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Fingers hold spatial information that toes do not

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Abstract

Fingers have preferential associations with relative spatial locations. Tactile localisation is faster when the fingers are in these locations, such as when the index finger is in a relatively higher spatial position, and the thumb in a relatively lower position. However, it is unclear whether these associations are related to hands specifically, or are a more general characteristic of limbs. The present study therefore investigated whether toes have similar spatial associations. If these associations reflect the statistics of natural limb usage, very different patterns of association would be expected for the fingers and toes, given their different functional roles in daily behaviour. We measured reaction time (RT) and error rates of responses to tactile stimuli applied to the middle finger/toe or thumb/big toe, when they were positioned in a relative upper or lower location. We replicated the finding that fingers have preferential associations that facilitates localisation—RT and error rate were lower when the index finger was in the top position, and the thumb in the bottom position. We found that toes do not hold the same spatial information, though it remains unclear whether toes hold different spatial information or none at all. These results demonstrate spatial information held by the fingers is stronger and more reliable than for the toes, so is not a general characteristic of limbs, but possibly related to hand use.

Keywords

Body representation; posture; touch; fingers; toes

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Introduction

There are striking similarities between the hand and foot: they are serially homologous (Rolian et al., 2010), both have hairy and glabrous skin on their alternate sides (Marieb, 2012), and share a qualitatively similar structural plan (Owen, 1849/2008). Yet they also have important differences. The bones of the hands and feet differ considerably in size and shape (Marieb, 2012). The nature of the mechanoreceptors on the two body parts differs (Kennedy & Inglis, 2002), resulting in differences in tactile sensitivity. Most obviously there are dramatic differences in the patterns of usage between the hand and foot in our everyday activities. At a psychological level, there are hints in the literature that there may be deep functional connections between the mental representations of the hands and feet. For example, Gerstmann's syndrome produces both finger agnosia (Kinsbourne & Warrington, 1962) and toe agnosia (Mayer et al., 1999; Tucha et al., 1997). Moreover, similar patterns of tactile confusions have been reported on the hand and foot (Cicmil et al., 2016; Manser-Smith, Tamè, & Longo, 2018; Schweizer et al., 2000), with shared individual differences in the pattern of mislocalisations between fingers and toes (Manser-Smith, Tamè, & Longo, 2019). Here, we investigated whether the hands and feet also share common associations between body parts and spatial locations.

There is a large body of evidence showing that tactile perception is modulated by specific body postures. For example, crossing the hands over the body midline reduces

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our efficiency in localising touch on the body (Yamamoto & Kitazawa, 2001), as does crossing the feet (Schicke & Röder, 2006), and crossing the fingers (de Haan et al., 2012). Romano et al. (2017) recently developed a novel method for measuring such associations between body parts and spatial locations. They found that participants responded to tactile stimulation faster when it was applied to the thumb when it was in a relative *bottom* position than top position, and responded faster to the index finger when it was in a relatively *top* position than bottom position. Romano and colleagues (2017, 2019) describe these preferential associations between body parts and spatial locations as standard representations of body-space relationships. Such standard representations may be embedded into body representation, and facilitate efficient localisation of tactile stimuli independent of ongoing postural changes.

How these standard representations emerge is not clear. One possibility is that they are general features of how the limbs are represented. Human hands and feet are serially homologous structures that co-evolved (Rolian et al., 2010), and so share a number of similarities such as those described above. Shared standard body-space representations between the hands and feet may also be a product of this co-development. In particular for our close non-human primate relatives such as chimpanzees, that use both their hands and feet dexterously (Holowka et al., 2017a, 2017b), it would be equally evolutionarily advantageous for hands and feet to have standard representations. However, as human hands and feet now have widely different uses, it is not clear whether standard associations would be conserved for the toes.

Another possibility is that standard body-space relationships are learned from frequent actions or postures, reflecting the statistics of natural hand usage. Natural use relationships have already been shown to be related to other somatosensory functions, such as transfer of tactile learning between fingers (Dempsey-Jones et al., 2016) and the representational structure of sensorimotor cortex (Ejaz et al., 2015). Given the fundamentally different patterns of usage between hands and feet in humans, we might expect the hands and feet to have different patterns of spatial association. It is also notable that there are dramatic differences between the upper and lower limbs in terms of their ability to rotate. The ability of the forearm to rotate allows us to position our hands and fingers in a range of postures, for example, with either the palm or dorsum facing upwards, with different postures used for different reaching and grasping behaviours depending on object affordances (Rosenbaum et al., 1990). The human legs, however, have a much more restricted ability to rotate (Marieb, 2012; Webb & Sparrow, 2007), meaning that the dorsal surface of the foot nearly always faces upwards, and the sole downwards, except when we are lying down.

The present study investigated whether standard body-space relationships, such as have been found for the hand, are also present in the feet. By using a method closely modelled on Romano and colleagues (2017), we aimed to investigate to what extent the toes have similar preferential body-space associations to the fingers. If there were similarities in standard body-space associations between these two body parts, this would provide evidence that standard representations are general features of the representation of the limbs. If we found that they were not similar, this would suggest that standard representations are learned from natural hand usage.

