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Concurrent use of somatotopic and external reference frames in a tactile mislocalization task

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Running head: REFERENCE FRAMES, TOUCH, MISLOCALIZATION, BODY POSTURE, FINGERS

Abstract

Localizing tactile stimuli on our body requires sensory information to be represented in multiple frames of reference along the sensory pathways. These reference frames include the representation of sensory information in skin coordinates, in which the spatial relationship of skin regions is maintained. The organization of the primary somatosensory cortex matches such somatotopic reference frame. In contrast, higher-order representations are based on external coordinates, in which body posture and gaze direction are taken into account in order to localise touch in other meaningful ways according to task demands. Dominance of one representation or the other, or the use of multiple representations with different weights, is thought to depend on contextual factors of cognitive and/or sensory origins. However, it is unclear under which situations a reference frame takes over another or when different reference frames are jointly used at the same time. The study of tactile mislocalizations at the fingers has shown a key role of the somatotopic frame of reference, both when touches are delivered unilaterally to a single hand, and when they are delivered bilaterally to both hands. Here, we took advantage of a well-established tactile mislocalization paradigm to investigate whether the reference frame used to integrate bilateral tactile stimuli can change as a function of the spatial relationship between the two hands. Specifically, supra-threshold interference stimuli were applied to the index or little fingers of the left hand 200 ms prior to the application of a test stimulus on a finger of the right hand. Crucially, different hands postures were adopted (uncrossed or crossed). Results show that introducing a change in hand-posture triggered the concurrent use of somatotopic and external reference frames when processing bilateral touch at the fingers. This demonstrates that both somatotopic and external reference frames can be concurrently used to localise tactile stimuli on the fingers.

Introduction

Localizing tactile stimuli on our body surface, despite its apparent simplicity, is a very complex process that requires the involvement of multiple representations of the tactile event using different coordinate systems (Azañón & Soto-Faraco, 2008; Azañón, Stenner, Cardini, & Haggard, 2015; Badde, Röder, & Heed, 2014; Longo, Azañón, & Haggard, 2010). At early stages of somatosensory processing information is represented in a body-centered, somatotopically organized reference frame in which tactile events are referred to distinct locations on the skin. This is reflected by the brain's somatotopic organization in the primary somatosensory cortex (Penfield & Boldrey, 1937; Tamè, Moles, & Holmes, 2014). In further stages of processing, however, the tactile event can be identified with respect to body-side (Farnè, Brozzoli, Làdavas, & Ro, 2007) or with respect to external space using an egocentric/allocentric reference frame (Azañón, Camacho, & Soto-Faraco, 2010). The transition from body-centered to allocentric coordinates is achieved by making use of postural information coming from proprioceptive, visual or vestibular inputs (Clemens, De Vrijer, Selen, Van Gisbergen, & Medendorp, 2011; Holmes & Spence, 2004) and it is likely to be mediated by sensory regions (Hamada & Suzuki, 2005) and associative brain areas in the posterior parietal cortex (Rusconi et al., 2014). This processing of tactile localization from one reference frame to another has been named tactile remapping (Driver & Spence, 1998).

The study of incorrect localizations of faint tactile stimuli to different regions of the body (i.e., tactile mislocalization), proved useful when studying the nature of representations underlying tactile processing at the fingers (Schweizer, Braun, Fromm, Wilms, & Birbaumer, 2001; Schweizer, Maier, Braun, & Birbaumer, 2000). In a typical tactile mislocalization task, near-threshold tactile stimuli are delivered to one fingertip at a time to evoke mislocalizations to the other (non-stimulated) fingers of the same hand. Incorrectly localized stimuli are predominantly attributed to fingers that are neighbored to the stimulated ones (e.g., the index or ring finger, when the middle finger is stimulated), thus revealing the dominance of a somatotopic representation when solving this tactile task (Schweizer et al., 2000). Tactile mislocalization profiles appear to be highly context dependent, as revealed by experiments employing interfering stimuli in

a mislocalization setup. For instance, Braun and colleagues (Braun, Hess, Burkhardt, Wühle, & Preissl, 2005) applied supra-thresholds interference stimuli on the left thumb or little finger either 200 or 500 milliseconds (ms) prior to presenting a near-threshold test stimulus on the right hand. Results showed that stimuli applied on the left hand strongly interfere with the mislocalization profile of the right hand in a finger-specific manner, namely as a function of the fingers' anatomical topology. Tactile stimulation of the left thumb increased mislocalizations to the right thumb. Similarly, stimulation of the left little finger caused a shift in localization responses towards the right ring finger. This suggests that bilateral interactions operate primarily on a skin-based representation – which is compatible with the organization of the primary somatosensory cortex. By skin-based coordinates we mean somatotopic representations that are present regardless of body sides (note that this representation has also been termed anatomical or somatotopic).

In all previous mislocalization studies conducted by Braun and co-workers (2000, 2001, 2005) the hands were always kept in their respective hemispace – the left hand on the left side, the right hand on the right side (Braun et al., 2005). As yet it is unclear whether and to what extent representations of bilateral tactile interactions based on skin coordinates dominate also when postural changes require the adoption of external reference frame coordinates. A first possibility is that the sensory representations are updated by posture changes (e.g., Azañón & Soto-Faraco, 2008; Gallace & Spence, 2005; Heed & Röder, 2010; Longo, 2015; Shore, Gray, Spry, & Spence, 2005; Zampini, Harris, & Spence, 2005). An alternative possibility, however, is that the fingers of the two hands are more strongly constrained into a somatotopic representation and much less sensitive to posture changes (e.g., Longo & Haggard, 2010, 2011; Mancini, Longo, Iannetti, & Haggard, 2011; Tamè, Farnè, & Pavani, 2011).

