Journal of Experimental Psychology:
Human Perception and Performance
2016, Vol. 42, No. 9, 1320–1331

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0096-1523/16/$12.00 http://dx.doi.org/10.1037/xhp0000206

Does the Crossed-Limb Deficit Affect the Uncrossed Portions of Limbs?

Elena Azañón and Svetla Radulova
Birkbeck, University of London

Patrick Haggard
University College London

Matthew R. Longo
Birkbeck, University of London

When locating touch, we remap its location from skin-based to external coordinates as a function of body posture. While remapping is thought to occur whenever there is tactile input, research has focused on a special case, the crossed-hands deficit, where tactile localization is impaired when the limbs are crossed compared with uncrossed. To date, these studies have always stimulated portions of the limbs that are crossed, such as a finger of each hand. It is therefore unknown whether the deficit induced by arm crossing is specific to the crossed portion of the limb or affects the limb as a whole. In Experiments 1 and 2, we stimulated the shoulders and elbows and found that tactile localization, measured with temporal order judgments, was unaffected by crossing the forearms. In Experiment 3, a crossed-limbs deficit was observed for touches on a single skin location when that location was distal—but not proximal—to the crossing point of the arms. In Experiment 4, we found a similar crossed-limbs deficit irrespective of how far distally to the crossing point touch was applied. Together, these results demonstrate that crossing the limbs affects tactile perception only distal to the point of crossing. The process of remapping tactile events does not take into account the end-point location of the limb, but an extremely precise metric description of the touch relative to the configuration of both arms.

Keywords: remapping, tactile processing, crossed-hands deficit, temporal order judgment, spatial reference frame

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As we move and explore the world that surrounds us, our limbs and bodies come into contact with innumerable objects. Each momentary contact evokes cutaneous activity that conveys information about the location of the stimulus on the body surface in a somatotopic (or skin-based) reference frame, independent of body posture (Penfield & Rasmussen, 1950). Each new movement, however, changes the relation between the location of a touch on the skin surface and the location of that touch in external space (Driver & Spence, 1998; Yamamoto & Kitazawa, 2001a). As a consequence, the brain must take current posture into account when calculating the location of touch (Azañón & Soto-Faraco, 2008; Azañón, Stenner, Cardini, & Haggard, 2015; Heed, Buchholz, Engel, & Röder, 2015; Heed & Röder, 2010), and compute tactile coordinates within a reference frame that is shared with other sensory modalities (Röder, Rösler, & Spence, 2004).

Somatotopic and external reference frames for touch are easily dissociated by simply moving the limbs. Indeed, the literature contains many curious demonstrations of tactile mislocalization that arise from incongruence between the somatotopic and external spatial coordinates of tactile stimuli, such as in the Japanese and the Aristotle illusions (e.g., Benedetti, 1985, 1988; Zampini, Harris, & Spence, 2005). One phenomenon that has raised particular interest is the crossed-hands deficit, which is typically studied in bimanual tactile temporal order judgment (TOJ) tasks (see Heed & Azañón, 2014, for a review). When the hands are crossed, a touch on the right hand (in somatotopic coordinates) is located on the left hemispace (in external space), creating an incongruence between reference frames (Shore, Spry, & Spence, 2002).

In most studies of the crossed-hands deficit, participants judge the order of two tactile stimuli applied in rapid succession to different hands while the arms are crossed or uncrossed (Heed & Azañón, 2014). Logically, the posture of the limbs is irrelevant to this task, and participants could in principle solve the task based on somatotopic coordinates alone. Posture of the limbs nevertheless has a massive effect on performance, indicating that external coordinates are in fact computed automatically: when the arms are uncrossed, participants correctly report the order of the two touches, but often misreport their order when the arms are crossed, even when the interval between the touches are twice or three times longer than with the arms uncrossed (Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001a).

This article was published Online First March 17, 2016.

Elena Azañón and Svetla Radulova, Department of Psychological Sciences, Birkbeck, University of London; Patrick Haggard, Institute of Cognitive Neuroscience, University College London; and Matthew R. Longo, Department of Psychological Sciences, Birkbeck, University of London.

Supported by a European Union Seventh Framework Programme (Grant FP7-PEOPLE-2011-IEF) under Agreement No. 302277, by the European Research Council (Grant ERC-2013-StG-336050), an Economic and Social Research Council Professorial Fellowship, and by a European Research Council Advanced Grant (HUMVOL). We thank Max-Philipp Stenner and three anonymous reviewers for their helpful comments on previous drafts of this article.

Correspondence concerning this article should be addressed to Elena Azañón, Department of Psychological Sciences, Birkbeck, University of London, London, WC1E 7HX, England. E-mail: eazanyon@gmail.com

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The high consistency of the crossed-hands deficit across individuals has proven particularly valuable for the investigation of tactile remapping. Consequently, many studies of remapping have compared conditions in which the limbs are crossed versus uncrossed (Heed & Azañón, 2014; Shore et al., 2002; Yamamoto & Kitazawa, 2001a). To date, crossed TOJ studies have always stimulated portions of the limbs that are crossed, such as a finger of each hand. It is, therefore, unknown whether the deficit induced by arm crossing in TOJ is specific to the crossed portion of the limb or affects the limb as a whole, and whether this affectation is gradual or not.

There is evidence that muscles work in functional groups, rather than individually, to achieve actions (d'Avella, Saltiel, & Bizzi, 2003; Lemon, 1988; see Cheung et al., 2009, for evidence in humans). This seems to produce considerable overlap in the cortical territories of adjacent body parts in the primary motor cortex (Rathelot & Strick, 2006). It is therefore plausible that tactile spatial localization, which is fundamental for perception during action (Brozzoli, Cardinali, Pavani, & Farnè, 2010; Dijkerman & de Haan, 2007; Hermosillo, Ritterband-Rosenbaum, & van Donkelaar, 2011), is influenced by functional units encompassing the entire limb (Reed, McGoldrick, Shackelford, & Fidopiastis, 2004). This is supported, for instance, by the presence of corticomotoneuronal cells for hand muscles at sites where stimulation produces shoulder movements (Rathelot & Strick, 2006). These two muscle groups have to work in a highly coordinated way to produce stable movements and postures, such as stabilizing the arm to execute precision finger movements (Lemon, 1988; Rathelot & Strick, 2006). Furthermore, some neurons in the monkey superior parietal cortex react to complex body postures involving the combination of tactile input and specific configurations of joints that could include the entire limb (Sakata, Takaoka, Kawarasaki, & Shibutani, 1973). Thus, it is plausible that postural/proprioceptive information about the crossed configuration of the limbs could affect tactile localization, irrespective of whether touch is applied on the crossed or on the uncrossed portion of the limb. This is depicted by the factor *spatial extent of the deficit* in Figure 1.

