cortex. Studies of perceptual decision-making in the somatosensory system have found that at successive processing stages from SI, to SII, to the posterior parietal cortex, that neuronal activity correlates progressively less with processing of the tactile stimulus itself and more with the animal's behavioural decision (e.g., de Lafuente & Romo, 2006; Romo, Lemus, & de Lafuente, 2012). As such, the findings of our experiment may reflect the organisation of a mental representation of the limbs which is used by participants to transform the raw sensory information they receive into a perceptual decision about which digit was stimulated. Overall, the distinction between perceptual and decision-making processes is not a clear one, in relation to localising tactile stimuli on the body. Overall, in this study we showed that idiosyncratic differences in performance on a tactile localisation task can be identified between the fingers and the toes, despite their divergent form and use. This provides the first evidence that there is a shared high-level mental representation of the fingers and toes. Such shared structure may relate to the ability for compensatory use of the feet for skilled behaviours in one-handed individuals (Hahamy et al., 2017).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actpsy.2019.102900.

References

Akselrod, M., Martuzzi, R., Serino, A., van der Zwaag, W., Gassert, R., & Blanke, O. (2017). Anatomical and functional properties of the foot and leg representation in areas 3b, 1 and 2 of primary somatosensory cortex in humans: A 7T fMRI study. *NeuroImage, 159*, 473–487. https://doi.org/10.1016/j.neuroimage.2017.06.021.

Braun, C., Hess, H., Burkhardt, M., Wühle, A., & Preissl, H. (2005). The right hand knows what the left hand is feeling. *Experimental Brain Research, 162*(3), 366–373. https://doi.org/10.1007/s00221-004-2187-4.

Cicmil, N., Meyer, A. P., & Stein, J. F. (2016). Tactile toe agnosia and percept of a "missing toe" in healthy humans. *Perception, 45*(3), 265–280. https://doi.org/10.1177/0301006615607122.

de Haan, A. M., Anema, H. A., & Dijkerman, H. C. (2012). Fingers crossed! An investigation of somatotopic representations using spatial directional judgements. *PLoS One, 7*(9)https://doi.org/10.1371/journal.pone.0045408.

de Lafuente, V., & Romo, R. (2006). Neural correlate of subjective sensory experience gradually builds up across cortical areas. *Proceedings of the National Academy of Sciences, 103*(39), 14266–14271.

Dietz, V. (2002). Do human bipeds use quadrupedal coordination? *Trends in Neurosciences, 25*(9), 462–467.

Disbrow, E., Roberts, T., & Krubitzer, L. (2000). Somatotopic organization of cortical fields in the lateral sulcus of Homo sapiens: Evidence for SII and PV. *The Journal of*

Comparative Neurology, 418(1), 1–21. Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1002/(SICI)1096-9861(20000228)418:1%3C1::AID-CNE1%3E3.0.CO;2-P.

Duncan, R. O., & Boynton, G. M. (2007). Tactile hyperacuity thresholds correlate with finger maps in primary somatosensory cortex (S1). *Cerebral Cortex, 17*(12), 2878–2891. https://doi.org/10.1093/cercor/bhm015.

Elias, L. J., Bryden, M. P., & Bulman-Fleming, M. B. (1998). Footedness is a better predictor than is handedness of emotional lateralization. Neuropsychologia, 36(1), 37–43. https://doi.org/10.1016/S0028-3932(97)00107-3.

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behaviour Research Methods, 39*(2), 175–191.

Fox, P. T., Burton, H., & Raichle, M. E. (1987). Mapping human somatosensory cortex with positron emission tomography. *Journal of Neurosurgery, 67*(1), 34–43.

Gerstmann, J. (1939). Syndrome of finger agnosia, disorientation for right and left, agraphia and acalculia: Local diagnostic value. *Archives of Neurology and Psychiatry, 44*(2), 398–408.

Hahamy, A., Macdonald, S. N., van den Heiligenberg, F., Kieliba, P., Emir, U., Malach, R., Johansen-Berg, H., Brugger, P., Culham, J. C., & Makin, T. R. (2017). Representation of multiple body parts in the missing-hand territory of congenital one-handers. *Current Biology, 27*(9), 1350–1355.

