# The Standard Posture of the Hand

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Perceived limb position is known to rely on sensory signals and motor commands. Another potential source of input is a standard representation of body posture, which may bias perceived limb position toward more stereotyped positions. Recent results show that tactile stimuli are processed more efficiently when delivered to a thumb in a relatively low position or an index finger in a relatively high position. This observation suggests that we may have a standard posture of the body that promotes a more efficient interaction with the environment. In this study, we mapped the standard posture of the entire hand by characterizing the spatial associations of all 5 digits. Moreover, we show that the effect is not an artifact of intermanual integration. Results showed that the thumb is associated with low positions, while the other fingers are associated with upper locations.

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*Public Significance Statement*
Recent results have shown that the thumb and index fingers have preferred spatial locations, with touch being perceived more quickly on the thumb when it is in a relatively low position and on the index finger when it is in a relatively high position. In this study, we mapped spatial associations across all five fingers. We report clear associations for all five fingers, with the thumb being associated with a relatively low position and all four other fingers being associated with a relatively high position. We propose that this position corresponds to the default posture of the hand, biasing perception, and potentially action, in all other postures.

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The perception of limb position in space relies on sensory signals from joints, skin, and muscle spindles, as well as efferent copies of motor commands (Proske & Gandevia, 2009). Another potential source of input is default representations of body posture (i.e., "standard posture"), which may function as Bayesian priors, biasing perceived limb position toward more common positions. The use of such priors is well known in other spatial domains (Cheng, Shettleworth, Huttenlocher, & Rieser, 2007), but has received little attention in the context of proprioception. There is, however, evidence that the brain may code default representations of body posture. For example, in the 1970s, Melzack and his colleagues found that after deafferentation by brachial plexus or subarachnoid anesthesia participants reported feeling their "phantom" body in a stereotyped posture, independent of the actual position of the body at the time of anesthesia (Bromage & Melzack, 1974; Melzack & Bromage, 1973 see Inui, Masumoto, Ueda, & Ide, 2012, for more complex changes after ischemic anesthesia).

There are also some behavioral results supporting the idea of a standard posture. For example, crossing the arms, as compared to having them in a standard uncrossed posture, impairs tactile localization on the hands, suggesting a conflict between actual limb posture and a representation of a standard posture (Yamamoto & Kitazawa, 2001). Similarly crossing two fingers induces similar impairments localizing touch in external coordinates (de Haan, Anema, & Dijkerman, 2012; Heed, Backhaus, & Röder, 2012). Indeed, experiments investigating visual-tactile interactions with crossed hands have found stronger interactions with visual stimuli near the usual location of the hand, not its actual crossed location, during the immediate period following touch (Azañón & Soto-Faraco, 2008). Furthermore, saccades directed toward a crossed hand, are initially directed toward the opposite hand (as if it was uncrossed), and then corrected online, several hundred milliseconds later (Groh & Sparks, 1996; Overvliet, Azañón, & Soto-Faraco, 2011). Other studies have reported patterns of constant error of perceived joint angle. For example, in the study of Gritsenko, Krouchev, and Kalaska (2007), participants had to estimate the joint angle of the elbow after a passive or active movement. Systematic biases toward the central point of the range of motion were found following both the active and passive movement condition. This regular tendency can be interpreted as a bias toward a standard posture.

In the current study, we aimed to map the standard posture of the hand. The rationale of our experiments assumes that when the internal spatial representation of the stimulated hand matches the sensory feedback, stimuli are detected faster and more accurately relative to when internal and sensory-driven spatial information do not match. This is in analogy to the rationale of the hand laterality task (Parsons, 1987), in which participants discriminate whether a seen image is of left hand or a right hand. Typically, reaction times (RTs) increase when the displayed hand is misaligned with one's own hand (Ionta & Blanke, 2009; Parsons, 1987), and this deficit has been explained as reflecting the time-consuming operation of mental rotation necessary to match visual information of the displayed hand with the proprioceptive information coming from one's own body. Following this idea, we recently found that the thumb and index fingers have preferential associations with relative low or high spatial positions, respectively (Romano, Marini, & Maravita, 2017). In that study, participants held their hands so that one was above the other (see Figure 1) and discriminated the
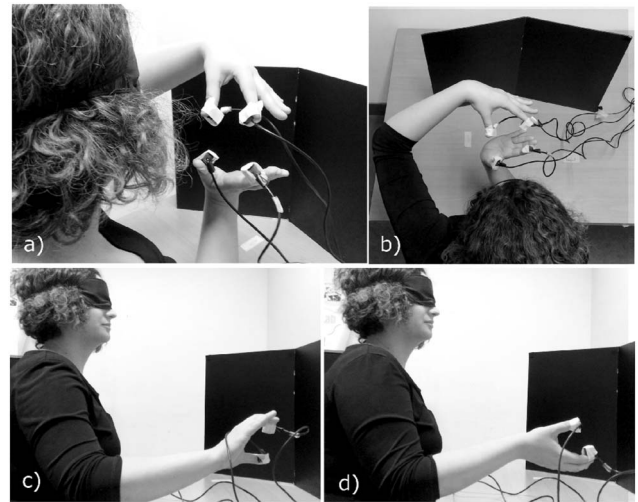


*Figure 1.* (a, b) Hand posture held during Experiments 1 and 2. Specifically, the situation with the solenoid attached to the thumb and the index finger is shown. One hand was held above the other and the distance was equivalent between the different stimulators. (c, d) Hand postures held during the two blocks of Experiment 3. The posture of Panel (c) corresponds to the one hypothesized to be the standard posture of the hand.

spatial position (high/low) of a tactile stimulus delivered to the thumb or index finger of one of the two hands. We found that tactile discrimination was faster and more accurate when the stimulated finger was a thumb in a relative low position or an index finger in a relative high position.