Furthermore, larger crossing effects have been found when both hands and fingers are crossed and smaller when only hands or fingers lay in contralateral hemifield (Heed, Backhaus, & Röder, 2012). This suggests that separate representations of the external positions of a finger and of a hand are integrated to localize a tactile stimulus (Badde, Röder, & Heed, 2014; Heed et al., 2012). Note that this idea is plausible because coding the position of a finger, for instance, requires the combination of proprioceptive information from the entire musculoskeletal chain of the limb (Heed et al., 2012; Longo, Azañón, & Haggard, 2010). Under a similar integrative model, we could expect differences in the degree that touch is influenced by posture of the limbs, with stronger modulations for skin sites that are far from the crossed point of the limbs. This is so, because distal areas from the crossing point would contain more crossed body parts contributing to the posture of the touched area. Similarly, a proximodistal gradient could also be found if tactile localization in a particular body area is influenced by its manipulative function. One could hypothesize that the greater motility of the hands, and their large manipulative role, could bias tactile location on the more distal locations of the limb toward an external reference frame. In contrast, for more proximal locations of the arm, like the forearm, it is more likely that tactile stimuli are less coded in external reference frames, and more in terms of somatosensory information. This is depicted by the factor *spatial gradient of the deficit* in Figure 1.

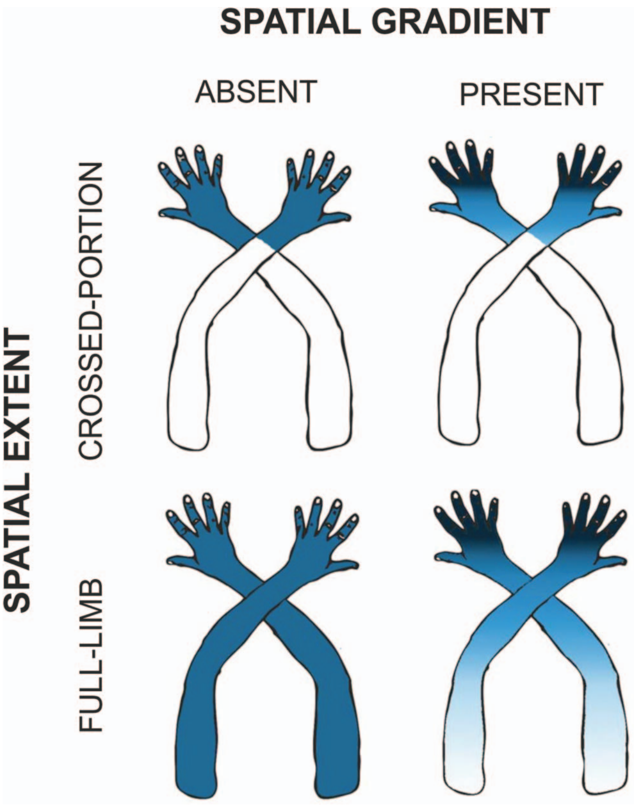

Figure 1. A 2 × 2 factorial model of the effects of limb crossing on tactile localization. In blue (dark) are areas that would be affected by crossing the arms in a tactile temporal order judgment task. The crossing deficit could affect the crossed portion of the limb or the limb as a whole (as depicted by the dimension spatial extent of the deficit). Additionally, the deficit could be equal or differ across distances to the crossing point, as denoted by the factor spatial gradient absent and present, respectively. The strength of the shadow indicates the degree of affectation, with larger deficit in darker colors. See the online article for the color version of this figure.

This study investigated whether the crossed-limb deficit affects the uncrossed portions of limbs, and whether this affectation is gradual or not. By measuring the localization of touch applied to locations that are not crossed, we can test the extent to which the end-point location of the arm affects tactile localization performance on different skin regions. In four experiments, participants crossed or uncrossed their hands and were asked to report the order of two touches applied to different sections of their limbs, including the shoulders, elbows, forearms, hands, and fingers. If the arm is treated as a single functional unit, or posture information about the entire limb is used to estimate the location of touch, we should observe deficits in localization performance when the limbs are crossed, even in locations of the limbs that are uncrossed. If, on the other hand, the deficit reflects a spatially fine-grained modulation of processing specifically on the crossed portion of the limbs, then performance should only be affected when touch is applied to the crossed portion of the limbs. These two outcomes are depicted in

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Figure 1 under the dimension "spatial extent" of the deficit. Furthermore, the degree of affectation when crossing the hands could be constant or gradual and differ across distances from the crossing point, as depicted by the dimension "spatial gradient" of the deficit in Figure 1. It might be influenced by factors such as closeness to end-point location, or the role that different body parts have for action.

Experiment 1

In Experiment 1, we tested whether crossing the arms had an effect on tactile localization on skin areas not crossed. To measure this, we tested participants in a TOJ task with arms crossed and uncrossed, and varied the skin sites where touch was applied. Specifically, tactile stimuli were presented to the fingers or to the shoulders in separate blocks, and participants responded with the stimulated body area.

Method

Participants. Eighteen (11 female) healthy volunteers participated ($M_{\text{age}} = 34$ years, $SD = 8.5$). All participants reported that they were right-handed and had normal tactile sensitivity. All participants were naive to the purpose of the experiment and gave written informed consent to participate. The study was conducted in accordance with the Declaration of Helsinki and was approved by the local ethics committee.

Procedure. Two successive tactile stimuli were presented at 14 different stimulus onset asynchronies (SOAs): −960, −480, −240, −120, −60, −30, −10, 10, 30, 60, 120, 240, 480, and 960 ms (negative values indicate that the first stimulus was presented to the left hand). Tactile stimuli consisted of a 10-ms stimulus at suprathreshold intensity delivered through 9-mm diameter solenoid tappers (rounded tip, 0.2-mm skin contact; M&E Solve, Kent, England). In the fingers condition, touch was presented to the dorsal surface of the middle phalanx of each ring finger. In the shoulders condition, touch was presented to the anterior fibers of the deltoid muscle. Participants were asked to perform the task either with their arms in a parallel posture or with the arms crossed over the body midline.

Each participant's task was to move without time restriction the finger (or shoulder) that he or she perceived to have been stimulated first. As in previous experiments, the response button and the tactile stimulator were close in external space. With this manipulation, we wanted to reduce compatibility effects between the location of the body part that received the stimulus and the location of the body part used to respond (Medina, McCloskey, Coslett, & Rapp, 2014). Each condition was presented twice in blocks of 140 trials (which corresponded to 20 trials per SOA and condition) using an ABCD−ABCD design, with the order of the first and the last four blocks independently randomized for each subject. Prior to each block, participants performed six practice trials. The experimenter entered responses manually using the keyboard. White noise was presented continuously through headphones to mask any sound made by the tactile stimulation.