Hashimoto, T., Ueno, K., Ogawa, A., Asamizuya, T., Suzuki, C., Cheng, K., ... Iriki, A. (2013). Hand before foot? Cortical somatotopy suggests manual dexterity is primitive and evolved independently of bipedalism. *Philosophical Transactions of the Royal Society B, 368*(1630), 1–12.

Hunt, K. D. (1994). The evolution of human bipedality: Ecology and functional morphology. *Journal of Human Evolution, 26*(3), 183–202. https://doi.org/10.1006/jhev.1994.1011.

Iwamura, Y. (2000). Bilateral receptive field neurons and callosal connections in the somatosensory cortex. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 355*(1394), 267–273.

Iwamura, Y., Iriki, A., & Tanaka, M. (1994). Bilateral hand representation in the postcentral somatosensory cortex. *Nature, 369*(6481), 554–556.

Kolasinski, J., Makin, T. R., Jbabdi, S., Clare, S., Stagg, C. J., & Johansen-Berg, H. (2016). Investigating the stability of fine-grain digit somatotopy in individual human participants. *Journal of Neuroscience, 36*(4), 1113–1127. https://doi.org/10.1523/JNEUROSCI.1742-15.2016.

Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational similarity analysis – Connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience, 2*, 1–28. https://doi.org/10.3389/neuro.06.004.2008.

Lewis, O. J. (1989). *Functional morphology of the evolving hand and foot.* Oxford: Clarendon Press.

Mancini, F., Bauleo, A., Cole, J., Lui, F., Porro, C. A., Haggard, P., & Iannetti, G. D. (2014). Whole-body mapping of spatial acuity for pain and touch. *Annals of Neurology, 75*(6), 917–924. https://doi.org/10.1002/ana.24179.

Manser-Smith, K., Tamè, L., & Longo, M. R. (2018). Tactile confusions of the fingers and toes. *Journal of Experimental Psychology: Human Perception and Performance, 44*(11), 1727–1738.

Martuzzi, R., van der Zwaag, W., Farthouat, J., Gruetter, R., & Blanke, O. (2014). Human finger somatotopy in areas 3b, 1, and 2: A 7T fMRI study using a natural stimulus. *Human Brain Mapping, 35*(1), 213–226. https://doi.org/10.1002/hbm.22172.

Mayer, E., Martory, M. D., Pegna, A. J., Landis, T., Delavelle, J., & Annoni, J. M. (1999). A pure case of Gerstmann syndrome with a subangular lesion. *Brain, 122*(6), 1107–1120. https://doi.org/10.1093/brain/122.6.1107.

McNutt, E. J., Zipfel, B., & DeSilva, J. M. (2018). The evolution of the human foot. *Evolutionary Anthropology, 27*(5), 197–217. https://doi.org/10.1002/evan.21713.

Merzenich, M. M., Kaas, J. H., Sur, M., & Lin, C.-S. (1978). Double representation of the body surface within cytoarchitecture areas 3b and 1 in "S1" in the owl monkey (Aotus trivirgatus). *Journal of Comparative Neurology, 181*(1), 41–73. https://doi.org/10.1002/cne.901810104.

Mountcastle, V. B. (2005). *The sensory hand: Neural mechanisms of somatic sensation.* Cambridge, MA: Harvard University Press.

Nelson, R. J., Sur, M., Felleman, D. J., & Kaas, J. H. (1980). Representations of the body surface in postcentral parietal cortex of Macaca fascicularis. *Journal of Comparative Neurology, 192*(4), 611–643. https://doi.org/10.1002/cne.901920402.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia, 9(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4.

Owen, R. (1849). *On the nature of limbs.* Chicago, IL: University of Chicago Press.

Rolian, C. (2009). Integration and evolvability in primate hands and feet. *Evolutionary Biology, 36*(1), 100–117. https://doi.org/10.1007/s11692-009-9049-8.

Rolian, C., Lieberman, D. E., & Hallgrímsson, B. (2010). The coevolution of human hands and feet. *Evolution, 64*(6), 1558–1568. https://doi.org/10.1111/j.1558-5646.2010.00944.x.