While the study of Romano and colleagues (2017) provided clear evidence for preferential associations between thumb and index fingers with spatial positions, the exact nature of these associations remains uncertain and the standard posture of the hand remains unknown. If these results truly reflect a standard posture of the whole hand, the other fingers should also show preferential spatial associations. This is crucial because the thumb and index finger are probably the most important fingers for skilled actions in humans as they are crucial for both power and precision grips (MacKenzie & Iberall, 1994; Napier, 1965). Moreover their primary role in both phylogenetic and ontogenetic development is well established, considering the use of the index finger for example for pointing (Bates, Camaioni, & Volterra, 1975; Leavens, 2004). Additionally, having an opposable thumb has likely been crucial for the evolution of the human species (Young, 2003). It is therefore possible that these two fingers have special features because of their different status, and the existence of a standard posture of the hand still needs further evidence. We sought evidence in support or against a standard posture of the entire hand by conducting three experiments applying the experimental paradigm of Romano and colleagues (2017) to map spatial associations across the entire hand. Experiment 1 investigated whether finger/space preferential associations extend to the middle finger. To further characterize the global configuration of the hand, in Experiment 2, we investigated the standard spatial position of all five fingers. Notably, in Experiment 1, we tested pairs of fingers, which involved the processing of a larger portion of the hand instead of a single finger. In Experiment 2, we explored the effect

at the single finger level, thus testing whether standard posture effects characterize each finger or whether they are a property detectable exclusively when the global hand configuration is processed. Finally, in Experiment 3, we tested whether the standard posture of the hand relies on intermanual relation or it is independent from the other hand posture. The perception of tactile events can be influenced by concurrent tactile or visual stimuli co-occurring on the same hand. This intermanual (or interhemispheric) interaction may impact the processing of every bodily related signal (Dupin, Hayward, & Wexler, 2015; Magosso, Serino, Di Pellegrino, & Ursino, 2010). Similarly, hand posture may further modulate interhemispheric competition for tactile events (Moro, Zampini, & Agliotti, 2004) in a space/finger-specific manner (Tamè, Farnè, & Pavani, 2011). The standard posture might be expressed as a property of the single specific limb, thus being detectable studying only one hand. Alternatively, it is potentially dependent on the integration of the postural signals coming from both hands following a logic of intermanual competition that highlights a preferential posture only under potential competitive targets. In this case, when only one hand is tested, no preferential location is expected. We thus clarify the role of intermanual interaction for the effect we found to date in Experiment 3.

## Experiment 1: Extending Finger-Space Associations to the Middle Finger

Experiment 1 was similar to the study of Romano and colleagues (2017), except that instead of just testing associations for the thumb and index finger, we assessed whether the effects generalize to the middle finger. In separate blocks, participants made speeded elevation judgments about tactile stimuli presented on (a) the thumb and index finger, (b) the thumb and middle finger, or (c) the index and middle fingers.

## Materials and Method

This experiment was preregistered on the Open Science Framework using the Narrative Preregistration option (osf.io/hhz4d). Preregistration included the definition of the sample size, the procedures, and the main statistical approach. The raw data from the three experiments are open and freely available at the following link: https://osf.io/kd57c/?view_only=c286dd25adf942f4bc38 e3f104b7eded.

**Participants.** Twenty members of the Birkbeck community participated in Experiment 1 (13 female; $M_{age}$ = 28.8 years, range = 19–42). One additional participant was excluded because she was unable to complete the task and was replaced. The effect found in our previous study was strikingly strong (Romano et al., 2017). A formal power analysis with the previous effect size of $\eta_p^2 = 0.80$ and setting $\alpha = .05$ and $\beta = .95$ showed that just four participants were required (G*Power 3.1 software). This shows that the current experiment is very well-powered to replicate the results of Romano and colleagues (2017) and to extend their results to the middle finger. The study was approved by the local ethics committee (Birkbeck, University of London). All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; $M$ = 86.5, range = 70–100). All participants were naïve to the scope and the hypothesis of the study.

**Stimuli.** Tactile stimuli were delivered through four 9-mm diameter solenoid tappers (rounded tip, 0.2-mm skin contact; M&E Solve, Kent, England). Stimulators were controlled by an I/O box (National Instruments USB-6341) under control of a custom MATLAB (Mathworks, Natick, MA) script. Each stimulus consisted of three square-wave pulses with 30-ms on-phases (single pulse) and two interleaved 30-ms off-phases, resulting in a 150-ms vibration with a frequency of 17 Hz. This stimulation is similar to that used in our previous work (Romano et al., 2017), and other experiments involving suprathreshold tactile stimulations (e.g., Azañón, Radulova, Haggard, & Longo, 2016; Marini, Romano, & Maravita, 2017).