Analyses. TOJ performance was quantified using probit analysis of the data (Badde, Heed, & Röder, 2014; Heed et al., 2012; Shore et al., 2002). Mean percentages of "right first responses" were first calculated for each participant, condition, and SOA. These proportions were then transformed into their standardized *z*-score equivalents and then linearly regressed onto the SOA values (in seconds) for each participant and condition. Because the longest SOAs showed evidence of a ceiling effect in both postures, only the intermediate eight points were used (−120 to 120 ms; see Badde, Röder, & Heed, 2015; Heed et al., 2012; Spence, Shore, & Klein, 2001). SOAs whose proportions of right hand first responses were 0 or 1 were corrected using Laplace's rule of succession formula (Zabell, 1989; which calculates the probability that the next observation will be a success. The number of successes plus 1 is divided by the number of observations plus 2). The slope of each individual line was used as a measure of performance, with steeper slopes (and larger slope values) indicating better performance. Individual slopes were submitted to an analysis of variance (ANOVA) with posture (crossed, uncrossed) and stimuli site (fingers, shoulders) as within-subject factors. This was followed by planned two-tailed *t* test comparisons across conditions.

Results and Discussion

As shown in Figure 2A, performance was impaired in the crossed compared to the uncrossed arm posture when touches were applied to the fingers ($M_{\text{slope crossed}} = 1.76$, $SD = 2.94$; $M_{\text{slope uncrossed}} = 9.83$, $SD = 3.81$). This replicated the well-established crossed-hands deficit for touch on the fingers (Shore et al., 2002; Yamamoto & Kitazawa, 2001a). Posture of the limbs, however, did not affect tactile localization performance at the shoulders ($M_{\text{slope crossed}} = 10.25$, $SD = 4.28$; $M_{\text{slope uncrossed}} = 9.70$, $SD = 3.53$). There was a significant two-way interaction, $F(1, 17) = 34.01$, $p < .001$, mean square error (MSE) = 334, $\eta_p^2 = .67$. The two main effects of stimulus site, $F(1, 17) = 33.40$, $p < .001$, $\eta_p^2 = .66$, and posture, $F(1, 17) = 33.45$, $p < .001$, $\eta_p^2 = .66$, were also significant, though both effects were driven by the drop in TOJ performance observed at the fingers, when the limbs were crossed. Performance was similar across touches on the shoulders and fingers in the uncrossed posture, $t(17) = .22$, $p = .82$, $d_z = .05$. This suggests that the different pattern of results observed between shoulders and fingers was not caused by differences in the ability to perform TOJs in different skin sites. Planned two-tailed *t* test confirmed the crossing effect for hands, $t(17) = 6.08$, $p < .001$, $d_z = 1.43$, but not for shoulders, $t(17) = 1.31$, $p = .21$, $d_z = .31$. Previous reports have found sex differences in the crossed-hands deficit (Cadieux, Barnett-Cowan, & Shore, 2010). We did not find any significant interaction or main effect with the sex of the participant in this or any of the following experiments ($ps > .16$).

The results of Experiment 1 showed that crossing the arms did not affect localization of touches on the uncrossed part of the limb. This suggests that crossing the limbs only affects skin areas distal to the crossed point.

Experiment 2

One possible explanation for the observed lack of crossing effects at the shoulders is that touch is far from the end-point location of the limb. This distance might prevent any modulation of touch at the shoulders by the location of the finger tips. Another possibility is that shoulders and arms are represented as separate body parts or encoded as belonging to separate functional units by

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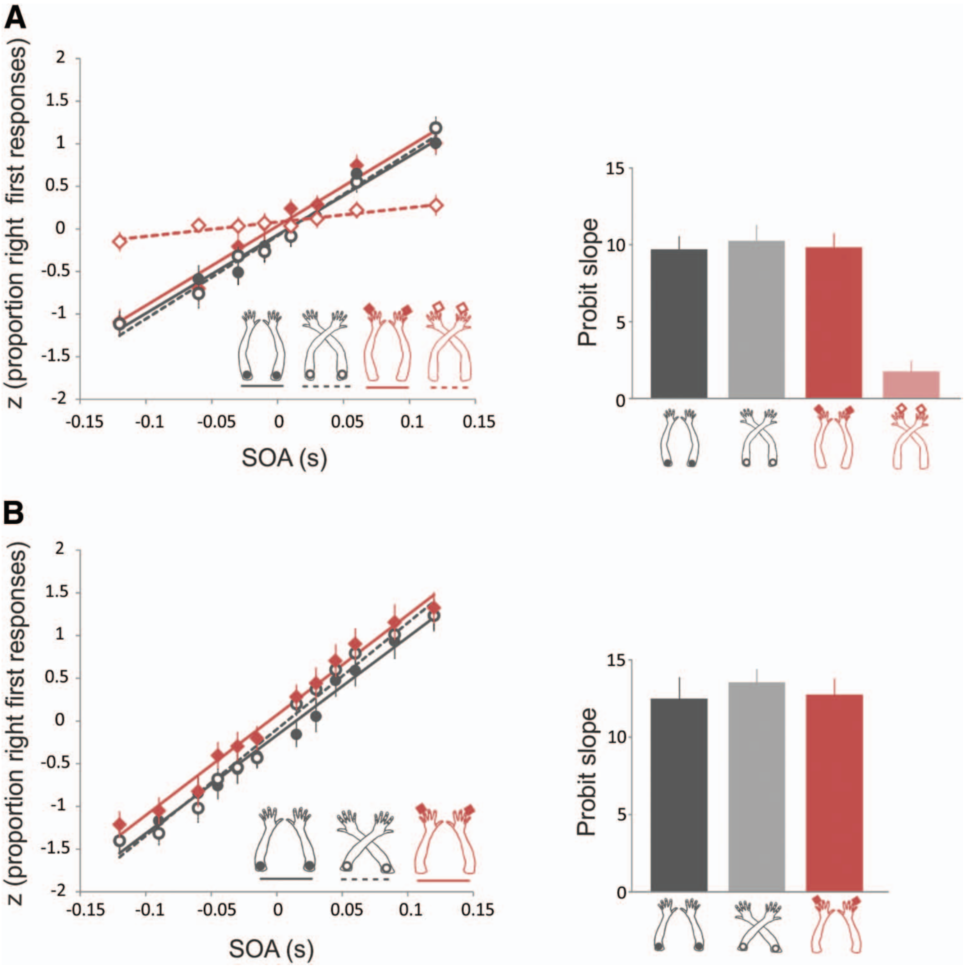

Figure 2. Results of Experiments 1–2. Data of Experiment 1 (A). Left panel: Standardized *z*-score equivalences of the mean proportions of right first responses and best-fitting linear regression lines for the uncrossed (solid lines) and crossed postures (dotted lines) when touch was on the shoulders (in gray, circles) or when touch was on the ring fingers (in red, diamonds). Right panel: Mean probit slopes across subjects. Larger slope values indicate better performance. Data of Experiment 2 (B). Touch was presented just above the elbows (gray, circles) or on the ring fingers (only in the uncrossed posture; red, diamonds). Left panel: Standardized *z* scores and best-fitting linear regression lines. Right panel: Mean probit slopes across subjects. Error bars depict the *SEM*. See the online article for the color version of this figure.

the brain. For example, the shoulder might be coded as being part of the torso, rather than part of the arm. If either of these explanations were correct, then proprioceptive input derived from the distal part of the arm would not necessarily influence tactile localization at the shoulders. In Experiment 2, we excluded this possibility by testing a more distal part, with stimuli placed at the distal section of the upper arm.