In the present study, we tested this question directly by examining the effect of posture changes (crossed vs. uncrossed hand posture) on the mislocalization profile at the right hand, while the left hand is concurrently stimulated or not stimulated. If the skin-based coordinate representation underlying finger interactions between the two body-sides is preserved regardless of hands posture in external space, the same finger-specific mislocalization profile should emerge regardless of posture. By contrast, if changing

hands' posture triggers a representation remapping also for bilateral tactile interactions a different mislocalization profile should emerge when the hands are crossed compared to when they are uncrossed. Finally, if skin-based and external-based coordinates can be concurrently used, the mislocalization profile should be modulated by changes in hands' posture while keeping trace of the finger-specific interactions.

Materials and Methods

Participants

Twenty participants (mean \pm SD=23.0 \pm 4.2 years; range 19-37 years; 11 females) took part in the study. Participants gave their informed consent prior to participation and reported normal or corrected to normal vision and normal somatosensation. The study was approved by the local ethics panel. Only participants that were right handed by self-report were enrolled in the study. A formal assessment of their handedness was done by the Edinburgh Handedness Inventory on 15 out of 20 participants (Oldfield, 1971; M=94, range 61-100). Data of five participants were lost due to flawed data storage.

Stimulation

During the experiment participants placed both hands palms down onto the hand supports of the stimulation apparatus (Figure 1). Piezoelectrical stimulators were placed on four fingers of the right hand and two fingers of the left hand. Tactile stimulators were modified Braille elements of computer keyboards for the blinds (QuaeroSys Medical Devices UG, Schotten, Germany). Stimulation units were placed beneath four fingers of the right hand (i.e., index finger (R-D2), middle finger (R-D3), ring finger (R-D4) and little finger (R-D5)) and beneath the index finger (L-D2) and little finger (L-D5) of the left hand. For the supra-threshold (maximal intensity 17 cN) stimuli applied to the left hand, the 2 x 2 centre rods out of the 2 x 8 matrix were used in order to assure that the intensity of these prime stimuli were well above the localization threshold. Spacing of the rods was 2.45 mm. For the supra-threshold stimulation on the left hand, rods were maximally protruded (1 mm). For right hand finger stimulation with near-threshold

intensities only one rod out of the 2 x 8 matrix was activated. The graded protrusion in steps of 10 μm of each rod was computer controlled. The intensity of the stimulus applied to the fingers of the right hand was adjusted to the participants' individual perceptual thresholds for each finger. By applying near-threshold stimuli at the right hand we measured the mislocalization profile, i.e., the probability of erroneously localizing a tactile stimulus applied to a certain finger to another finger. The localization threshold is defined as the stimulation intensity at which the stimulus can be correctly localized with a probability of 50%. The localization threshold is slightly higher than the detection threshold, corresponding to the intensity at which the stimuli can be detected regardless of the stimulus localization (Harris, Thein, & Clifford, 2004). Importantly, the mislocalization profile at the right hand was studied in the context of a priming stimulus applied to the index or to the little finger of the left hand – thus introducing a bilateral tactile stimulation – or without any previous prime stimulus. The priming stimulus on the left hand was always presented 200 ms prior to the near-threshold stimulus on the right hand. The duration of all prime and near-threshold stimuli was 50 ms. Across blocks, hands were positioned in an uncrossed or crossed position (Figure 1). Note that the spatial relationship between the fingers receiving the prime stimuli on the left hand and fingers receiving the near-threshold targets on the right hand change as a function of posture. Specifically, the index fingers are close to one another in the uncrossed posture, but farther apart in the crossed posture. Conversely, the little fingers are farther apart in the uncrossed posture but close to one another in the crossed posture.

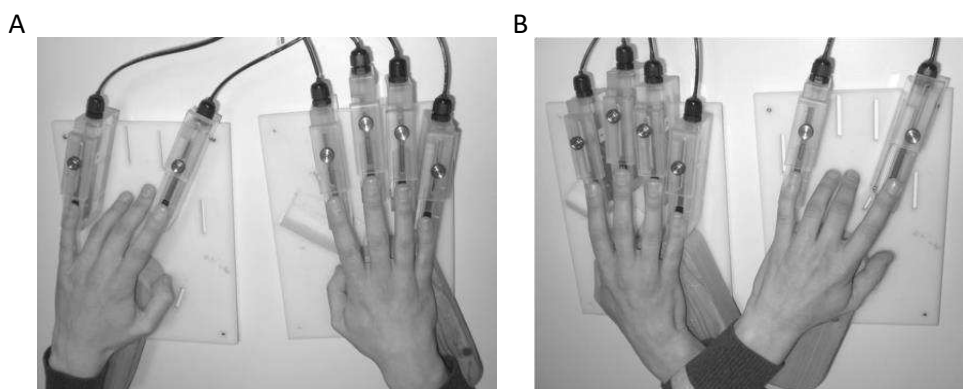


Figure 1. Illustration of the stimulation devices and the hand's posture across conditions. The blanket covering the hands during the experiment, and the numbers assigned to each finger for the response are not shown. (A) Hands uncrossed. (B) Hands crossed. Note that the spatial relationship between the fingers receiving the prime stimuli on the left hand and fingers receiving the near-threshold targets on the right hand change as a function of posture. Index fingers are close to one another in the uncrossed posture, but farther apart in the crossed posture; whereas little fingers are farther apart in the uncrossed posture but close to one another in the crossed posture.