Experiment 1

Methods

Participants. Twenty-one individuals participated at Birkbeck, University of London (8 female, mean age = 33 years). All had normal touch and gave written informed consent. Twenty were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; $M=73$) and all were right-foot dominant as assessed by the Waterloo Footedness Questionnaire (Elias et al., 1998; $M=59$). The study was approved by the Birkbeck Psychological Sciences ethics committee.

The effects reported by Romano and colleagues (2017) were very strong—the critical interaction having partial eta-squared values of 0.80 and 0.83 in two experiments. A power analysis using G*Power 3.1 (Faul et al., 2007) with the smaller of these effect sizes, an alpha value of 0.05, and power of 0.95, indicated six participants were required. We aimed for 20 participants, but ended up with one extra. As such, our experiment is appropriately powered to replicate the basic effect of Romano and colleagues on the hands, and investigate the presence of the same effect on the feet. It is worth noting, however, that no existing studies have investigated spatial associations on the toes, so effect size estimates from the fingers have been used. It is possible, of course, that potential effects on the toes are smaller than on the fingers.

Task. Procedures were similar to those used by Romano et al. (2017, 2019). Participants sat in a chair with tactile stimulators applied to the tip of the glabrous skin surface of the thumb and middle finger of both hands, or the tip of the glabrous skin surface of the big toe and third toe of the feet. The middle finger was used instead of the index finger, as pilot participants reported difficulty in distinguishing the big toe and second toe. This is consistent with previous findings of patterns of tactile confusions across the toes (Cicmil et al., 2016; Manser-Smith, Tamè, & Longo, 2018). Importantly, Romano and colleagues (2019) showed that similar spatial associations are found for the middle finger as were found for the index finger in Romano et al. (2017).

Figure 1 shows the posture used for testing the hands (left panel) and the feet (right panel). Hands were held one

Figure 1. The left panel shows the posture held while testing the hands. The right panel shows the posture held while testing the feet. In both postures, the hands/feet were held one above the other, without touching, in front and aligned with the body midline.

above the other, without touching, in front of the body midline, separated by approximately 15 cm. The feet were also held one above the other, with the heel of the top foot resting on a stool to reduce fatigue. Participants were tested in the same postures, but with the left and right hand/foot positions reversed in half the blocks. The posture we used for the hands was different to that used by Romano et al. (2017), wherein the thumb and index finger were positioned in two "L" shapes, with the two thumbs and two index fingers positioned one above the other as if to form a square. As it was not possible for the feet to be held in the position they used a position was chosen that could comfortably be held by both the hands and feet, as shown in Figure 1. Vision was occluded using a blindfold.

The experiment consisted of four blocks—in two blocks only the fingers of both hands were stimulated, and in two blocks only the toes were stimulated. Alternate participants started by performing either both hand or both foot blocks. Tactile stimulators could only be applied to either the fingers or the toes at one time (to allow responses to be made with the alternate body part), and was a time consuming process, so AABB counterbalancing was used to minimise the number of times changing the stimulator locations. There were two of each hand and foot blocks so that limb position could be varied between the blocks, eliminating the possibility of a left/right compatibility bias in responding. In one block the left limb was in the "top" position and the right limb in the "bottom" position, and in the second block the right limb was in the "top" position and the left limb in the "bottom" position. Order of the two hand or foot blocks was randomised for each participant. Each block contained 160 trials in random order, resulting in 640 trials per participant.

On each trial, the participant received a touch at one of four locations on the fingers or toes—first or middle digit, in the top or bottom position. They were asked to respond as quickly as possible by judging whether the stimulation occurred on a digit in the top or bottom position (regardless of which digit was stimulated or whether it was the left or right hand/foot).

Apparatus and stimuli. Tactile stimuli were delivered through four solenoid tactile stimulators (8 mm in diameter; M & E Solve, UK), controlled by a National Instruments I/O Box (NI USB-6341) driven using a custom MALTAB script (Mathworks, Natick, MA). Each stimulus consisted of a train of three 30 ms stimuli interleaved with an off phase of 30 ms, resulting in a vibro-tactile stimulation of 150 ms.

When stimulation was applied to the hand, responses were collected using two foot-pedals—one below the toe and one below the heel of the right foot. Participants responded to the "top" position by lifting the toe, and to the "bottom" by lifting the heel. When tactile stimulation was applied to the toes, a number pad was used. Participants responded to the "top" using their right middle finger, and "bottom" using their right thumb. Stimulus-response compatibility bias (that responses using the toe of the foot and middle finger always corresponded to "top" judgements, and using the heel and thumb always corresponded to "down" judgements) are