**Procedure.** Procedures were similar to those used in our previous study (Romano et al., 2017). A unimodal tactile position discrimination task was used, similar to the one previously used to investigate cross-modal effects (Maravita, Spence, Sergent, & Driver, 2002; Marini et al., 2017; Spence, Pavani, & Driver, 2004). Participants sat in front of a table with their eyes closed. Tactile stimulators were attached with surgical tape to the fingertips of the two fingers under investigation in the current block. The participant's arms were extended in front of them in a comfortable position and their hands were placed one on top of the other in such a way that the four stimulators corresponded to the vertices of an imaginary square of around 8 cm of side. Each finger was on top of its contralateral homologue so that, for example, one thumb was just above the thumb of the other hand (see Figure 1; Marini et al., 2017; Romano et al., 2017). We adopted a symmetric set up, in terms or right–left and up–down distances; because it was shown that stimulator distances might affect perceptual judgment in similar setups (Marini et al., 2017).

On each trial, participants received a tactile stimulus at one of the four possible locations on their fingertips and were asked to discriminate, as quickly and accurately as possible, the location of the stimulation (top or bottom), regardless of the stimulated finger, side (left/right), or hand (left/right). Each block was characterized by the stimulation of a different pair of fingers of both hands comprising four possible targets during each block: (a) thumb/index, (b) index/middle, and (c) thumb/middle. There were three independent experimental blocks, each involving the same pair of fingers of each hand (i.e., thumb vs. index, thumb vs. middle, index vs. middle). The sequence of the blocks was randomly assigned. A total of 160 trials per block (40 trials per stimulator) were delivered in random order.

The hand that was kept above (i.e., right hand on top or left hand on top) was always the same for one participant, so that the hand position mapping did not change across the blocks. Which hand was above was counterbalanced across participants. Responses were recorded through two foot-pedals, one below the toe and one below the heel of the dominant foot. Participants raised the toe to respond "top" or the heel to respond "bottom."

**Analysis and predictions.** The preprocessing and statistical analysis were described in the preregistration document and followed the approach used by Romano et al. (2017). RTs were first trimmed to eliminate outliers, which were defined as trials faster than 200 ms (anticipatory responses) and trials exceeding 3 SD above the mean of each participant (late responses). Following this procedure we excluded 4% of the trials because of anticipated responses and 2% of the trials because of late responses. RTs were then log-transformed to overcome the typical asymmetry of the RT

distribution (Ratcliff, 1993). Error rates were transformed using the arcsine of the square root, a mathematical transformation that improves the distribution to fit with the assumption of parametric analysis (Zubin, 1935). Participants with mean error rate exceeding 3 *SD* above the group average would have been excluded from the analysis. However, none of our participants had to be excluded for this reason.

Statistical analyses used repeated-measure analysis of variance (ANOVA) with factors relative position (top, bottom) and finger (thumb/index, index/middle, thumb/middle) depending on the tested block. Average RTs and error rate were tested separately as dependent variables. The expected interaction was explored with planned comparisons, corrected for multiple comparisons using Tukey's honest significant difference test. While, inferential statistics were conducted on transformed data that fits better parametric statistics assumptions, plots represent nontransformed data, which are easier to read graphically and hold meaningful metric units (see Figure 2).

To address the question of whether the processing of touch on a specific finger is affected by being paired in a block with another specific finger, we applied a second statistical approach developed after submission of the preregistration document. RT for the discrimination of tactile stimulation on each specific finger was investigated as a function of the factors position (top/bottom) and by the opposed finger stimulated (e.g., index when matched with thumb/index when matched with middle).

We predicted that we would replicate the finger-space associations for the thumb and index finger (Romano et al., 2017) in the block involving the thumb and the index finger. Moreover if the finger-space association extends to other fingers, we should expect a significant interaction also for the block involving the middle finger. The general logic of the experiment is that tactile stimuli are discriminated more efficiently when a finger is in a spatial location, which is associated with the potential preferential spatial location. Because the conclusion drawn on error rates are basically

the same of RT analysis, for concision, we report the results of RT analyses in the main text, and error rates results only in the online supplemental materials.

## Results

**Basic contrasts (block analyses).** The results of Experiment 1 are shown in Figure 2. We first analyzed the thumb-index condition, which was identical to Romano et al. (2017). These results show strong associations between fingers and spatial positions and provide a clear replication of the main results of Romano and colleagues (2017). Indeed, the ANOVA showed significant main effects of both position, $F(1, 19) = 5.33$, $p = .032$, $\eta_p^2 = .219$, and finger, $F(1, 19) = 9.09$, $p < .010$, $\eta_p^2 = .324$, and, most crucially, an interaction between the two factors, $F(1, 19) = 101.06$, $p < .001$, $\eta_p^2 = .842$. Consistent with previous results, planned comparisons revealed that the thumb-bottom ($M = 615$ ms, $SE = 29$) and the index-top ($M = 563$ ms, $SE = 29$) associations had faster responses (all $ps < .010$) than the thumb-top ($M = 729$ ms, $SE = 37$) and the index-bottom ($M = 733$ ms, $SE = 34$) associations.