Experimental setup

The stimulator units were mounted on two supports, one for each hand, such that participants were able to position their hands comfortably on the stimulator pads (Figure 1). By means of guiding slots in the support, stimulators were individually adjusted to participants' hands size. The adjustment was done such that the piezoelectric stimulators could stimulate all the fingers optimally at the individual fingertips.

In order to allow for comfortable hand positions arms were supported by small cushions. Each finger of the right hand was assigned a number in order to speed up participants' responses. Numbers were *one* for the stimulus applied on the index finger (R-D2), *two* for the stimulus applied on the middle finger (R-D3), *three* for the stimulus applied on the ring finger (R-D4) and, finally, *four* for the stimulus applied on the little finger (R-D5). In order to ease the assignment of numbers to stimulus locations, numbers were attached to the piezoelectric stimulators. To avoid cooling-off and to suppress acoustic noise accompanying the tactile stimulation, both hands were covered with a blanket. It was made sure not to cover the enumeration of the response pads in order to allow the subject to indicate the locus of the perceived stimulation by telling the corresponding number to the experimenter.

Participants had a screen positioned in front of them by which they received feedback on their performance. In particular, they saw a sketch of a hand presented on the computer screen. Whenever they named the correct finger location the corresponding finger turned green. In case the localization was wrong, the finger that had to be chosen turned red. Feedback had the purpose of keeping high the participants' motivation to detect the correct location. Participants' responses were registered by the

experimenter by inserting their responses into the computer controlling the task. The program registered how many stimuli at a certain finger had been localized wrongly or correctly, and chose the finger to be stimulated in the next trial. The program also adjusted and stored stimulus intensity for the right hand automatically, based on performance in the previous trials (see procedure). The experiment terminated automatically either as soon as 5000 trials were collected or alternatively if 24 correct and 8 erroneous localizations to any of the non-stimulated fingers of the right hand were reached for each stimulated finger. Throughout the experiment, white noise was presented over closed-ear headphones (Sennheiser XL-300, Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany), connected to a custom-built white noise generator, to mask any sounds made by the tactile stimulators.

Procedure

Before starting the main experiment, each participant performed a series of 20 practice trials in order to familiarise with the task. Participants were seated at a table with the stimulation devices placed in front of them. After placing the screen of the computer controlling the experiment in front of the participant, the meaning of the feedback display that appeared after each trial was explained.

Participants were informed that they had to perform a localization task to indicate which of the right hand fingers had been stimulated, and to tell the experimenter verbally their response (i.e., one, two, three or four). Accuracy was stressed over speed. In case participants did not feel the stimulus they were instructed to guess the stimulated site (i.e., forced choice). During the experiment, stimulation intensity for the near-threshold stimuli was adapted continuously depending on the participants' responses. To this end, the stimulation intensity was increased by an individual step whenever a stimulus had not been correctly localized, and vice versa it was decreased by an individual step following a correct localization. The intensity was tracked and adapted separately for each finger. The initial intensity of the near-threshold stimuli of the staircase procedure was 50% of the maximum intensity. These variations ensured sufficient incorrect localizations. Supra-threshold prime stimuli delivered to the left hand were always at the maximum intensity possible.

Each experimental trial started with a 523 Hz tone, followed by the near-threshold tactile stimulus. Depending on the stimulation condition, 200 ms before a supra-threshold tactile prime stimulus (i.e., L-D2 or L-D5) was or was not applied. Only localization responses that occurred between 300 ms and 5000 ms after the presentation of the near-threshold stimuli were regarded as valid. The different stimulation conditions were presented in randomized order. At the beginning of the experiment the stimulation probability for each finger and condition was the same. In order to obtain a comparable number of mislocalizations for each stimulated finger on the right hand the probability to stimulate a certain finger changed according to how many mislocalizations had been recorded. If the minimum number of mislocalizations was reached for a certain finger the stimulation frequency for this finger dropped to 50 %. This procedure guaranteed that those fingers were more stimulated for which not enough mislocalizations had been occurred. Participants were allowed short breaks between blocks. The duration of the experiment varied across participants, since the required minimal number of trials for the individual stimulation condition was reached after different times. The duration of the experiment ranged from 90 to maximally of 120 minutes including breaks. The experimenter remained in the room throughout the session to ensure that participants complied with the instructions and to register their responses.

Analysis

To study whether hand posture (uncrossed, crossed) and the presence of a prime stimulus to either L-D2 or L-D5 affect the profile of erroneously localized near-threshold stimuli, we determined the average profile to where near-threshold stimuli were mislocalized. Since for any stimulated finger of the right hand a minimum number of mislocalization was requested, the number of trials for each stimulated finger, as well as for the different experimental conditions was not fixed (Table 1a). Let n_{ik} be the number of how often finger i was named when stimulating finger k then $N_k = [n_{1k}, \dots, n_{4k}]$ represents the

absolute (mis)localization profile. In order to weight the mislocalization profiles for all stimulated fingers equally, the absolute numbers of mislocalizations for one stimulated finger to the other non-stimulated fingers was transformed into percentage values:

$$P_k = [p_{1k}, \dots, p_{4k}] \text{ , with } p_{ik} = \frac{n_{ik}}{\sum_{i=1}^4 n_{ik}}$$

Note, that for correctly localized stimuli the mislocalization frequency n_{kk} was set to $n_{kk} = 0$ before normalizing the response. Finally, profiles for the individual fingers were averaged across the stimulated fingers k , yielding one relative mislocalization profile P_i for each of the six experimental conditions (i.e., three prime stimuli conditions x two hand postures) (Table 1b). The relative mislocalization profile for a single condition $p_i = \frac{1}{4} \sum_{k=1}^4 p_{ik}$ indicates to where erroneously localized stimuli were preferentially assigned independently from the finger to which the near-threshold stimulus was applied. The profile reflects participants' response bias in the presence of near-threshold stimuli.