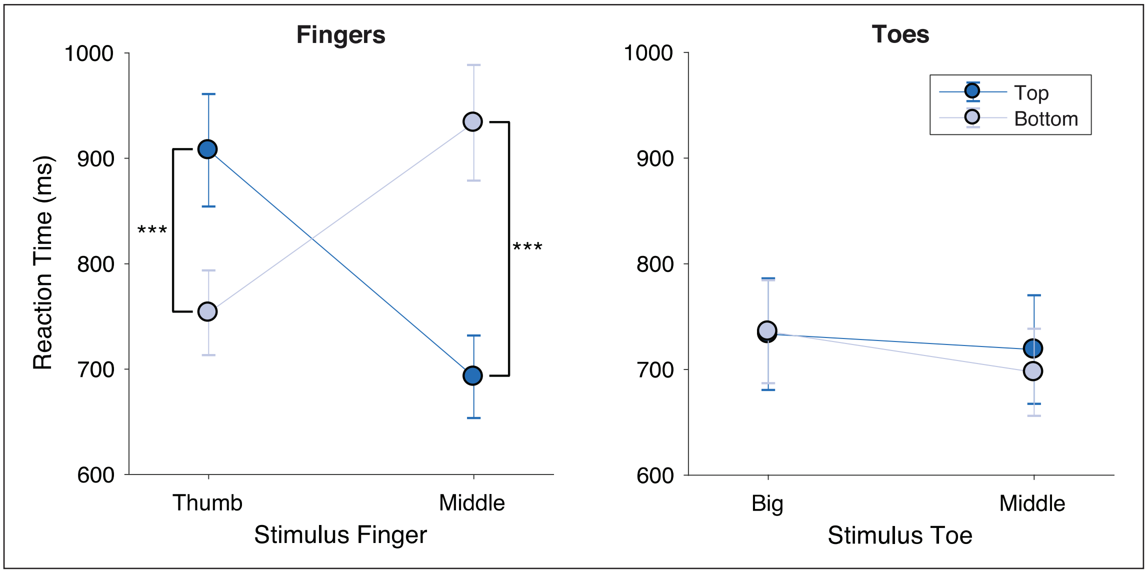

Figure 2. Grand average RTs in Experiment 1 for the fingers (left panel) and toes (right panel). Error bars represent standard error of the mean. Participants were considerably faster at responding to the fingers when the thumb was in a relative bottom position, and the middle finger in a relative top position, than vice versa. Participants were equally fast at responding to the toes in all locations.
$^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

unlikely to influence pattern of results given the robust findings of Romano et al. (2017) using both the paradigm used in the present experiment and using an implicit association task (IAT). The IAT measured the strength of conceptual associations between body parts and spatial concepts using an association task—RTs were faster to images of index fingers when the word "up" was present, and images of middle fingers when the word "down" was present. These findings suggest that spatial associations are also present at the level of implicit conceptual associations.

Analysis. Analyses were modelled on those of Romano et al. (2017). RTs were trimmed to remove outliers, defined as trials faster than 200 ms (anticipatory responses; 0.3% of trials) as well as trials exceeding three standard deviations above the individuals' mean (late responses; 1% of trials; range of cut-offs: 1,070–4,881 ms). Remaining responses were log-transformed to address the asymmetrical distribution of RT responses (Ratcliff, 1993). Accuracy scores were transformed using the arcsine of the square root, to align the distribution to meet the assumptions of analyses of variance (ANOVAs) (Zubin, 1935), as participants often scored at 100% accuracy.

To assess whether we replicated the associations for the fingers reported in our previous studies (Romano et al., 2017, 2019), we first conducted a repeated-measures ANOVA on data from the fingers with two factors: relative POSITION (top/bottom) and DIGIT (first/middle) receiving tactile stimulation. RTs and error rate were dependent variables in separate analyses. To assess whether similar associations occur for the toes, we then conducted an analogous ANOVA on data from the toes. For each interaction, we carried out Bayesian repeated measures ANOVAs (Wetzels et al., 2012) to quantify evidence for or against the null hypothesis (H_0). The BF_{10} (Bayes factor) expresses the likelihood of H_1 relative to H_0 given the current data. Bayesian statistics were carried out using JASP (version 0.8.2.0) with the default parameters.

To more directly compare the patterns of associations for the fingers and toes, we then conducted a three-way repeated-measures ANOVA, with factors BODY PART (fingers/toes), POSITION (top/bottom) and DIGIT (first/middle). We predicted faster and more accurate discrimination of tactile stimuli when the middle finger was in a relative top position than when it was in a relative bottom position, and vice versa for the thumb, as found by Romano et al. (2017). This would be reflected in an interaction between the POSITION and DIGIT factors. If the toes also hold similar spatial information, then the same interaction should be present in the ANOVA on the toes. If standard postures were different for the fingers and toes, this would be evident in a significant interaction between BODY PART, POSITION and DIGIT. Follow-up *t*-tests to explore significant interactions were corrected for multiple comparisons using the Holm-Bonferroni procedure. The data associated with this research are available through the Open Science Framework (OSF; osf.io/t4rnm).

Results and discussion

Fingers hold spatial information

We started by analysing just the data from the fingers to compare our results to those of Romano and colleagues