Method

Participants. Twelve (eight female) new participants from the same pool as the previous experiment ($M_{\text{age}} = 23$ years, $SD = 3.4$) were tested. All participants reported that they were right-handed and had normal tactile sensitivity.

Procedure. The procedure and analyses were similar to those of Experiment 1, except that now two solenoids were attached to the distal section of the upper arm (on the dorsal part and close to the elbow) rather than to the shoulders. This area was always kept uncrossed, while the configuration of the lower forearm could be crossed or uncrossed. To maximize the amount of data collected in the most informative conditions, and because we were mainly interested in a modulation at the elbows, we did not use a full factorial design that included the crossed and uncrossed TOJ conditions at the fingers, as we did in Experiment 1. We, nonetheless, included the uncrossed TOJ at the fingers, as a measure of standard tactile TOJ performance.

The number of short SOAs was increased (±15, ±30, ±45, ±60, ±90, ±120, and ±240 ms) to allow for a better sampling of the relevant intervals. In three separate conditions (uncrossed-elbows, crossed-elbows, and uncrossed-fingers), participants were instructed to judge which stimuli came first with no time restric-

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tion, by depressing a response button placed beneath the stimulated body area. When use of a response button was not possible due to biomechanical constraints, the experimenter introduced the responses manually using the keyboard. Participants completed two blocks in each condition (order counterbalanced) using an ABC−ABC design (where the first and the last three blocks were independently randomized per each subject). Twenty trials per SOA were tested, for a total of 840 trials, excluding practice.

Results and Discussion

Tactile localization performance was similar in the three conditions, regardless of posture or stimulated skin area (see Figure 2B). This was confirmed by a one-way, repeated-measures ANOVA, $F(2, 22) = 1.84$, $p = .18$, $MSE = 3.7$, $\eta_p^2 = .14$. Thus, the crossed position of the arm did not affect tactile localization at the elbows. Performance in this condition was indeed numerically better than any of the other two (uncrossed) conditions. Performance at the elbows and fingers was comparable (comparison uncrossed-elbows vs. uncrossed-fingers: $t(11) < 1$), confirming that the lack of effect was not driven by poor TOJ performance at the elbows.

The results of Experiment 2 are consistent with those observed in Experiment 1 and suggest that the process of tactile localization is not influenced by the entire configuration of the limb in space or by the end-point location of the limb. Rather, the results suggest the integration of precise metric information about the relative location of the point of limb crossing and the point of stimulation.

Experiment 3

In Experiment 3, we tested the possibility that crossing effects only arise on skin areas that could potentially be crossed. The underlying idea is that the entire configuration of the limb (or end-point location) might only be functionally relevant for tactile localization in body areas with high mobility, such as the forearms and hands. That is, for areas that could easily cross the midline. In Experiment 3, we applied two tactile taps to the middle part of the forearms. Participants' arms were always crossed, with the crossing point above the wrists or below the elbows. Thus, taps (fixed on the same skin area across conditions) could be applied to the crossed or uncrossed sections of the arms, depending on the crossing point at which the arms crossed each other. If tactile information, at the time of remapping, takes into account postural information relative to the entire limb as a functional unit, we would expect to find similar localization performance regardless of the actual position of the taps with respect to the crossed portion of the limbs. On the contrary, if tactile remapping relies on precise metric information about the relative posture of the limbs with respect to touch, we would expect to find a larger crossed deficit when the taps are on the crossed section of the forearms.

Method

Participants. Sixteen (eight female) new participants ($M_{\text{age}} = 22$ years, $SD = 3.9$) were tested in Experiment 3. All participants reported that they were right-handed and had normal tactile sensitivity. Fourteen (seven female) participants ($M_{\text{age}} = 21$ years, $SD = 3.0$) performed a second part 1−3 months later.

Procedure. Participants were tested in two crossed conditions in which the arms were crossed above the wrist or below the elbows, with stimuli fixed on the middle of each forearm (dorsal part; see Figure 3A). Distance between the taps was set to 12 cm. We used the same SOAs as in Experiment 2 (±15, ±30, ±45, ±60, ±90, ±120, and ±240 ms) and conducted the same type of analyses. Participants performed two blocks in each condition with an ABAB design, for a total of 560 trials, excluding practice. The order of the first condition was counterbalanced across participants. Results of a pilot test suggested differences in the TOJ crossed-deficit, depending on whether participants' arms were or were not in contact at the crossing point. Thus, half the subjects performed the two crossed conditions with physical contact between the arms (at the crossing point) and half the subject without. Physical contact was avoided by using a bridge over the lower arm (leaving the upper middle arm free of contact) and the vertical distance between the forearms was about 2 cm.

Results and Discussion

A mixed repeated-measures ANOVA with the within-subject factor of portion (crossed portion, uncrossed portion) and the between-subjects factor of physical contact (contact, no contact) returned a significant main effect of portion, $F(1, 14) = 11.11$, $p = .005$, $MSE = 236$, $\eta_p^2 = .44$, and of physical contact, $F(1, 14) = 15.67$, $p = .001$, $MSE = 255$, $\eta_p^2 = .53$. Thus, overall, participants showed a clear crossed deficit when the stimuli was presented to the crossed portion of the limb compared to the uncrossed portion ($M_{\text{slope uncrossed}} = 13.07$, $SD = 2.87$; $M_{\text{slope crossed}} = 7.64$, $SD = 7.24$), $t(15) = 2.88$, $p = .01$, $d_z = .72$ (see Figure 3B). Furthermore, participants whose hands were touching each other performed worst overall. Nonetheless, both effects were driven by a significant two-way interaction, $F(1, 14) = 6.06$, $p = .027$, $MSE = 129$, $\eta_p^2 = .30$. That is, participants who performed the task with physical contact between the arms ($n = 8$) showed a crossed deficit (i.e., uncrossed minus crossed performance; $M_{\text{crossed deficit}} = 9.45$, $SD = 8.75$), $t(7) = 3.05$, $p = .018$, $d_z = 1.07$, whereas the deficit was not significant in participants whose arms did not contact each other ($n = 8$; $M_{\text{crossed deficit}} = 1.42$, $SD = 2.91$), $t(7) = 1.38$, $p = .21$, $d_z = .49$.