Table 1a.

Prime stimulus to L-D2, hands parallel subject 01					
	Response				Sum
Stimulation	R-D2	R-D3	R-D4	R-D5	
R-D2	30	2	3	4	9
R-D3	0	46	5	1	6
R-D4	11	6	28	8	25
R-D5	6	2	6	27	14
Sum	17	10	14	13	54

Table 1b. Correctly localized stimuli are set to 0% mislocalization

Normalized Mislocalizations in Percent					
	Response				Sum
Stimulation	R-D2	R-D3	R-D4	R-D5	
R-D2	0.0 %	2/9 = 22.2 %	3/9 = 33.3 %	4/9 = 44.5 %	100 %
R-D3	0/6 = 0.0 %	0.0 %	5/6 = 83.3 %	1/6 = 16.7 %	100 %
R-D4	11/25 = 44.0 %	6/25 = 24.0 %	0.0 %	8/25 = 32.0 %	100 %
R-D5	6/14 = 42.9 %	2/14 = 14.2 %	6/14 = 42.9 %	0.0 %	100 %
Mean	21.7 %	15.1 %	39.9 %	23.3 %	100 %

An example of the calculation of the mislocalization profiles is presented in Table 1a and 1b. In a final step of the data analysis, difference profiles between mislocalization for prime stimuli either to L-D2 or L-D5 with respect to no prime stimuli were determined both, for uncrossed and crossed hand postures.

Statistic

Mislocalization values of all the near-thresholds stimulated fingers when no prime was present were entered into a two-way analysis of variance (ANOVA) with FINGER (R-D2, R-D3, R-D4, R-D5) and POSTURE (uncrossed, crossed) as within-participant variable. To calculate mislocalizations induced by the presence of the prime stimuli, mislocalization values when there was no prime were subtracted from mislocalization values when a prime stimulus was present (i.e., L-D2 or L-D5). The resulting mislocalization values were entered into three-way repeated-measures ANOVA with FINGER (R-D2, R-D3, R-D4, R-D5), PRIME (L-D2 - no, L-D5 - no) and POSTURE (uncrossed, crossed) as within participant variable. Two-tailed paired *t*-tests were used for all planned comparisons.

Results

The ANOVA with the mislocalization profile values for the conditions in which there was no prime stimulus (i.e., right hand stimulation only) revealed a significant main effect of FINGER, $F(3,57)=7.83$, $p<.0001$, $MSE=97.89$, $\eta_p^2=.29$. As shown in Figure 2, participants significantly show a systematic mislocalization profile for all the four fingers (R-D2: $M\pm SE=24.1\pm 1.23$, $t(19)=19.63$, $p<.0001$; R-D3: $M\pm SE=27.1\pm 1.03$, $t(19)=26.43$, $p<.0001$; R-D4: $M\pm SE=29.4\pm 1.08$, $t(19)=27.16$, $p<.0001$; R-D5: $M\pm SE=19.3\pm 1.90$, $t(19)=10.17$, $p<.0001$) as documented by the comparisons against zero. Participants significantly mislocalized more on the ring finger than on the index ($t(19)=2.94$, $p=.008$), middle ($t(19)=2.18$, $p=.04$) and little ($t(19)=3.66$, $p=.002$) fingers, and more on the middle compared to the little fingers ($t(19)=2.68$, $p=.009$). Neither the main effect of POSTURE nor the interaction between POSTURE and FINGER were significant (all $p > .49$).

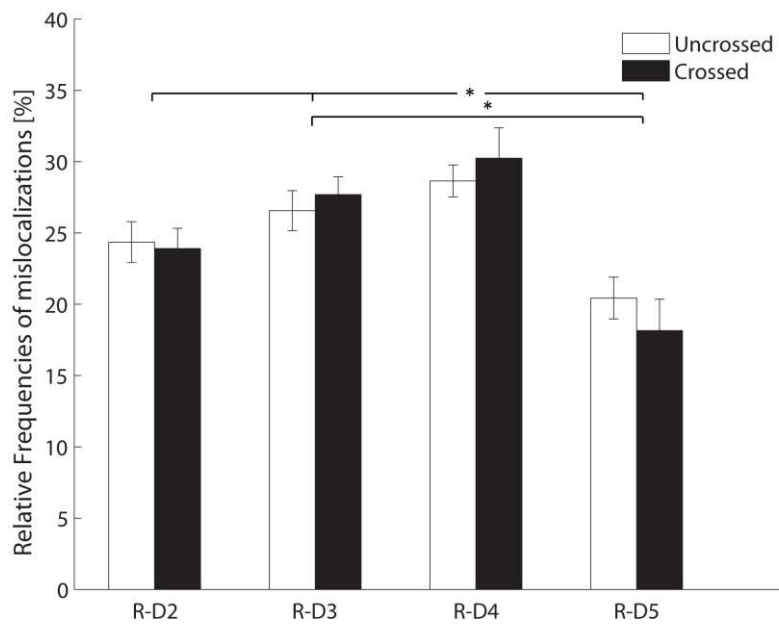


Figure 2. Mislocalization profile for the crossed (white bars) and uncrossed (black bars) conditions when only the right hand was stimulated. Error bars represent the standard error of the mean (\pm SEM) across participants. *denotes $P < 0.05$.