We next investigated the condition in which the thumb was paired with the middle finger. The results were very similar to the index/thumb comparison. There were clear main effects of finger, $F(1, 19) = 11.10$; $p < .010$; $\eta_p^2 = .369$, and position, $F(1, 19) = 6.05$; $p = .024$; $\eta_p^2 = .241$, and an interaction, $F(1, 19) = 104.87$; $p < .001$; $\eta_p^2 = .847$. The planned comparisons support the association of thumb with bottom and the middle finger, analogously to the index, with top. The thumb-bottom ($M = 600$ ms, $SE = 22$) and the middle-top ($M = 539$ ms, $SE = 21$) conditions had faster responses than the thumb-top ($M = 682$ ms, $SE = 27$) and the middle-bottom ($M = 674$ ms, $SE = 27$) conditions (all $ps < .010$). Thus, the spatial associations we reported previously are not specific to the thumb and index finger, but generalize at least to the middle finger as well.

Finally, we looked at the condition in which the index and middle fingers were stimulated. The key question here is what happens with the index finger. If the associations we have reported are specific to each finger, then the index finger should remain associated with the top position. If, in contrast, the associations are based on the relative position of the fingers being stimulated in the task, then the association of the index finger should switch, now that it is paired with the middle finger. The ANOVA showed significant main effects of finger, $F(1, 19) = 6.57$; $p = .019$; $\eta_p^2 = .257$, and position, $F(1, 19) = 13.01$; $p < .010$; $\eta_p^2 = .406$, and the interaction Finger × Position, $F(1, 19) = 6.80$; $p = .017$; $\eta_p^2 = .263$. Planned comparisons of index/middle contrasts showed that both fingers have worse performance detecting the stimuli in a relative lower position (index-bottom: $M = 654$ ms, $SE = 32$; middle-bottom: $M = 643$ ms, $SE = 30$) than an relative high position (index-top: $M = 626$ ms, $SE = 29$; middle-top: $M = 570$ ms, $SE = 26$), with a larger difference between the two locations for the middle than the index (all $ps < .050$) suggesting that both fingers have preferential standard association with a relative higher location which is possibly stronger for middle finger.

**Single finger approach.** With these analyses, we tested the role of the paired finger at each condition on the localization of the tactile event of the stimulated finger. If the spatial association is a standard property of each finger then the spatial associations should not change depending on the other finger stimulated.



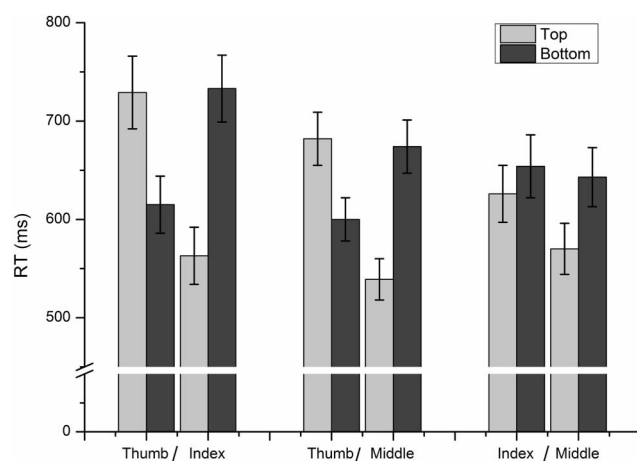*Figure 2.* Results from Experiment 1. Bars represent average reaction times (RTs) for the tactile discrimination task. Error bars indicate one standard error. Light gray columns report RTs when the finger occupies a relative higher position; dark gray columns represent the performance when the finger was in a relative lower position. The three different pairs of fingers tested are indicated on the *x*-axis.

Results of the thumb analysis suggest that the thumb has a constant strong association with lower position that does not change based on the other finger involved. The ANOVA showed significant effects for the main factor position, $F(1, 19) = 28.28$, $p < .001$, $\eta_p^2 = .598$, with top position ($M = 705$ ms, $SE = 35$) slower than bottom ($M = 607$ ms, $SE = 26$), while the factor contrasted finger, $F(1, 19) = 1.02$, $p = .326$, $\eta_p^2 = .051$, and the interaction between the two main factors, $F(1, 19) = 1.15$, $p = .298$, $\eta_p^2 = .057$, were not significant.

In contrast, the analysis of the index finger suggest that it was associated with relative upper location showing a significant main factor position, $F(1, 19) = 33.76$; $p < .001$; $\eta_p^2 = .640$, while the main effect of the contrasted finger was not significant, $F(1, 19) = 0.30$; $p = .592$; $\eta_p^2 = .015$. Moreover the association is partially influenced by the other finger involved as shown by a significant interaction, $F(1, 19) = 31.13$; $p < .001$; $\eta_p^2 = .621$. Post hoc comparisons showed that the index finger is always faster when it is in an upper position (compared to thumb: $M = 563$ ms, $SE = 29$, compared to middle: $M = 626$ ms, $SE = 29$) than in a lower location (compared to thumb: $M = 733$ ms, $SE = 34$, compared to middle: $M = 654$ ms, $SE = 32$), but the difference between top and bottom position decreases when the index is matched with the middle finger instead of the thumb (all $ps < .05$).