To better understand the effect of physical contact, we invited the same participants to perform the two crossed conditions again (1−3 months later). Participants who performed the two conditions with physical contact of the arms in the first session conducted the task without contact, and vice versa for the other group of participants. Two participants were unable to return (remaining sample: $n = 14$, seven female; $M_{\text{age}} = 21$ years, $SD = 3.0$). We first analyzed the overall data of this session, independent of the variable physical contact, and found again a crossed deficit when the stimuli were presented to the crossed portion of the limb ($M_{\text{slope}} = 9.39$, $SD = 4.25$) compared to the uncrossed portion ($M_{\text{slope}} = 13.24$, $SD = 3.04$), $t(13) = 3.94$, $p < .002$, $d_z = 1.05$. As shown in Figure 3C, a 2 × 2 repeated-measures ANOVA with the within-subject factors of portion and physical contact showed both a main effect of portion, $F(1, 13) = 9.78$, $p = .008$, $MSE = 260$, $\eta_p^2 = .43$, and a main effect of physical contact, $F(1, 13) = 17.25$, $p = .001$, $MSE = 146$, $\eta_p^2 = .57$. Interestingly, the two-way interaction was significant, $F(1, 13) = 5.28$, $p = .039$, $MSE = 36$, $\eta_p^2 = .29$. Post hoc t test (Bonferroni-corrected threshold at .013 for four comparisons) indicated that the crossed deficit was larger when the arms were in contact ($M_{\text{crossed deficit}} = 5.91$, $SD = 7.20$),

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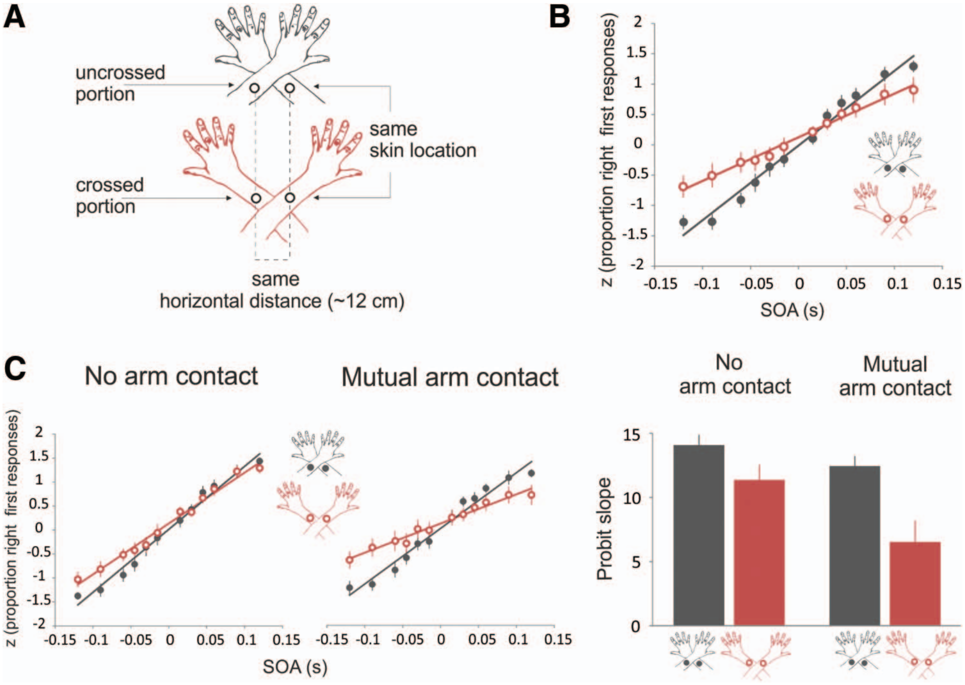

Figure 3. Setup and results of Experiment 3. Aerial view of the setup used in Experiment 3 (A). The two touches were presented on the same skin locations. The crossed posture varied, so the two touches could be on the crossed or on the uncrossed portion of the limbs. The external (horizontal) distance between touches was kept constant at 12 cm. Standardized *z*-score equivalences of the mean proportions ($n = 16$, first session) of right arm first responses and best-fitting linear regression lines for the condition where touch is presented to the uncrossed portion of the limb (black lines, filled circles) and the condition where touch is presented to the crossed portion (red lines, open circles) (B). Participants ($n = 14$) who performed the two conditions with arms crossed with mutual contact in the first session conducted the task with arms crossed but avoiding contact in a second session, and vice versa for the rest of participants (C). Left panel: Standardized *z* scores in each condition. Right panel: Mean probit slopes across subjects. Error bars depict the *SEM*. See the online article for the color version of this figure.

$t(13) = 3.07$, $p = .009$, $d_z = .82$, than when they were not ($M_{\text{crossed deficit}} = 2.70$, $SD = 3.85$), $t(13) = 2.63$, $p = .021$, $d_z = .70$. Furthermore, the benefit of noncontact (mutual vs. nonmutual contact) was mainly observed in conditions where the touches were applied to the crossed portion of the limbs (crossed portion: $M = 4.84$, $SD = 5.01$, $t(13) = 3.61$, $p = .003$, $d_z = .97$; uncrossed portion: $M = 1.63$, $SD = 2.34$, $t(13) = 2.60$, $p = .022$, $d_z = .70$).

The same pattern of results was obtained when the proportion of correct responses over all SOAs was calculated (i.e., accuracy; see Cadieux, Barnett-Cowan, & Shore, 2010; Cadieux & Shore, 2013; Heed et al., 2012). Comparable results were also found when the full range of SOAs (−240 to 240 ms) was used to calculate the probit slopes, rather than just the intermediate SOAs. The ANOVA for both dependent variables showed a main effect of limb portion ($ps < .02$) and of physical contact ($ps < .001$). Importantly, the two-way interaction was also significant, probit: $F(1, 13) = 8.08$, $p = .014$, $MSE = 18$, $\eta_p^2 = .38$; accuracy: $F(1, 13) = 9.88$, $p = .008$, $MSE = 286$, $\eta_p^2 = 0.43$, indicating that the crossed deficit was larger when the arms were in contact, probit: $t(13) = 2.97$, $p = .011$, $d_z = .79$; accuracy: $t(13) = 2.94$, $p = .011$, $d_z = .79$, than when they were not ($ps > .06$, $d_z\text{s} < .54$). Again, the benefit of noncontact (mutual vs. nonmutual contact) was observed in conditions where the touches were applied to the crossed portion of the limbs (crossed portion: $ps < .005$, $d_z\text{s} > .91$; uncrossed portion: $ps > .06$, $d_z\text{s} < .54$).