The ANOVA with the mislocalization profile values for the conditions in which prime stimuli were present revealed a significant main effect of FINGER, $F(3,57)=9.73$, $p<.0001$, $MSE=152.2$, $\eta_p^2=.34$. Participants made significantly more mislocalization on the index finger compared to all the other fingers (All $ps<.005$). The interaction between PRIME and FINGER was also significant, $F(3,57)=29.38$, $p<.0001$, $MSE=61.7$, $\eta_p^2=.61$. Overall, mislocalizations were maximal at the finger homologous to the primed one. Specifically, mislocalizations for R-D2 were larger when the prime stimulus was L-D2 ($M\pm SE=11.6\pm 1.79$) compared to when it was L-D5 ($M\pm SE=1.73\pm 1.51$, $t(19)=5.01$, $p<.0001$). Conversely, mislocalizations for R-D5 were larger when the prime stimulus was L-D5 ($M\pm SE=3.2\pm 1.62$) compared to when it was L-D2 ($M\pm SE=-8.4\pm 1.30$, $t(19)=-9.24$, $p<.0001$). Importantly, the two-way interaction between POSTURE and FINGER, $F(3,57)=29.38$, $p<.0001$, $MSE=61.7$, $\eta_p^2=.61$, and the three-way interaction between POSTURE, PRIME and FINGER, $F(3,57)=2.85$, $p=.04$, $MSE=35.5$, $\eta_p^2=.13$, also reached significance. The two-way interaction was caused by lower mislocalizations to R-D5 in the uncrossed ($M\pm SE=-5.5\pm 1.28$) compared to the crossed condition ($M\pm SE=0.3\pm 2.02$, $t(19)=-2.77$, $p=.01$). The three-way interaction is illustrated in Figure 3.

Figure 3A shows the mislocalization results when the prime was delivered on the left index finger (i.e., L-D2). In this condition, mislocalizations on R-D2 were larger in the uncrossed ($M \pm SE = 14.1 \pm 2.58$) compared to the crossed hands' posture ($M \pm SE = 8.13 \pm 1.70$, $t(19) = 2.32$, $p < .031$). By contrast, mislocalizations on R-D5 were larger in the crossed ($M \pm SE = -6.1 \pm 1.93$) compared to the uncrossed condition ($M \pm SE = -10.8 \pm 1.42$, $t(19) = 2.14$, $p = .045$). Note that in all cases the percentage of mislocalizations were significantly different than zero from the percentage of mislocalizations in the no-prime condition ($ps < .0003$). Figure 3B shows the mislocalization results when the prime was delivered on the left little finger (L-D5). Again, mislocalization on the (R-D5) were larger in the crossed ($M \pm SE = 6.7 \pm 2.37$) compared to the uncrossed condition ($M \pm SE = -0.3 \pm 1.50$, $t(19) = -3.07$, $p = .006$). In fact, the percentage of mislocalizations for R-D5 in the uncrossed condition were at the same level as the percentage of mislocalizations in the no-prime condition (one-sample t-test against zero: $t(19) = 1.19$, $p = .28$). In addition, there was a tendency for the two postures of a different mislocalization profile for R-D3 (crossed: $M \pm SE = -7.48 \pm 1.21$; uncrossed: $M \pm SE = -3.59 \pm 1.42$, $t(19) = 1.97$, $p = .06$).

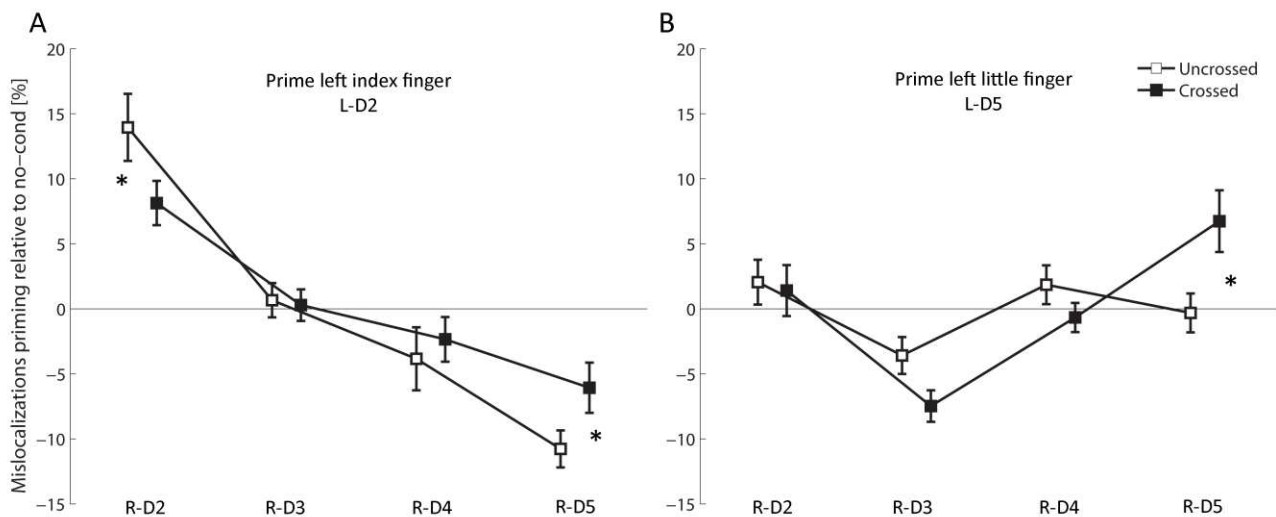


Figure 3. Mislocalization profile when the prime stimulus was on the left index finger (A) and when it was on the left little finger (B) when the hands were uncrossed (white lines) or were crossed (black lines), expressed in number of mislocalization relative the no-prime stimulation condition. A negative mislocalisation index means that there are less mislocalizations in the prime condition compared to the no-prime condition. Error bars represent the standard error of the mean ($\pm SEM$) across participants. *denotes $P < 0.05$.