Romo, R., Lemus, L., & de Lafuente, V. (2012). Sense, memory, and decision-making in the somatosensory cortical network. *Current Opinion in Neurobiology, 22*(6), 914–919. https://doi.org/10.1016/j.conb.2012.08.002.

Sathian, K., & Zangaladze, A. (1996). Tactile spatial acuity at the human fingertip and lip: Bilateral symmetry and inter-digit variability. *Neurology, 46*, 1464–1466.

Schicke, T., & Röder, B. (2006). Spatial remapping of touch: Confusion of perceived stimulus order across hand and foot. *Proceedings of the National Academy of Sciences of the United States of America, 103*(31), 11808–11813. https://doi.org/10.1073/pnas.0601486103.

Schmitt, D., Zeininger, A., & Granatosky, M. C. (2016). Patterns, variability, and flexibility of hand posture during locomotion in primates. In T. L. Kivell, P. Lemelin, B. G. Richmond, & D. Schmitt (Eds.). *The evolution of the primate hand* (pp. 345–369). New York, NY: Springer. https://doi.org/10.1007/978-1-4939-3646-5.

Schweizer, R., Braun, C., Fromm, C., Wilms, A., & Birbaumer, N. (2001). The distribution of mislocalizations across fingers demonstrates training-induced neuroplastic changes in somatosensory cortex. *Experimental Brain Research, 139*(4), 435–442. https://doi.org/10.1007/s002210100793.

Schweizer, R., Maier, M., Braun, C., & Birbaumer, N. (2000). Distribution of mislocalizations of tactile stimuli on the fingers of the human hand. *Somatosensory & Motor Research, 17*(4), 309–316. https://doi.org/10.1080/08990220020002006.

Schweizer, R., Voit, D., & Frahm, J. (2008). Finger representations in human primary somatosensory cortex as revealed by high-resolution functional MRI of tactile stimulation. *Neuroimage, 42*(1), 28–35. https://doi.org/10.1016/j.neuroimage.2008.04.184.

Szalay, F. S., & Dagosto, M. (1988). Evolution of hallucial grasping in the primates. *Journal of Human Evolution, 17*, 1–2), 1–33.

Tamè, L., Braun, C., Holmes, N. P., Farnè, A., & Pavani, F. (2016). Bilateral representations of touch in the primary somatosensory cortex. *Cognitive Neuropsychology, 33*(1–2), 48–66. https://doi.org/10.1080/02643294.2016.1159547.

Tamè, L., Farnè, A., & Pavani, F. (2011). Spatial coding of touch at the fingers: Insights from double simultaneous stimulation within and between hands. *Neuroscience Letters, 487*(1), 78–82. https://doi.org/10.1016/j.neulet.2010.09.078.

Tamè, L., Wühle, A., Petri, C. D., Pavani, F., & Braun, C. (2017). Concurrent use of somatotopic and external reference frames in a tactile mislocalization task. *Brain and Cognition, 111*, 25–33. https://doi.org/10.1016/j.bandc.2016.10.005.

Tocheri, M. W., Orr, C. M., Jacofsky, M. C., & Marzke, M. W. (2008). The evolutionary history of the hominin hand since the last common ancestor of Pan and Homo. *Journal of Anatomy, 212*(4), 544–562. https://doi.org/10.1111/j.1469-7580.2008.00865.x.

Tucha, O., Steup, A., Smely, C., & Lange, K. W. (1997). Toe agnosia in Gerstmann syndrome. *Journal of Neurology, Neurosurgery & Psychiatry, 63*(3), 399–403. https://doi.org/10.1136/jnnp.63.3.399.

Wagenmakers, E.-J., Love, J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., ... Morey, R. D. (2018). Bayesian inference for psychology. Part II: Example applications with JASP. Psychonomic Bulletin & Review, 25(1), 35–57. https://doi.org/10.3758/s13423-017-1323-7.

Weinstein, S. (1968). Intensive and extensive aspects of tactile sensitivity as a function of body part, sex, and laterality. In D. R. Kenshalo (Ed.). *The skin senses* (pp. 195–222). Springfield, IL: Thomas.

Yamamoto, S., & Kitazawa, S. (2001). Reversal of subjective temporal order due to arm crossing. *Nature Neuroscience, 4*(7), 759–765. https://doi.org/10.1038/89559.