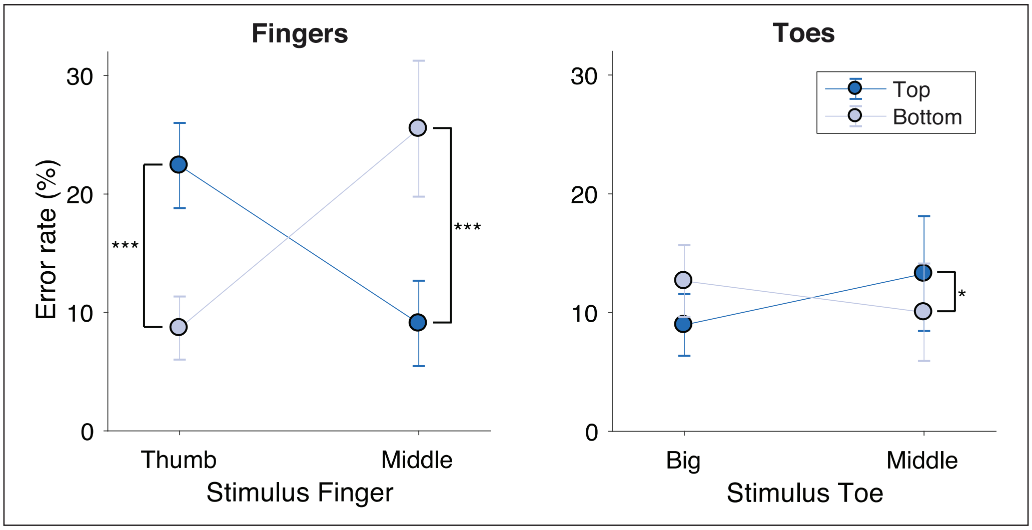

Figure 3. Grand average error rates in Experiment 1 for the fingers (left panel) and toes (right panel). Error bars represent standard error of the mean. Participants made considerably fewer errors in responding to the thumb when it was in a relative bottom position, and the middle finger in a relative top position, than vice versa. Participants made fewer errors overall when responding to the toes in all locations. *$p < .05$, **$p < .01$, ***$p < .001$.

(2017). The left panel of Figure 2 shows RTs in each of the four conditions. An ANOVA showed a significant main effect of POSITION, $F(1, 20)=7.18$, $p=.01$, $\eta^2 p=.26$, and a nearly significant effect for DIGIT, $F(1, 20)=4.06$, $p=.06$, $\eta^2 p=.17$. Most critically, the interaction between POSITION and DIGIT was highly significant, $F(1, 20)=63.36$, $p<.0001$, $\eta^2 p=.76$. As can be seen in Figure 2, there was a clear crossover interaction. Follow-up tests, using Holm-Bonferroni multiple-comparison correction, showed that responses on the thumb were faster when it was in a relative bottom position than a relative top position, 753.53 and 907.61 ms, $t(20)=5.26, p<.001, d_z=1.15$. Conversely, responses on the middle finger were faster when it was in a relative top than bottom position, 692.71 and 933.67 ms, $t(20)=7.36$, $p<.001$, $d_z=1.61$. A Bayesian repeated-measures ANOVA revealed very strong evidence for the alternative against the null hypothesis for the interaction, $BF_{10}=5.64 \text{ x } 10^{11}$.

The left panel of Figure 3 shows error rate in each of the four conditions. The ANOVA with error rate as dependent variable also showed a significant interaction between the two factors, $F(1, 20)=117.81$, $p<.001$, $\eta^2 p=.86$, while the two main effects were not significant, POSITION: $F(1, 20)=0.34$, $p=.57$, $\eta^2 p=.02$; DIGIT: $F(1, 20)=0.06$, $p=.80$, $\eta^2 p<.01$. Follow-up paired t-tests revealed that responses were more accurate on the thumb when it was in a relative bottom position (error rate ± standard error: 8.68% ± 2.66) than top position, 22.40% ± 3.60, $t(20)=9.61$, $p<.001$, $d_z=2.10$. Again, responses to the middle finger were more accurate when it was in a relative top position (9.07% ± 3.61) than a relative bottom position, 25.51% ± 5.74, $t(20)=6.89$, $p<.001$, $d_z=1.50$. A Bayesian repeated-measures ANOVA suggested that there is very strong evidence for the alternative against the null hypothesis for the interaction, $BF_{10}=1.23 \text{ x } 10^9$. Importantly, the consistent patterns seen in the RT and error data suggest that the effects we report are not due to a speed-accuracy trade-off.

These results extend the results of Romano and colleagues (2017) using the thumb and index finger, and replicate the findings of Romano and colleagues (2019) using the thumb and middle finger, that as well as being faster, responses were more accurate when the thumb was in the bottom position, and the middle finger in the top position, than vice versa. This further supports the conclusion that there are standard body-space relationships that facilitate responding to tactile stimuli.

Toes do not hold the same spatial information as fingers

Our novel question was whether the toes also hold spatial information. The right panel of Figure 2 shows RTs for the toes. In contrast to the fingers, there was only a significant main effect of DIGIT, $F(1, 20)=10.82$, $p<.01$, $\eta^2 p=.35$. Responses to the middle toe were faster regardless of whether it was in the top or bottom (718.64 and 697.34 ms) position, compared to the big toe in the top or bottom position (733.36 and 735.65 ms). The main effect of POSITION, $F(1, 20)=0.05$, $p=.83$, $\eta^2 p<.01$, and the interaction between DIGIT and POSITION, $F(1, 20)=0.84$, $p=.37$, $\eta^2 p=.04$, were not significant. To further investigate the non-significant results of the interaction, we conducted a Bayesian repeated-measures ANOVA. The results indicated that there was weak evidence for the null over the alternative hypothesis, $BF_{10}=0.463$.