In sum, while mislocalizations were maximal to the finger homologous to the prime (i.e., R-D2 when the prime was L-D2, and R-D5 when the prime was L-D5), there was a clear effect of posture. Bilateral stimulation on homologous fingers led to largest mislocalization effects when the posture brought the finger near to one another (i.e., the index fingers in the uncrossed posture; the little fingers in the crossed posture), compared to when they were far apart (i.e., the index finger in the crossed posture; the little fingers in the uncrossed posture; see Figure 1).

Discussion

In the present study, we investigated whether the skin-based representation of bilateral tactile interactions at the hands is updated as a function of hand posture (i.e., uncrossed vs. crossed hands). To this aim, we delivered near-threshold tactile stimuli to the index, middle, ring or little fingers of the right hand, and asked participants to perform a tactile localization task. We examined the distribution of mislocalizations in this task as a function of hand posture and as a function of the presence or absence of a prime stimulus delivered on the opposite hand, 200 ms prior to the target. Supra-threshold prime stimuli were delivered either to the left index (L-D2) or the left little finger (L-D5). When a prime stimulus was not present (i.e., single hand stimulation, with no bilateral tactile interaction involved) the mislocalization profile of the right hand was not affected by changes in hand posture. Mislocalizations occurred to all fingers (i.e., index, middle, ring and little fingers) and were more pronounced for the ring finger compared to the index and little fingers. However, this mislocalisation profile emerged regardless of whether the hand were uncrossed or crossed (Figure 2). The fact that the mislocalization profile was not altered when the spatial relationships between the fingers changed suggests that unilateral tactile stimuli were coded using a skin-based reference frame based on somatotopic coordinates.

An effect of posture emerged instead when bilateral tactile stimulation was present (i.e., the primed conditions). Overall, we found that the mislocalization profile that was biased towards the finger of the right hand homologous to the primed one. For instance, when the prime stimulus was delivered to the left

index finger (i.e., L-D2), mislocalizations occurred mostly towards the right index finger (i.e., R-D2). Importantly, posture modulated this effect. When the prime stimulus was delivered to the left index finger, mislocalizations to the right index finger were more pronounced when the hands were uncrossed (index fingers spatially close) compared to when the hands were crossed (index fingers far apart; Figure 3A, R-D2). This suggests a role of finger spatial-proximity in external space that was confirmed also when considering mislocalization towards the right little finger. Regardless of which finger was primed (i.e., L-D2 or L-D5), mislocalizations towards the right little finger were greater when the hands were crossed (little fingers spatially close) compared to when the hands were uncrossed (little fingers far apart; Figure 3A-B, R-D5).

These results show two distinct effects. First, a finger-specific modulation with changes in the mislocalization profile directly related to the identity of the fingers primed; second, a spatially specific modulation with changes in the mislocalization profile as a function of the physical distance between the fingers. The presence of modulatory effects that can be ascribed to both fingers identity and the spatial position between them suggests that participants concurrently adopted different reference frames during the task. The persistence of finger-specific interactions indicates that somatotopic based coordinates are used to map the tactile stimuli on the fingers. However, the modulatory effect of the mislocalization profile when the fingers were located in different position with respect to each other in external space (i.e., close or far apart), suggests that also external based coordinates were adopted when mapping tactile stimuli on the fingers.

Overall, these results indicate that when a single hand is stimulated the coding of tactile stimuli is persistently based on skin reference frames coordinates. By contrast, when both hands are stimulated tactile coding is based jointly on skin- and external-based reference frames coordinates. Therefore, the characteristics of the task, here the presence of bilateral tactile stimulation, determine the nature and the contribution of the adopted reference frames (for a review on the role of type of task in tactile coding see Tamè, Braun, Holmes, Farnè, & Pavani, 2016).

Unilateral tactile stimuli are localised using skin-based coordinates

The distribution of tactile mislocalization when no prime was present and touches were delivered to the right hand only revealed a clear prevalence of mislocalizations towards the ring finger and to some extent towards the middle finger. These results are in accordance with previous reports on tactile mislocalization at the fingers (Schweizer et al., 2000) that documented more mislocalization to the most central compared to the most lateral fingers of the hand (Schweizer et al., 2001, 2000). This higher prevalence of mislocalizations towards the ring and middle fingers probably derives from the greater uncertainty in localizing the fingers that are positioned at the centre of the hand, compared to ones that are more external such as the index and little fingers.

Interestingly, when the hands assumed a crossed posture, the pattern of results was not altered in the single hand stimulation condition. This indicates that tactile remapping was not required when only one hand was stimulated, and the somatotopic reference frame persisted despite the change in hands' posture. This is in accordance with the results of Medina and colleagues (2014), who used a modified version of the Simon effect in the tactile domain. Tactile stimuli were presented at the hands, with the arms in uncrossed or crossed postures, and responses were given using the two feet. Participants were faster in the congruent conditions, in which the stimulated hand and the response foot were on the same side, compared to the incongruent ones, in which the stimulated hand and the response foot were on different sides. Notably, this occurred regardless of the position of arms and legs position (i.e., uncrossed or crossed), leading the authors to conclude that tactile stimuli and response codes were primarily coded using an anatomical reference frames, based on the somatotopic identity (Medina, McCloskey, Coslett, & Rapp, 2014). Moreover, Röder and colleagues (2002) studying the effect of postural changes on the tactile inhibition-of-return, found that detection of a tactile stimulus at a target finger (e.g., left index finger) was slower when it was preceded (e.g., 500 ms) by a tactile stimulus on the same or an adjacent finger of the primed hand (e.g., left index or middle fingers) than on a finger of the unprimed hand. However, when participants assumed a position with the fingers of the two hands interleaved on the midline, stimulation on the finger of the other hand that spatially corresponds with the previous adjacent finger (i.e., right index finger) did not impair participants performance (Röder, Spence, & Rösler, 2002), suggesting a tactile coding based on