In Experiment 3, localization performance varied depending on whether the touches were applied to the crossed or uncrossed portion of the arms, even though the arms were crossed in both conditions. This excludes the possibility that crossing the arms per se induces a deficit in tactile localization. The results further demonstrate that tactile remapping does not take into account the end-point location of the limb, but a precise metric description of the touch relative to the configuration of both arms.

Experiment 4

In Experiment 3, we found that tactile localization performance with arms crossed improved when the arms of the participant were not touching each other. One explanation is that the lack of mutual contact of the arms adds uncertainty to the actual crossing point with respect to the location of the tactile stimuli at the time of remapping. Adding uncertainty might increase the probability that touches presented distal to the crossed point are actually perceived as located on the uncrossed portion, thus, reducing the crossing deficit, overall. In Experiment 4, we tested whether the perceived location of touches presented close to the crossed point would be

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more uncertain with respect to the crossed point than touches presented further away, reducing therefore the crossed deficit. In other words, whether there would be a gradient in the crossed-hands deficit as a function of how distal, relative to the crossing point, touch is applied (see Figure 1, variable "spatial gradient" of the deficit). As noted in the Introduction, the position of a finger requires the combination of proprioceptive information from the entire musculoskeletal chain of the limb (Heed et al., 2012; Longo et al., 2010). Therefore, a similar gradient might also be found, based on the number of crossed body parts (see Heed et al., 2012). It is possible that stronger modulations of the crossed posture of the limbs are found for skin sites far from the crossed point of the limbs than close. This is so as distal areas from the crossing point would contain more crossed body parts that contribute to the posture of the touched skin area (Badde, Röder, et al., 2014; Heed et al., 2012). Finally, another possibility for such a gradient might be differences in the mobility and the manipulative role of the different body parts tested, as pointed out by an anonymous reviewer. It seems intuitive, for instance, that tactile location on the hand and fingers is coded in an external reference frame. In contrast, for less manipulative body parts, like the forearm, it is more likely that tactile stimuli are less coded in external reference frames, but more in terms of skin-based information.

It is known that increasing the external horizontal distance between two touches in external space improves tactile localization performance (Gallace & Spence, 2005; Roberts, Wing, Durkin, & Humphreys, 2003; Shore, Gray, Spry, & Spence, 2005). Thus, we could not test different points on the arm keeping the same crossing point, because any increase in the distance from touch to the crossed point would also imply an increase in the horizontal external distance between the two touches. We tested the hands and fingers instead, keeping the crossing point stable across conditions. The independent mobility of the hands with respect to the arms allowed us to place the hands in a way that the horizontal distance between the touches at the fingers and at the hands was constant. We also added a condition in which the touches were presented at the forearms, at the same distal distance from the crossed point than the distance used at the hand condition (about 4 cm) to allow for a comparison of the crossed-hands deficit across different body parts (see Figure 4A). All conditions were tested with arms crossed and uncrossed, and allowing mutual contact of the limbs.

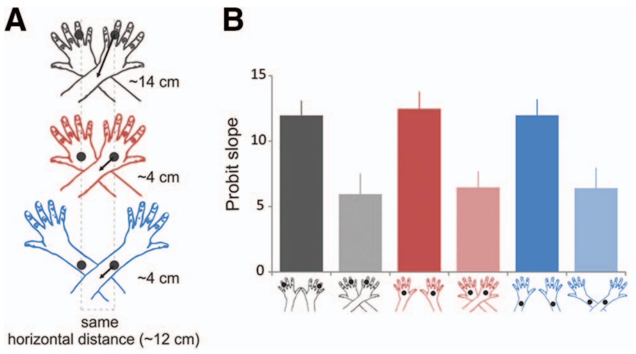

Figure 4. Setup and results of Experiment 4. Aerial view of the setup used in Experiment 4 (A). Mean probit slopes across subjects in the six conditions (B). Error bars depict the *SEM*. See the online article for the color version of this figure.

Method

Participants. Twelve (four females) new participants were tested in Experiment 4. One subject was removed from the data analyses due to an error in the code at the time of testing (remaining sample: $M_{\text{age}} = 25$ years, $SD = 3.7$). All participants reported that they were right-handed and had normal tactile sensitivity.

Procedure. Participants were tested in three blocked crossed conditions, with stimuli fixed on the middle phalanx of each ring finger, the center of the hands, or the distal part of each forearm (see Figure 4A). The stimuli were always attached to the dorsal part of the skin (hairy skin). Participants' arms could be uncrossed or crossed. When crossed, the limbs touched each other at the crossed point. To keep the distance between the two touches constant in external space (horizontal distance about 12 cm), participants crossed their arms at the wrists for the hands and fingers conditions (about 4 cm and about 14 cm away from the crossed point, respectively), and at the middle of the forearms for the arms condition (about 4 cm away; see Figure 4A). In the crossed conditions of Experiment 3, some participants were unable to perceive the correct order even at the longest SOA of 240 ms. For this reason, we included two new SOAs in Experiment 4, for a total of 18 SOAs (±15, ±30, ±45, ±60, ±90, ±120, ±240, ±500, and ±900 ms). Participants performed two blocks in each condition using an ABCDEF−ABCDEF design, with the order of the first block counterbalanced within and between AB, CD, and EF pairs using a Latin square design. The order of the blocks was equal across the first and last series. There were a total of 1,296 trials, excluding practice trials.

Results and Discussion

A 2 × 3 repeated-measures ANOVA with the factors stimulation site (forearms, hands and fingers) and posture (crossed, uncrossed) revealed a main effect of posture, $F(1, 10) = 20.33$, $p = .001$, $MSE = 566$, $\eta_p^2 = .67$. The Posture × Stimulation Site interaction was not significant, $F(2, 20) < 1$, (see Figure 4B). Thus, the crossing effect was similar across conditions, $M_{\text{crossed-deficit fingers}} = 6.01$, $SD = 5.35$, $t(10) = 3.72$, $p = .004$, $d_z = 1.12$; $M_{\text{hands}} = 6.0$, $SD = 5.06$, $t(10) = 3.94$, $p = .003$, $d_z = 1.19$; $M_{\text{forearms}} = 5.56$, $SD = 3.47$, $t(10) = 5.32$, $p = .0003$, $d_z = 1.60$. A planned t test comparison of the crossed deficit (uncrossed minus crossed performance) between finger and hand conditions confirmed that the deficit was similar irrespective of how distal, relative to the crossing point, touch was applied ($p > .99$).