The ANOVA for the middle finger showed significant results for the main factors position, $F(1, 19) = 53.70$; $p < .001$; $\eta_p^2 = .739$, and the interaction Position $\times$ Contrasted Finger, $F(1, 19) = 15.46$; $p < .001$; $\eta_p^2 = .449$, while the main effect contrasted finger was not significant, $F(1, 19) = 0.08$; $p = .785$; $\eta_p^2 = .004$. Post hoc comparisons for the interaction showed that the middle finger analogously to the index finger is always faster when it is in an upper position (compared to thumb: $M = 539$ ms, $SE = 20$, compared to index: $M = 570$ ms, $SE = 26$) than in a lower location (compared to thumb: $M = 674$ ms, $SE = 27$, compared to index: $M = 643$ ms, $SE = 29$), but the difference between top and bottom position decreases when the middle finger is in contrast with the index finger as compared to when it is matched with the thumb (all $ps < .050$). Thus, the index and middle fingers both have a strong spatial association with the top location, which is more evident when they are contrasted with the thumb, and less strong when they are compared to each other.

The results of Experiment 1 suggest that the standard posture of the hand when processing touch has the thumb below the index and middle fingers. This configuration makes the hand to appear as a pair of pliers. Although it is just a speculation, the fact that the thumb can be opposed to each of the other fingers may suggest a potential role of grasping (or more likely a specific grasping action with the thumb down) in the standard postural representation.

## Experiment 2: Specific Spatial Preference for Each Finger of the Hand

The results of Experiment 1 showed that the associations reported by Romano and colleagues (2017) are not specific to the thumb and index finger, but generalize at least to the middle finger. In this experiment, we aimed to extend this conclusion to all five fingers.

## Materials and Method

Experiment 2 and 3 were preregistered on the Open Science Framework using the Narrative Preregistration option (osf.io/2m6yq). Preregistration of Experiment 2 and 3 was done after the analysis of Experiment 1 and included the definition of the sample size, the procedures, and the main statistical approach.

**Participants.** Twenty new right-handed (Oldfield, 1971; $M = 94$, range $= 80–100$) participants were tested in Experiment 2 (12 female; $M_{age} = 28$ years, range $= 19–42$).

**Procedure.** The task, the tactile stimulus features and response modalities were the same of Experiment 1, except that now, only homologous fingers were tested (in five separate blocks, one per finger; order of the fingers randomized). This manipulation avoids the possibility that the preferences emerge as a result of relative position of one finger as compared to another one. By doing so we controlled whether the association between fingers and the spatial locations is a property of the hand posture or it is a characteristic of each specific digit. The hand positioned above was counterbalanced across participants.

Participants were asked to judge the relative elevation of the tactile stimulation, while keeping their eyes closed. Responses were delivered through two foot-pedals, one below the toe and one below the heel of the dominant foot. Participants raised the toe to respond "top" or the heel to respond "bottom." Forty trials per condition were collected, resulting in 80 trials per block.

**Analysis and predictions.** Preprocessing of data was the same as Experiment 1. 4% of trials were identified as anticipated responses, whereas 1% of trials was identified as a late response for a total of 5% of trials excluded. In addition to the analyses described in the preregistration document, we first ran a global analysis at first with a $5 \times 2$ repeated measures ANOVA including the factors finger (thumb, index, middle, ring, little) and position (top, bottom). The global approach led us to match not only the preference for a spatial location for each finger, but also a potential difference in the strength of these associations between different fingers (e.g., the interaction). To unpack any eventual interaction we ran a second one-way ANOVA contrasting the proportion of change of RT. We applied a logarithmic transformation to overcome the asymmetric distribution that typically characterizes ratios. Log transformation centers the proportion on zero (instead of one) and distributes values around the 1:1 ratio symmetrically. Thus values were calculated as log (bottom/top), with positive values indicating that the top is faster than the bottom for each finger. We then ran the one-way ANOVA including the factor finger, which was followed by a series of $t$ test applying the Bonferroni–Holm procedure for multiple comparison correction to match all the pairs of fingers as post hoc testing if the factor finger was significant.

As in Experiment 1, similar results can be obtained analyzing error rates. This analysis is reported in the online supplemental materials.

If associations depend only on the tested finger, we should replicate the results of Experiment 1 when testing a single finger and its contralateral homologue. Alternatively, if the association depends on the position of a given finger relative to the other finger tested, or the entire hand more generally, the single finger test should not produce any significant preference and difference between the fingers.

## Results

The ANOVA showed significant effects both for the main effect of position, $F(1, 19) = 22.69$, $p < .001$, $\eta_p^2 = .539$, and for the interaction between the two factors position and finger, $F(4, 76) = 3.05$, $p = .022$, $\eta_p^2 = .138$. The main effect of finger, $F(4, 76) = .71$, $p = .587$, $\eta_p^2 = .032$, was not significant.