somatotopic rather than external reference frame coordinates. Finally, Tamè and colleagues (2011) using a double simultaneous stimulation (DSS) paradigm have shown that when the spatial relationship between the hands in the external space are changed (i.e., one hand rotated upside down) the pattern of results at the within-hand level (i.e., how much the target finger was masked by the stimulation of the adjacent finger) was not altered (Tamè et al., 2011; Tamè, Farnè, & Pavani, 2013). Instead, when the masker stimulus was delivered on the fingers of the opposite hand the finger-specific interaction between the fingers was altered. This latter effect will be discussed extensively in the next section.

Overall, we have shown that, in line with previous literature on this topic, localization of tactile stimuli delivered at the fingers of a single hand is not altered by the different hands' posture. These results suggest that under unilateral tactile stimulation an anatomical coordinate system based on somatotopy is consistently used to locate touches at the hands.

Bilateral tactile stimuli are localised using concurrent anatomical and external coordinates

When a prime stimulus was delivered on the left hand and targets occurred on the right hand – hence, bilateral stimulation occurred – the distribution of mislocalization responses was modulated by hands posture. A clear effect of physical proximity between the primed fingers (i.e., L-D2 or L-D5) and the homologous tested fingers of the right hand (i.e., R-D2 or R-D5) emerged. Our results are in accordance with previous reports, using different approaches (e.g., Temporal Order Judgment, TOJ; Double Simultaneous Stimulation, DSS) that have shown that altering the spatial relations between the hands in external space significantly affects how stimuli on the two sides of the body interact (Azañón & Soto-Faraco, 2008; Heed & Azañón, 2014; Schicke & Röder, 2006; Tamè et al., 2011).

The timing between the prime and target stimuli that we have adopted may have played an important role in determining these results. Throughout our study, prime stimuli were delivered 200 ms before the target, a temporal window that it is at the limit of the estimated time required for tactile-remapping to be completed (Azañón & Soto-Faraco, 2008; Overvliet, Azañón, & Soto-Faraco, 2011). The temporal time-course of tactile remapping has been investigated by several studies (e.g., Yamamoto and Kitazawa 2001;

Kitazawa 2002; Azañón and Soto-Faraco 2008). The beginning of this process is assumed to occur between 100-140 ms from tactile stimulus onset, as shown by attentional modulatory effects of the somatosensory evoked potentials (SEPs) as a function of limb posture at this timing (Eimer, Cockburn, Smedley, & Driver, 2001; Heed & Röder, 2010). The end of this process appears to be fully achieved between 190-300 ms from tactile stimulus onset (Kitazawa, 2002; Overvliet et al., 2011; Yamamoto & Kitazawa, 2001). In particular, Overvliet and colleagues (2011), in a series of experiments, examined the time-course of tactile remapping by studying saccadic responses to tactile stimuli delivered at the hands. They observed that participants were postponing the saccades until the remapping was completed. The ending time for the remapping was therefore estimated in about 190 ms at the net of the time needed to accomplish the motor planning and execution as estimated from monkey research data (Overvliet et al., 2011). Therefore, the time in which we present our prime stimulus (200 ms prior the near-threshold stimulus) is likely to fall on the border at which the tactile remapping is completed. Compatible with our results, Braun and colleagues (2005) have shown stronger finger-specific modulatory effects on the mislocalization profile for stimuli delivered on one hand, when a prime stimulus was delivered 200 ms prior to the target compared to when the prime was presented 500 ms prior to the target (Braun et al., 2005). Indeed, in the latter case (i.e., 500 ms) the greater time lag between the two stimuli is certainly sufficient to allow tactile remapping to be completed.

Interactions between the two sides of the body while the position of the hands is altered has been largely investigated using a temporal order judgment (TOJ) paradigms with the aim of characterising the reference frames in which the location of touch is coded (for a review see Heed and Azañón 2014). However, in the present work we used a different paradigm, namely the mislocalization task, which is thought to reflect low level processing of the tactile representation, as shown in several previous reports (Braun et al., 2011, 2005, Schweizer et al., 2001, 2000). Intriguingly, the finger-specific effect of the left hand prime-stimulus application on the distribution of mislocalizations for near-threshold stimuli delivered to the right hand is maintained, though attenuated by the postural modulation. This indicates that postural remapping is required only when both hands are tactilely stimulated with the presence of concurrent influence of somatotopic and non-somatotopic bodily representations, namely based on anatomical and

external spatial coordinates. Previous behavioural studies have shown that both anatomical and external coordinates can be jointly used in some circumstances. In a behavioural investigation using a DSS paradigm, Tamè and colleagues (2011) asked participants to detect tactile stimuli at a pre-defined target finger that was stimulated alone or concurrently with another finger, either on the same or the opposite hand. For instance, when the target finger was the right index, the concurrent stimulation was presented to the middle finger of the same hand, or alternatively to the index or middle finger of the other hand. Results showed interference effects of the concurrent tactile stimulation both within and between hands. Interference was comparable when the distracting stimulation was on the non-homologous finger of the same hand, and when it was on the non-homologous finger of the opposite hand with respect to the target. By contrast, when the distracting stimulus was applied to the homologous finger of the opposite hand, the amount of interference was considerably reduced. Using this paradigm, Tamè et al. also examined the effects of hand posture, asking participants to perform the task either with both hands palm down, or with one hand palm up. With the latter posture manipulation, DSS interference remained unchanged within-hands, but became less consistent between hands. Indeed, when concurrent stimulation was delivered between-hands no significant interference was observed in terms of change in accuracy for either homologous or non-homologous finger stimulation. This posture-dependent modulation indicates a role for non-somatotopic spatial representations for touch, which takes into account the overall structure of the body as well as its layout in space (Tamè et al., 2011).