The right panel of Figure 3 shows error rates for the toes. The ANOVA with error rate as the dependent variable showed a significant interaction, $F(1, 20)=5.64$, $p=.03$, $\eta^2=0.22$, but no significant main effect for either the factor POSITION, $F(1, 20)=0.49$, $p=.49$, $\eta^2p=.02$, or DIGIT, $F(1, 20)=0.05$, $p=.82$, $\eta^2p<.01$. The pattern of results on the toes was inverted from error rate on the fingers: responses were *less* accurate to the big toe when it was in a relative bottom position (12.66% ± 3.03) than top position (8.96% ± 2.60). Responses to the middle toe were also less accurate when it was in the top position (13.73% ± 4.83) than bottom position (10.03% ± 4.10). However, this difference was only significantly different between the middle toes, $t(20)=-2.66$, $p=.02$, $d_z=-0.58$, $BF_{10}=0.429$, and not the big toes, $t(20)=1.17$, $p=.26$, $d_z=0.26$, $BF_{10}=0.230$. A Bayesian repeated-measures ANOVA indicated that there was weak evidence for the alternative over the null hypothesis for the interaction, $BF_{10}=1.17$.

Differences in spatial information held by fingers and toes

To directly compare performance on the fingers and toes, we conducted a 2*2*2 ANOVA. There was a significant main effects of BODY PART, $F(1, 20)=7.50$, $p=.01$, $\eta^2p=.27$, as well as a significant three-way interaction between POSITION, DIGIT, and BODY PART, $F(1, 20)=79.04$, $p<.0001$, $\eta^2p=.80$. This three-way interaction verifies that the fingers and the toes hold different spatial information (these differences are described in the specific body part analyses).

A 2*2*2 ANOVA with error rates as the dependent variable again showed a significant effect of BODY PART, $F(1, 20)=6.62$, $p=.02$, $\eta^2p=.25$, and a significant three-way interaction between POSITION, DIGIT, and BODY PART, $F(1, 20)=82.93$, $p<.0001$, $\eta^2p=.81$. The main effect of BODY PART and significant three-way interaction again verifies that the fingers and toes hold different spatial information.

These results indicate that while the toes may hold weak spatial information, this information is different to that held by the fingers. This suggests that standard body-space relationships of the digits are not only a general characteristic of the limbs, but are learned through actions and postures used by the hands, but not the feet. However, the data do not allow a clear determination of whether these differences result from the toes having a qualitatively different pattern of spatial associations from the fingers (as suggested by the modest interaction for error rates), or having no associations at all (as suggested by the lack of interaction for RT). We replicated the pattern of spatial associations for the fingers that we have recently reported (Romano et al., 2017, 2019): responses were faster and more accurate to stimuli on the thumb when it was in a lower than in an upper location, and vice versa for the middle finger. In contrast, no such pattern was found for the big and middle toes, with some evidence that the pattern might even be reversed. One concern about this experiment, however, is that different modes of responding were used in the two conditions. When stimulated on the fingers, participants responded by lifting the heel or toes of their foot; when stimulated on the toes, participants responded by pressing buttons with their thumb and middle finger. This is a potential confound in the design of the experiment, and it is possible that the different modes of responding could contribute to the differences in the patterns of spatial associations that we find for fingers and toes. We therefore conducted a second experiment in which we used vocal responses, which allowed us to exactly match the manner of responding for fingers and toes.

Experiment 2

Method

Participants. Twenty individuals at the University of Milan Bicocca participated (13 female, mean age = 26 years). All had normal touch and gave written informed consent. The study was approved by the local ethics committee.

Apparatus and stimuli. Tactile stimuli were delivered through four tactile stimulators (custom-made electromagnetic solenoids, Heijo Electronics, Beckenham, United Kingdom, www.heijo.com), controlled by a custom-made I/O box and OpenSesame software (OpenSesame 3.1; Mathôt et al., 2012). The tactile pulse pattern was taken from our previous experiments, with each stimulus consisting of a train of 30 ms stimuli interleaved with an off-phase of 30 ms, resulting in a vibro-tactile stimulation of 150 ms. This produced a clearly perceivable tap delivered through a 4 mm diameter magnetic rod placed inside the solenoid. Note that while these stimuli are different from those used in Experiment 1, they are identical to those used by Romano and colleagues (2017) in the original experiments using this paradigm.

Task. The task and procedures were identical to Experiment 1 except that participants made responses verbally in all conditions. Participants responded using the Italian words "su" (i.e., top) or "giù" (i.e., bottom) to indicate whether they perceived the tactile stimulus on a digit on the top or bottom hand/foot. This made the manner of responding identical across both the finger and toe conditions. Vocal responses were collected using a pair of headphones (Logitech H390) with an attached microphone. The reaction time (RT) was recorded using a custom modification of the inline voicekey script for OpenSesame 3 which detected the response produced by the participant after the delivery of the tactile stimulus. The response time is taken at the time in which the recorded loudness is above the sound threshold. An initial calibration phase was used to set the sensitivity threshold and check that the voice onset was correctly detected. Before the beginning of the experiment, six stimuli were delivered to a single finger and participants were instructed to alternate the "su" and "giù" responses. Feedback of the response time was