A one-way ANOVA using the proportion of change as dependent variable showed a significant effect of finger, $F(4, 76) = 4.01$, $p < .010$, $\eta_p^2 = .174$. However, post hoc testing did not show any significant specific contrast after the correction for multiple comparisons, suggesting to explore the effect looking at the general response pattern and not at specific differences between fingers (Figure 3a).

Figure 3a shows a different pattern for the thumb compared to the rest of the other fingers. Our results also suggest that the index and middle fingers might have a stronger sensitivity to the preferred location than the ring and little fingers. Results show that all the fingers but the thumb are associated with the relative top position when the task did not require the processing of the entire hand posture, conversely the thumb has no association until it is opposed to one of the other fingers. In that case it has a strong preference for the bottom position, as highlighted in Experiment 1 and our previous study (Romano et al., 2017). The finding that we have stronger associations for the thumb down and another finger up when more than one finger has to be processed suggests that we are likely looking at the standard posture of the entire hand with our task. It is possible that the representation of each finger holds some spatial information on its own, but when the entire hand is processed, spatial properties of the body emerge more strongly.

## Experiment 3: Finger-Space Preferences Without Intermanual Interference

Body related signals can be modulated by intermanual interaction at a tactile (Moro et al., 2004), and crossmodal level (Magosso et al., 2010) in a space/finger-specific way (Tamè et al., 2011). We designed Experiment 3 to figure out the eventual contribution/interference of the other hand in determining the effect of standard posture.

## Materials and Method

**Participants.** The same 20 participants that took part in Experiment 2 also participated in Experiment 3. Ten of them were administered first with the five blocks of Experiment 2, while the other 10 started the experimental session with the two blocks of Experiment 3. Overall the entire session lasted around 30 min including Experiments 2 and 3.

**Procedure.** In Experiment 3, only one hand was involved in the task. The hand was kept in such a way that it had the thumb down and the index finger up, as in the crossmodal congruency task position (Maravita et al., 2002; Spence et al., 2004), or in the converse position (index down, and thumb up) in a separate block.

The order of the blocks was counterbalanced across participants. The tactile stimulations and response modalities were the same of Experiments 1 and 2. Again, participants were asked to localize the relative elevation of the tactile stimulation while keeping the eyes closed 40 trials per condition were collected, resulting in 80 trials per block.

**Analysis and predictions.** In Experiment 3, we used a $2 \times 2$ repeated-measure ANOVA with factors relative position (top/bottom) and finger (thumb/index). Preprocessing of data were the same of Experiments 1 and 2. 5% of trials were excluded because identified as anticipated responses, 2% of trials were excluded because they were late responses. We never diverged from the preregistration document in the analyses of Experiment 3.

If the effect is independent of intermanual interaction we should find a significant interaction of the factors finger and position, replicating the results of Experiment 1. Error rates results are reported in the online supplemental materials.
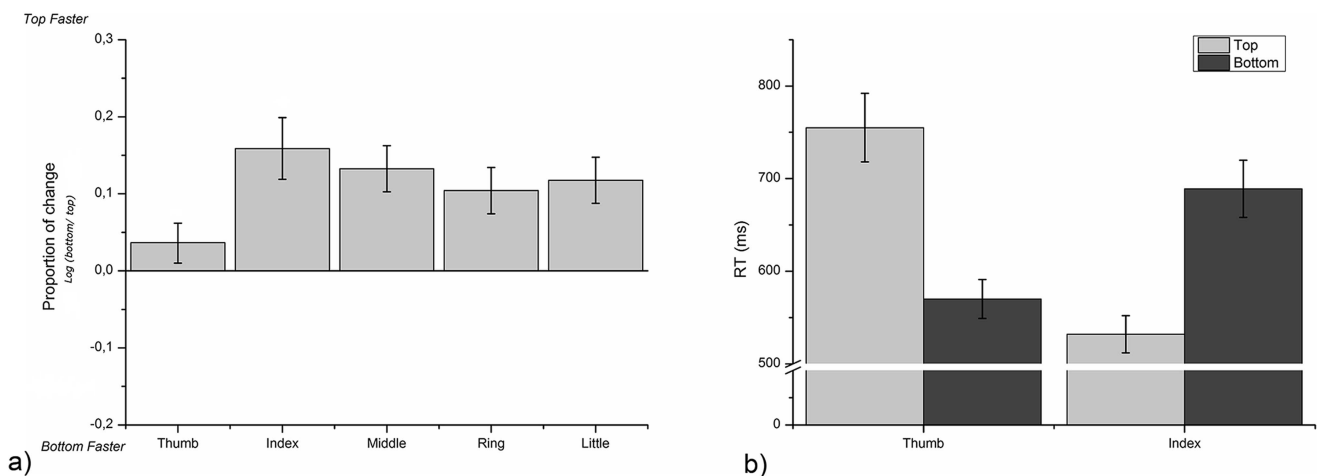


*Figure 3.* (a) Experiment 2 results. Columns represent the proportion of change between the reaction time (RT) for each finger held in the two positions. Ratios have been log transformed. Values > 0 suggest for a better performance in top position. (b) Experiment 3 results. Columns represent average RTs for the tactile discrimination task. Light gray columns report RTs when the fingers occupy a relative higher position; dark gray columns represent the performance when the fingers were in a relative lower position. Thin bars indicate the standard error of the mean in both panels.