On the same line, neuroimaging studies in humans support the notion of the concurrent presence of the anatomical and external coordinates to localise tactile stimuli on the body. For instance, Heed and Röder (2010) measured electroencephalography responses while participants performed a tactile task with their uncrossed or crossed hands near the feet. Participants were instructed to attend, in different blocks, a particular limb while receiving a series of tactile stimuli on all the limbs (i.e., left and right hands and feet). The task consisted in reporting deviants' stimuli on the attended limb. When participants attended a certain foot (e.g., left foot) the evoked response potentials (ERPs) showed a greater amplitude, in the time range of 100-140 ms post-stimulus, for the left compared to the right hand both when the left hand was

positioned far and near the attended foot, in this example the left foot. Therefore, this result reflects the presence of the response for both the spatial distance between the attended and stimulated locations. The authors interpreted this data as evidence that both the anatomical and external reference frames were affecting the ERPs responses (Heed & Röder, 2010). Other studies recorded brain oscillations, while participants performed a tactile localization task, and came to the same conclusion by showing the presence of concurrent brain activity that can be ascribed to anatomical and external spatial coding (Buchholz, Jensen, & Medendorp, 2011, 2013).

Altogether, these findings suggest that anatomical and external space based representations may coexist, possibly with different relative weightings as a function of tasks demands. In this respect, it has been shown that the use of different coordinates is weighted with respect to several factors, such as visual information (e.g., Kappers 2004; Ley et al. 2013), movement (e.g., Pritchett et al. 2012) and task context (Pavani, Farnè, & Làdavas, 2003). In our study, the type of stimulation applied, namely unilateral or bilateral determined the task context. It is possible that the mere presence of bilateral tactile stimuli on homologous fingers is interfering with the remapping of the sensory information in an external coordinate system. In this regard, Badde and colleagues (2015) have shown that in a dual task, irrelevant context of the second task can affect the way in which the anatomical and external coordinates are weighted to solve the first tactile localization task (Badde, Röder, & Heed, 2015). The same authors recently proposed a probabilistic model that can account for the tactile localization errors in the uncrossed and crossed hands posture by weighting the integration of the anatomical and external coordinates (Badde, Heed, & Röder, 2015). They tested participants' responses in several tactile localization tasks comparing different models. They found that the best fit was obtained by an integration model in which both reference frames, namely based on anatomical and external coordinates, were used with different weights to localise tactile stimuli in both crossed and uncrossed postures (Badde, Heed, et al., 2015).

Conclusion

The current results show that localization of tactile stimuli delivered on a single hand is coded using a skin-based reference frame even when position of the hands is changed and the physical distance between the fingers of the two hands is altered. Instead, localization of tactile stimuli on one hand, when prime stimuli are concurrently delivered on the opposite hand, determines the use of concurrent skin-based and external reference frames coordinates, at least when the time between the tactile stimuli is up to 200 ms. The use of one or more reference frames is affected by the specific context of the task, which in this case is represented by the unilateral or bilateral tactile stimulation. We suggest that the prime stimuli of one hand are interfering with the tactile remapping of the stimuli that have to be localised on the other hand. Therefore, tactile localization in the context of a mislocalization profile primarily occurs through skin-based reference frames when stimuli are unilateral, whereas relies on the concurrent presence of skin-based and external reference frames coordinates when both hands are stimulated. Although under bilateral tactile stimulation the remapping is taking place, triggered by the changes in hands' posture, fingers identity is maintained. This occurs most likely because of the need to maintain the fingers-identity, a relevant property functional to bimanual actions. Indeed, it is likely adaptive to keep the same hand-representation regardless of hands' posture.

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Figures Caption

Figure 1. Illustration of the stimulation devices and the hand's posture across conditions. The blanket covering the hands during the experiment, and the numbers assigned to each finger for the response are not shown. (A) Hands uncrossed. (B) Hands crossed. Note that the spatial relationship between the fingers receiving the prime stimuli on the left hand and fingers receiving the near-threshold targets on the right hand change as a function of posture. Index fingers are close to one another in the uncrossed posture, but farther apart in the crossed posture; whereas little fingers are farther apart in the uncrossed posture but close to one another in the crossed posture.

Figure 2. Mislocalization profile for the uncrossed (white bars) and crossed (black bars) conditions when no prime was present and only the right hand was stimulated. Error bars represent the standard error of the mean (\pm SEM) across participants.

Figure 3. Mislocalization profile when the prime stimulus was on the left index finger (A) and when it was on the left little finger (B) when the hands were uncrossed (white lines) or were crossed (black lines), expressed in number of mislocalization relative the no-prime stimulation condition. A negative mislocalisation index means that there are less mislocalizations in the prime condition compared to the no-prime condition. Error bars represent the standard error of the mean (\pm SEM) across participants.

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