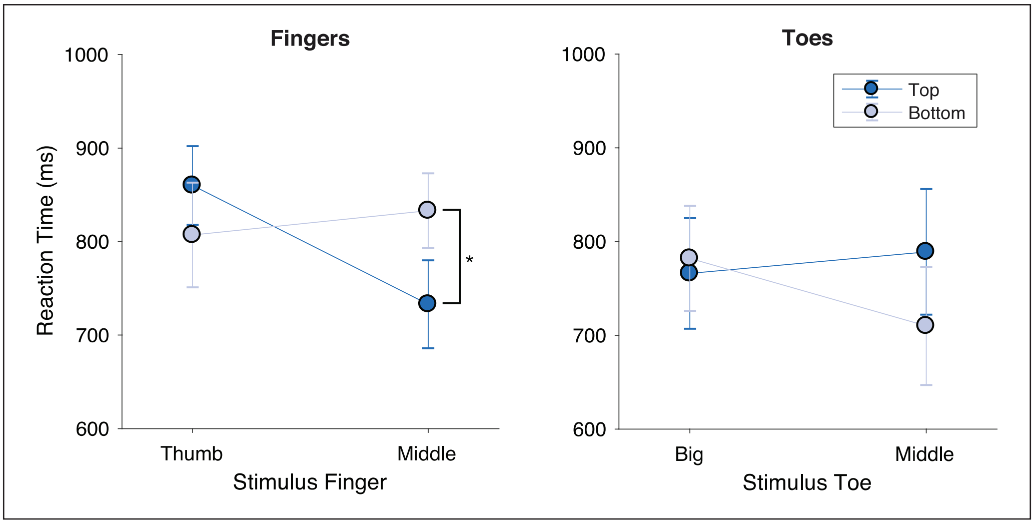

Figure 4. Grand average RTs for the fingers (left panel) and toes (right panel) in Experiment 2. Error bars represent one standard error of the mean. $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$.

visible on the computer screen of the experimenter and, soon after the response, the next stimulus was given to the participant. If the participants had to repeat one of the six answers, the sound threshold parameter (i.e., the one controlling the sensitivity of the voicekey script) was decreased making it more sensitive. Else, if one anticipated response was recorded (i.e., RT < 200 ms or a response was recorded before the actual response), the sound threshold was increased. In case of adjustment, the calibration procedure was repeated. The content of the response (i.e., top or bottom) was entered manually by an experimenter using the keyboard.

Analysis. All analyses were identical to Experiment 1. A total of 7% of trials were excluded as anticipations and 4% as outliers (range of cutoffs: 1,328–2,326 ms). The number of trials excluded is larger than in Experiment 1, presumably on account of issues related to audio recording of vocal responses.

Results and discussion

Analysis on fingers

The left panel of Figure 4 shows RT in each of the four conditions on the fingers. As in Experiment 1, there was a clear crossover interaction of POSITION and DIGIT, $F(1, 19) = 12.71$, $p < .005$, $\eta^2 p = .40$. There were no significant main effects of POSITION, $F(1, 19) = 0.60$, $p = .45$, $\eta^2 p = .03$, or DIGIT, $F(1, 19) = 2.65$, $p = .12$, $\eta^2 p = .12$. Follow-up tests showed that the interaction was similar to that in Experiment 1 and previous studies with this paradigm. For the middle finger, responses were faster in the top than in the bottom position, 732.75 and 832.91 ms; $t(19) = 2.87$, $p < .02$, $d_z = 1.12$, $\mathrm{BF}_{10} = 5.238$. In contrast, on the thumb responses were marginally faster when it was in the bottom than in the top position, 807.08 and 860.38 ms, $t(19) = 1.83$, $p = .08$ (2-tailed), $d_z = 0.41$, $\mathrm{BF}_{10} = 0.936$. A Bayesian repeated-measures ANOVA revealed strong evidence for the alternative hypothesis over the null hypothesis for the interaction, $BF_{10} = 64.23$.

The left panel of Figure 5 shows error rates for the four conditions on the hand. An ANOVA showed a clear interaction between POSITION and DIGIT, $F(1, 19) = 102.88$, $p < .0001$, $\eta^2 p = .84$. There were no significant main effects of either POSITION, $F(1, 19) = 0.429$, $p = .52$, $\eta^2 p = .02$, or FINGER, $F(1, 19) = 2.15$, $p = .16$, $\eta^2 p = .10$. Follow-up *t*-tests showed that responses were more accurate for the thumb in the lower than the upper position, 7.50% and 13.75%; $t(19) = 6.14$, $p < .0001$, $d_z = 1.37$, but more accurate for the middle finger in the upper than lower position, 7.63% and 16.00%, $t(19) = 8.69$, $p < .0001$, $d_z = 1.94$. A Bayesian repeated-measures ANOVA provided strong support for the alternative over the null hypothesis for the interaction, $BF_{10} = 55.50$.

Analysis on toes

The right panel of Figure 4 shows RT data for the toes. There was no significant main effect of POSITION, $F(1, 19) = 0.64$, $p = .43$, $\eta^2 p = .03$, or DIGIT, $F(1, 19) = 0.59$, $p = .45$, $\eta^2 p = .03$, nor their interaction, $F(1, 19) = 1.05$, $p = .32$, $\eta^2 p = .05$. A Bayesian ANOVA found weak evidence in favour of the null hypothesis over the alternative hypothesis for the interaction, $BF_{10} = 0.47$.