Tactile localization performance did not differ across conditions when the arms were uncrossed ($M_{\text{fingers}} = 11.96$, $SD = 3.72$; $M_{\text{hands}} = 12.47$, $SD = 4.33$; $M_{\text{forearms}} = 11.97$, $SD = 4.07$; $ps > .089$), showing that the lack of interaction was not given by differences in TOJ performance across body sites.

The results of Experiment 4 suggest that the crossed-hands deficit is similar irrespective of how distal, relative to the crossing point, touch is applied. It also reveals the same pattern of crossed deficit across different body parts.

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General Discussion

Using the TOJ crossing effect, we investigated the role that crossing the arms has in tactile remapping. In a series of experiments, we applied tactile stimulation to locations of the skin that were not crossed. We found that the crossed-hands deficit is specific to the crossed portion of a limb. In Experiments 1 and 2, we found that tactile localization was not affected by crossing the limbs when the stimulated skin site was on the shoulders or elbows. A similar pattern was found in Experiment 3, where stimulation was applied to the middle of the forearm. The crossed deficit was only observed when the touches originated from the crossed portion of the limbs. These results suggest that the process of remapping tactile events according to current proprioceptive input is not based on a coarse assessment of end-point location, but on the exact configuration of the relevant body parts (Heed et al., 2012; see also Badde et al., 2014). Moreover, in Experiment 4, we found no gradient in the crossed deficit along the different crossed sections of the limbs. Thus, crossing the limbs affects tactile perception in a metrically precise way and alters localization of touches equally and only distal to the point of crossing (see Figure 1).

It is assumed that the crossed-hands deficit in a TOJ task reflects an automatic encoding of posture (Azañón, Camacho, & Soto-Faraco, 2010; Kitazawa, 2002; Röder et al., 2004). That is, every time touch is presented, posture is taken into account. The encoding of posture could explain the appearance of the deficit, but it does not ensure that the output of the remapping process in a TOJ task is a precise coordinate estimate of the location of touch. To resolve the TOJ task, the brain only needs to compute categorical right or left spatial relations about the location of touch, because the participant is only required to move one of the hands, and a precise estimation of the location of touch is not needed. This is not a trivial issue, because it has been found that the processing of categorical and coordinate spatial relations, the latter believed to occur in tactile remapping, engage different lateralization patterns of neural activation, implying the use of distinct neural networks (Jager & Postma, 2003; Laeng, 1994). That is, judging whether a dot appears to the right or left of fixation, a task conceptually similar to the TOJ, preferentially activates the left hemisphere in functional magnetic resonance imaging experiments. The opposite is true when participants perform judgments based on the exact distance from fixation (see Jager & Postma, 2003, for a review). Interestingly, several studies have recently reported a left hemisphere advantage when comparing processing of touch on crossed and uncrossed hands (Soto-Faraco & Azañón, 2013; Takahashi, Kansaku, Wada, Shibuya, & Kitazawa, 2012; Wada et al., 2012). These results suggest that the crossed deficit in TOJ might preferentially reflect a deficit in the categorical processing of left and right relations rather than a computation of precise metric estimates. The results of the present study rule out this alternative explanation and suggest, indirectly, that the crossed-hands deficit is based on extremely precise spatial computations. This is so, by showing that the location of the touch is extremely well-defined in relation to the crossed point and the configuration of the other hand, even at skin sites where no near landmarks are available, like the middle of the forearms.

The present results also exclude the possibility that crossing the limbs induces a general deficit in tactile localization. Yamamoto and Kitazawa (2001a), for instance, found that the crossed-hands deficit emerged only when the two arms were crossed, but not when the hands were held in opposite hemispaces without crossing the limbs, even though in both cases there was a conflict between reference frames (the touched right hand was on the left hemispace and vice versa for the left hand; see also Auclair, Barra, & Raibaut, 2012). This could reflect, for instance, the engagement of a specific configuration of mental resources (e.g., attention, memory) when the hands are actually "crossed" that differs from that engaged when the arms do not cross each other. This idea is in analogy to "task set" in cognitive control, where each task requires an appropriate configuration of mental resources that changes the way stimuli is processed (Meiran, Chorev, & Sapir, 2000; Monsell, 2003; Wylie & Allport, 2000). In light of the results of Experiment 3, we suggest that the differences found in Yamamoto and Kitazawa's (2001a) study, between the actual crossing and not crossing of the arms, might be related to differences in the uncertainty that the two touches are placed in opposite hemispaces, in the later condition. A close inspection to Yamamoto and Kitazawa's Figure 5, shows that, when the hands were placed in the contralateral hemifield with noncrossed limbs, performance deteriorated slightly. Crossing the limbs makes the two touches at the fingers undoubtedly crossed, which facilitates the emergence of the crossed deficit. Under this hypothesis, one would expect to find a decrease in performance, without an actual crossing, the further the fingers are placed from each other in the opposite hemispace (note that this detrimental effect should be stronger than the benefit observed in tactile TOJ paradigms when increasing the distance between two touches; Roberts et al., 2003; Shore et al., 2005).

The Arm as a Functional Unit for Tactile Spatial Localization

Humans reference touch to a representation of the body that is segmented into discrete parts, which consequently influences the perception of tactile distance on the skin (de Vignemont, Majid, Jola, & Haggard, 2009; Knight, Longo, & Bremner, 2014). For instance, de Vignemont et al. showed that the distance between two touches was judged as larger when touches were applied across the wrist rather than either within the hand or arm, even though distances were in fact identical. These segmentation effects were weakened by action, which suggests that action brings body parts together into coherent functional units. Here we found that the limb is not treated as a single functional unit for tactile spatial localization and that the end-point location of the entire limb does not influence tactile localization. Interestingly, even the end-point location of the stimulated body section was irrelevant in Experiment 3 (because the forearm's end-point location was crossed in the two conditions). Our results clearly demonstrate a fine-grained computation of posture in relation to touch. It further suggests that a detailed representation of the relative positions of both limbs in space is available for remapping. It is worth mentioning that the lack of modulation of the end-point location might have been driven by the lack of movement of the arms. Movement of the arms during or just before touch could have pulled together the different sections of the arm as a functional unit, driving effects of the entire arms even in noncrossed sections of the arm (see de Vignemont et al., 2009).