## Results

The results are shown in Figure 3b. Results are in line with Experiment 1, showing a strong interaction between finger and position, and preferential associations remaining equal: thumb bottom/index top. Specifically, the ANOVA showed a significant main effect of finger, $F(1, 19) = 13.61$, $p < .010$, $\eta_p^2 = .417$, and a significant interaction Position $\times$ Finger, $F(1, 19) = 48.31$, $p < .001$, $\eta_p^2 = .718$, while the main effect of Position was not significant, $F(1, 19) = .77$, $p = .392$, $\eta_p^2 = .039$.

Planned comparisons for the interaction confirmed that the thumb-bottom ($M = 570$ ms, $SE = 21$) and the index-top ($M = 532$ ms, $SE = 20$) associations had faster responses (all $ps < .010$) than the thumb-top ($M = 755$ ms, $SE = 37$) and the index-bottom ($M = 689$ ms, $SE = 31$) associations (Figure 3b).

Results show that the standard posture affects the localization of tactile stimuli also when only one hand is involved in the task. This finding rules out a possible main role of intermanual interference causing the effect we observed, suggesting that the putative standard posture of the hand is a property embedded within each single hand.

## General Discussion

These results provide the first whole-hand maps of a possible standard posture. We used the paradigm of Romano and colleagues (2017) to identify spatial associations for each finger. We clearly replicated the finding that the thumb is associated with relatively lower spatial locations and the index finger with relatively higher locations (Romano et al., 2017). We further showed that these effects extend across the entire hand, with all nonthumb fingers associated with relatively higher spatial positions. By mapping these spatial associations we show that the standard representation of the hand holds the thumb opposed to all the other fingers: the thumb below and the four fingers lined up above. Our results also provide strong evidence for the generality of these effects, showing that they do not rely on contrast between the two hands.

The question whether the postural associations extend beyond the thumb and index finger is important because thumb and index finger are likely to be the most relevant fingers for both evolutionary and ontological development of humans, being special for actions like grasping and pointing (Bates et al., 1975; Leavens, 2004; Napier, 1965; Young, 2003). One possible hypothesis was that those fingers have special and dedicated representations holding additional characteristics (i.e., preferred spatial configurations), unlike the other fingers, and perhaps other body parts generally. Instead, we found that the middle finger also shows a preferential relative spatial location, which corresponds to the top elevation in a similar fashion to the index finger. The index and middle fingers did not show a clear difference from each other, ruling out the hypothesis that preferential associations result from the index finger being special, or from the middle finger being longer than the index finger. Our results support a whole hand preferred configuration with the thumb associated with the bottom position and opposed to the index and middle fingers that are readily associated with a relative upper position. This shape is evocative of a grasping configuration, although this link remains speculative. However, the orientation of the thumb down suggests that the configuration is even more specific than a general grasping movement.

In Experiment 2, we directly tested prototypical spatial associations across all five fingers. We found the thumb to be opposed to the other four fingers, which are associated with the upper location providing further evidence for the standard posture proposed in Experiment 1. Experiment 2 was designed such that only homologous fingers were tested in each block, avoiding the direct comparison with a second finger. Therefore, any preferential positions should be intrinsically coded in the finger representation independently of the rest of the hand. Experiment 2 highlights a clear association for the index, middle, ring, and little fingers with the top location, and mixed results for the thumb. The latter suggests that the processing of the thumb together with another finger is necessary to individuate the association of the thumb with a relative lower location, however a clear explanation for this specificity should be further investigated. It is possible that the thumb is a reference point for the hand, and thus has no preferential association per se. When tested alone it is not above or below something. Conversely, the other fingers are always represented in comparison to the thumb so that they are intrinsically coded as "above the thumb." Whatever the reason, our results suggest that standard spatial locations for each finger are better characterized when a larger portion of the hand is processed for both the thumb and the fingers.

Accordingly, the effects found in Experiment 2 were weaker than the results obtained in experiments involving two fingers from the same hand. The results of Experiment 3 confirmed the association for index-top and thumb-bottom once again, suggesting that the postural effects observed are more likely to be a within hand characteristic independent of the posture of the other limb. The whole hand configuration would not be necessary to detect the preferential spatial association for each finger (except the thumb) but plays an important role.

This study suggests the following standard posture: a hand configured like a pair of pliers, with the thumb in a lower location opposed to the four fingers occupying an upper position. The thumb opposing the other fingers suggests a hand likely being ready to grasp, however the precise orientation is evocative of a specific grasping action, potentially not the most frequent in everyday life. Indeed a mug is typically grasped with the thumb and index finger aligned horizontally, while a book is often held with the thumb above. Objects trigger specific preferential postures because of their specific affordances (Jeannerod, 1988). However, given that no object had to be grasped and any action was required with the hands our study is free from this potential confound. The hand posture that we identified is specifically evocative of grasping something like a branch of a tree.