The right panel of Figure 5 shows the corresponding data for error rates. There was a significant main effect of POSITION, $F(1, 19) = 7.43$, $p < .02$, $\eta^2 p = .28$, and a significant interaction of POSITION and DIGIT, $F(1, 19) = 7.07$, $p < .02$, $\eta^2 p = .27$. There was no main effect of digit, $F(1,$

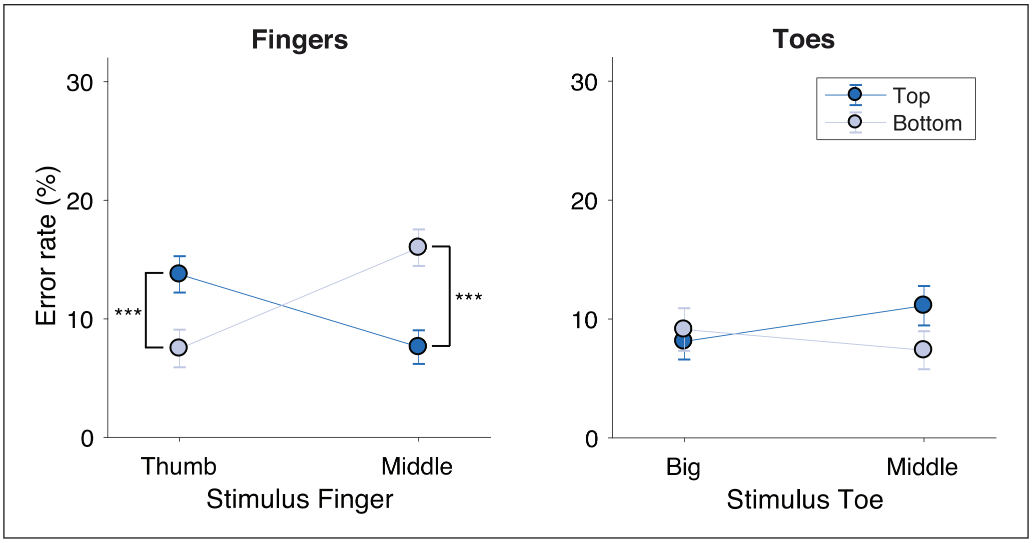

Figure 5. Grand average error rates in Experiment 2 for the fingers (left panel) and toes (right panel). Error bars represent one standard error of the mean. *$p < .05$, **$p < .01$, ***$p < .001$.

19)=0.24, p=.63, η^2p=.01. Follow-up t-tests showed no significant differences between the upper and lower locations for the big toe, 766.46 and 781.98 ms, $t(19)=0.25$, p=.81, d_z=0.06, nor for the middle toe, 789.32 and 709.80 ms, $t(19)=1.60$, p=.13, d_z=0.36. A Bayesian ANOVA found modest evidence in favour of the alternative hypothesis for the interaction, $BF_{10}=4.21$.

Comparison of fingers and toes

A full ANOVA comparing RT on the fingers and toes revealed a significant main effect of BODY PART, $F(1, 19)=6.18$, $p < .05$, η^2p=.25. More critically, as in Experiment 1 there was a significant three-way interaction of BODY PART, POSITION, and digit, $F(1, 19)=5.65$, $p < .05$, η^2p=.23. This interaction again demonstrates that the associations between digits and spatial locations differ systematically between the fingers and toes. There were no other significant main effects or interactions.

A similar ANOVA on error rates revealed significant main effects of BODY PART, $F(1, 19)=11.98$, $p < .01$, η^2p=.39, and POSITION, $F(1, 19)=5.26$, $p < .05$, η^2p=.22, as well as an interaction of POSITION and DIGIT, $F(1, 19)=15.51$, $p < .0001$, η^2p=.45, and a nearly significant interaction of POSITION and BODY PART, $F(1, 19)=3.95$, p=.06, η^2p=.17. Most critically, as with the RT data and as in Experiment 1, there was a significant three-way interaction of BODY PART, POSITION, and DIGIT, $F(1, 19)=129.23$, $p < .0001$, η^2p=.87.

General discussion

We investigated the existence of standard body-space relationships in two different body parts: the fingers and the toes. We showed that localisation of tactile stimuli was more efficient (faster RTs and lower error rate) when the thumb is in a relative bottom position, and the middle finger in a relative top position. This provides a clear replication of the pattern of results reported by Romano and colleagues (2017) when the thumb and index finger were tested, and shows that the same pattern of results holds for the thumb and middle finger. Moreover, our findings showed that the toes do not share the same standard body-space associations as the fingers, and error rate was lower for the middle toe in a relative bottom than top position (the inverse to results found on the hand), and all results on the feet showed only weak supporting evidence.

These results provide evidence that standard body–space relationships are *not* a general feature of the representation of the limbs, as patterns of results across the hands are not replicated across the feet. Our results instead suggest that standard representations of the limbs may be learned from frequent actions or postures. For example, most frequently used grasping postures using the hand occur with the thumb in a relatively lower position than the fingers (Cutkosky & Howe, 1990; Feix et al., 2016).

One potential interpretation of the weaker (or absent) body-space associations between the toes than between the fingers comes from the fact that the thumb has more flexibility and independence of movement relative to the other fingers than the big toe has to the other toes (Lewis, 1989). Thus, the relative position of the toes cannot change to as great an extent as relative position of the fingers. Not only do we find weaker standard associations between the toes than the fingers, we find a quantitatively different pattern of results: responses were faster to the middle toe regardless of its relative position, as least in Experiment 1. As noted above, while our experiments were clearly sufficiently powered to identify spatial associations on the fingers, it is possible that spatial associations on the toes exist, but are subtler and smaller in magnitude than those on the fingers. In that case, more highly powered experiments might be needed to detect such effects.

One possible explanation of this result that can be dismissed is that it is a result of differences in localisation accuracy across the toes. In this study, we found that responses were slower to the big toe than the middle toe, though previous studies have shown that localisation accuracy is higher for the big toe than the middle toe (Cicmil et al., 2016; Manser-Smith, Romano, et al., 2018). Moreover, accuracy results of this experiment did not indicate that participants were simply worse at responding to tactile stimuli on the big toe. Therefore, we can reliably say that the standard body-space relationships found for the toes are not simply due to differences in tactile acuity across the toes. Nevertheless, it is possible that biomechanical constraints make it more difficult to position the feet directly one above another than for the hands. While participants in our experiments did not complain about this, it is possible that it created a more awkward or uncomfortable posture, which could potentially have affected responses. Similarly, another difference between conditions is that the feet rested on the legs of a stool, whereas the hands were held freely in space. We consider this unlikely to play a meaningful role in the differences we observe. If anything, this should have added noise to the results for the fingers, the condition in which clear associations were found. It also notable that the hand posture used here with one hand held flat above the other is very different from that used in our previous studies with this paradigm where the fingers were held in an "L" shape one above the other (Romano et al., 2017) or just as just a single hand (Romano et al., 2019). Critically, very similar patterns of spatial associations for the fingers have been found in each of these cases.

The different patterns of results for response accuracy for hands and feet provides further evidence that standard body-space associations are learned from frequent actions or postures. In human and non-human primates, the anatomy of the hip, knee, and ankle joints constrains leg movement and posture in such a way that it is more comfortable for the outer edge of the foot to be angled towards the ground than the inner edge of the foot, resulting in the big toe being in a relative top position and middle toe in a relative bottom position (Marieb, 2012; Webb & Sparrow, 2007). For example, during arboreal locomotion, many non-human primates use the toes in these positions (Holowka et al., 2017b; Schmitt et al., 2016). In humans, most frequent seated postures involved the legs being crossed towards the midline of the body, again resulting in the big toe being in a relative top position and middle toe in a relative bottom position. This posture has less functional significance than hand grasping postures, which could explain why learned patterns of body-space associations are weaker for the toes than the fingers, and are only reflected in response accuracy and not RT.

Differential visual experience of the fingers vs. toes may also contribute to these associations. The hands are ubiquitous in our visual field, at least from the second-year of human life (Fausey et al., 2016). The toes, in contrast, are not only less likely to be in our visual field, but are commonly covered by socks and shoes which do not individuate the different toes. This could explain why the spatial associations of the toes are weaker, and possibly qualitatively different, than those of the fingers. These associations result from generalisation across the statistics of motor commands, proprioceptive feedback about limb position, or visual feedback from seeing the body, resulting in a sort of Bayesian prior of limb position. Indeed, studies using fMRI have found that the clear somatotopic organisation that characterises the representations of the fingers in primary somatosensory cortex may be less discretely organised for the toes (Akselrod et al., 2017; Hashimoto et al., 2013), though with the intriguing exception of individuals who habitually use their feet for skilled manipulative actions (Dempsey-Jones et al., 2019).

The possibility of such a standard, or default posture has been suggested based on a range of previous data, including the stereotyped posture of the "phantom" body following spinal anaesthesia (Melzack & Bromage, 1973), and impairments in tactile localisation (Yamamoto & Kitazawa, 2001) and visual-tactile interactions (Azañón & Soto-Faraco, 2008) with the limbs crossed. The idea that the perceived spatial location of limbs would involve a Bayesian process of integrating online proprioceptive signals with a default prior posture is analogous to findings that visual location memory is biased towards specific spatially prototypical locations (e.g., Azañón et al., 2020; Cheng et al., 2007; Huttenlocher et al., 1991).

One limitation of our first experiment was the use of different response effectors in the hand and foot blocks. Differences in RT and response accuracy between hands and feet may be related to the different response effectors, and not differences in standard associations. In our second experiment, we replicated these results using identical verbal responses in both conditions. This demonstrates that the differences between fingers and toes are not an artefact of different modes of response. Romano et al. (2017, 2019) have found consistent standard body-space associations using different response effectors and task paradigms. As well as the paradigm like that used in the present study, Romano and colleagues (2017) also found using an IAT that standard body-space relationships are present even on a conceptual level. The consistent results we found verbal responses used in Experiment 2 thus adds to the evidence that these effects generalise across of range of tasks and response modalities. Moreover, the similarity of the results we found in samples tested in the United Kingdom (Experiment 1) and Italy (Experiment 2) shows that these associations are not due to idiosyncratic associations or idioms present in any specific language.

In conclusion, our results support the hypothesis that standard body-space relationships are not a general feature of the representation of the limbs, as patterns of RT and accuracy results are different across hands and feet. Standard body-space relationships are much stronger and more reliable for the hands, suggesting a main role of ontological development and experience of grasping in their development.

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