How and why this specific grasping might be involved in the formation of this standard configuration, and the meaning of these associations, are questions that remain open for future research. We can hypothesize two possible reasons and mechanisms. The first one is connected to evolutionary development, so that our standard posture corresponds to that of a primate ready to grasp a branch of a tree like for arboreal locomotion (Schmitt, Zeininger, & Granatosky, 2016). Fastest responses should be available for the posture that is more frequent and/or need to move efficiently and safely in primate's environment. A second hypothesis is inherent to ontological development. It is possible that early experiences of active use of the hands include physical and functional constrains that induce the use of the hands with the thumb in a lower position.

Intriguingly in newborn infants (Cobb, Goodwin, & Saelens, 1966) and in fetuses (Hooker, 1938) the hand is more frequently held is a position like a fist with the thumb held under the third digit, a posture similar to the one that we described.

Yet this is a crucial question, indeed no physical or bodily constraints can directly motivate these associations as in adulthood humans efficiently and frequently use the hands in different postures not necessarily more frequently with the thumb down. In the resting position the relative elevation of the thumb with respect to the other fingers varies depending on the prono-supination of the hand, and the overall body posture. For example, the resting position of the hand when standing up has the thumb in a position physically higher than the other fingers because of the hand structure, but all of them are pointing down; so that a straightforward interpretation in terms of more frequent use, or resting position cannot be done. This is even more evident thinking about skilled use of tools where each instrument requires a preferential hand configuration.

In the general framework of body/space couplings, our associations differ from those that regard the position of hands in space relative to the body midline (Simon & Acosta, 1982; Tamè, Carr, & Longo, 2017). The more efficient responses obtained because of body/space couplings were possibly due to shorter intra- (vs. inter-) hemispherical brain processing time (Marzi, 1999; Tamè & Longo, 2015) and/or to stimulus-response compatibility effects (Berlucchi, Crea, di Stefano, & Tassinari, 1977). Regarding processing across the body midline, the spatial localization of somatosensory stimuli seems to be automatically referred to the location of the stimulated limb in the external egocentric space (Yamamoto & Kitazawa, 2001), although it has been proposed that tactile stimuli are initially unconsciously processed in a somatotopic frame of reference, and only at a second stage they are remapped and consciously reported in an egocentric spatial frame of reference (Azañón & Soto-Faraco, 2008). Also fingers were found to localize tactile stimuli on a somatotopic representations impairing the processing once fingers were crossed (de Haan et al., 2012; Heed et al., 2012). This finding are in line with the idea of a standard representation, however physical constraints certainly forced the creation of such preferences. Our findings bring the idea of a standard posture to a different level that extends beyond the rigid anatomical or gravitational constraints (van Elk & Blanke, 2011; Yamamoto & Kitazawa, 2001; de Haan et al., 2012; Heed et al., 2012), pointing toward a stable standard hand posture that could potentially extend to other body parts. The standard posture would not be based on physical constraints (or not only at least), but on functional advantages.

The fact that our task involved an explicit spatial judgment might somehow trigger the activation of the standard postural representation, that otherwise would remain silent and not affect other tactile tasks. At the moment, we can only hypothesize two scenarios: a) the effect might depend on a low-level processing of somatosensory information, impacting all the subsequent processing stages, including those that do not require spatial processing; b) the effect is related to remapping of touch from a skin-centered to an external reference frame. This function likely depends on multisensory processing occurring on a later stage of processing of touch (see, e.g., Azañón & Soto-Faraco, 2008), so that only tasks requiring an explicit localization of touch would be affected by a standard posture. Further studies may clarify whether the standard posture affects remapping of touch, so that when a participant is asked to actively manipulate and track body parts, localization and their spatial framework, or it affects tactile processing at a more basic level like biasing all the tactile perceptions like in simple detection task.

A potential limit of our procedure is that we adopted a fixed mapping of the response effector, namely the toe was always used to respond up, and the heel was always used to respond down. This response mapping has been universal in studies using the classical procedure of the cross-modal congruency task (Holmes, Calvert, & Spence, 2004; Maravita et al., 2002; Spence et al., 2004; Spence, Pavani, Maravita, & Holmes, 2004). Moreover, it was crucially shown that responses given with foot pedals or verbal responses identify the same effects during tactile elevation discrimination tasks, although less precisely following verbal responses (Gallace, Soto-Faraco, Dalton, Kreukniet, & Spence, 2008). Consistent with these considerations, in our previous study (Romano et al., 2017), we measured thumb/index preferential spatial associations also with an Implicit Association Test (Greenwald, McGhee, & Schwartz, 1998). In that IAT, responses were given with the index finger or the thumb instead of the foot pedals, and results confirmed the same association for thumb-down and index-up. These observations suggest that it is unlikely that the standard posture effect described so far depends uniquely from a compatibility effect of the response effector of the foot with the stimulated finger or the spatial location.

Our results strengthen the theoretical framework of a standard bodily spatial preferences (Romano et al., 2017) that adds to the somatotopic cortical mapping and the spatial localization relative to the egocentric space coordinates (de Vignemont, 2010; Longo, Azañón, & Haggard, 2010). Those levels of spatial somatosensory analysis are known to promote the efficient interaction with external world and especially with object manipulation and recognition. This study clarifies that a putative standard representation of the hand may exist with one's hands with the thumb in a relatively lower position and the other fingers in a relative upper position.

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