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Precise Encoding of Tactile Localization

Interestingly, the results of Experiments 1 and 2 agree with the finding that tactile extinction in patients with spatial neglect occurs on the contralesional hand when touches are delivered beyond the crossing point, but not before (Auclair et al., 2012; Medina & Rapp, 2008). This neurologic deficit is characterized by the limited conscious access to information coming from the contralesional side of space, when the stimulus is presented simultaneously with other competing stimuli on the ipsilesional side (Bisiach & Vallar, 1988; Driver & Vuilleumier, 2001). The close results obtained here and in the patient studies suggest that tactile extinction occurs after remapping has taken place. Compelling evidence that these two processes are related is the fact that there was no extinction in patients in the Auclair et al. (2012) study when the left hand was placed in the left hemispace without arm crossing, which is similar to the lack of crossing effect in TOJ under this configuration (Yamamoto & Kitazawa, 2001a). Nonetheless, this relation has to be taken with caution, because extinction in patients in the Auclair et al. (2012) study was only observed with hands crossed, not uncrossed. Moreover, in this same study, extinction appeared when the contralesional hand was placed in ipsilesional space, which should have had induced an amelioration of the deficit, if extinction was based on the allocation of attention to the remapped stimuli alone.

On the other hand, the results of Experiments 1 and 2 contrast with the results of tool use experiments with crossed sticks (Yamamoto & Kitazawa, 2001b; Yamamoto, Moizumi, & Kitazawa, 2005). Yamamoto and Kitazawa (2001b) showed that the judgment of the temporal order of two successive stimuli, delivered to the tips of sticks held in each hand, is dramatically altered by crossing the sticks without changing the positions of the (uncrossed) hands, where the actual mechanoreceptors are located. This suggests that an end-point location—the position of the tool in Yamamoto and Kitazawa's study and the position of the fingers in our study—is taken into account in the calculation of the external location of touch. This contrasts with our own findings. A possible explanation for these seemingly divergent results in the two studies is the behavioral relevance that the integration of an end-point location might have: whereas the location of the tip of a tool (as an extension of our own arms) might be relevant to localize tactile events through sensations at the hands, the location of the hands might not be directly relevant to locate a touch at the shoulders. Note that, in the experiments with tools, subjects perceived the touch as being applied to the end of the sticks (which were crossed), though the mechanoreceptors were in the hand, and, in our case, subjects clearly perceived the touch on the shoulders or elbows. Related to this, in our experiments, responses were given by lifting the body area judged to have been stimulated first, to avoid stimulus-response compatibility effects (Medina et al., 2014). Making such atypical responses might have forced participants to adopt a reference frame biased to the body surface, as pointed out by an anonymous reviewer. Because we do not typically act in the world with our shoulders or elbows, focusing on the body surface might have reduced, and even eliminated, the deficit. Hence, a different response demand, such as verbal, might have revealed a different finding.

Spatial Uncertainty and Tactile Remapping

In Experiment 3, we also found that adding uncertainty to the actual crossing point with respect to the location of the tactile stimuli, by avoiding mutual contact of the arms, improved localization performance and reduced the crossed-limb deficit. This suggests that contact information (from self-touch) facilitated the formation of a detailed representation of the relative positions of both limbs in space. Note that all conditions were blocked, and therefore participants were explicitly aware of the location of the touches relative to the crossed portion of the limbs. Thus, uncertainty about the location of the two touches probably originates at the time of remapping each individual tactile stimulus.

One possibility is that, when detailed information about the configuration of the limbs is not present, touches on the crossed portion of the limb are more often perceived as coming from the uncrossed portion, thus reducing the global deficit in this condition. Another possibility is that no systematic bias is present, but the perception of the origin of the two touches is more variable when there is no self-touch. Thus, touches on the crossed portion of the limb would be as likely perceived as coming from the uncrossed portion as from the crossed portion, reducing the overall crossed deficit. However, if the perception of stimulus location in the absence of self-touch was more variable, we should have found a decrease in performance when touch originated from the uncrossed portion of the limbs, because some touches would have been computed as if occurring on the crossed portion. This was not the case, and we found a trend in the opposite direction. Thus, the effect of contact was mainly unidirectional, suggesting that with more ambiguous information about whether the stimulated portion of the limbs is crossed, the default interpretation appears to be that that portion of the limbs remains uncrossed. The use of a default representation of the limbs as uncrossed has been suggested in tactile remapping (Bremner, Holmes, & Spence, 2008; Bremner & van Velzen, 2015; Longo et al., 2010; Overvliet, Azañón, & Soto-Faraco, 2011; Rigato, Ali, van Velzen, & Bremner, 2014). The underlying idea is that tactile localization is influenced by a prior expectation that a tactile sensation originates from where the touched limb is typically located in external space, for example, from the right side of space for the right arm (Bremner et al., 2008).

It could still be argued, however, that it was not ambiguity about the spatial location of the two touches, but the difference in limb elevation, that was responsible for the difference in performance. Differences in arm elevation might have facilitated the encoding of touch in external space, through the computation of an extraspatial (vertical) dimension. This hypothesis seems unlikely in this case, for several reasons. First, the position of touch in the vertical dimension was minimal, differing about 2 cm between conditions. Second, slight differences in elevation are irrelevant when touches originate from unambiguously crossed portions of the limbs, such as the hands when crossing the lower arms. This has been shown elsewhere (Yamamoto & Kitazawa, 2001a) and has been recently replicated in our lab using the same paradigm and stimuli as those presented here. In this study, we compared the judgments of temporal order at the fingers in the crossed condition with mutual and nonmutual contact of the arms (about 2 cm higher) and found no differences between conditions. This suggests that contact information from self-touch is relevant for tactile spatial percep-

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tion when the localization of touch is ambiguous, possibly by disambiguating the position of touch in space.

Tactile Remapping and the Distance to the Crossed Point

In Experiment 4, we tested whether the perceived location of touches presented distal, but close to the crossed point, were more ambiguous with respect to the crossed point than distal touches presented further away. Following the idea of a default expectation that touch originates from body parts in an uncrossed configuration (see previous section), we hypothesized that touches presented nearer the crossed point would be more likely perceived as located on the uncrossed portion, which would reduce the crossed deficit. However, we found a similar deficit regardless of the distal distance of touch relative to the crossed point of the limbs. This might be due to several issues related to our design. First, it is possible that the shorter of the two distances to the crossed point was already too large to observe any difference between the far and close conditions, that is, our design may not have created sufficient ambiguity. Second, the fact that the crossed and uncrossed conditions were blocked might have eliminated, in a top-down fashion, any possible uncertainty about the location of the touches with respect to the crossed point in the hand condition. This effect of prior knowledge seems more likely in Experiment 4 than in Experiment 3, in which conditions were also blocked, because of differences in the design of the two experiments. In particular, in Experiment 3, both touches and the crossed point were located on the forearm and did not span any joint. In Experiment 4, by contrast, participants crossed their arms at the wrist. Under these conditions, mislocating touch proximal to the crossed point would mean attributing tactile sensations that originate from the hand to the forearm. Joints are important landmarks for tactile localization (Cholewiak & Collins, 2003), and their influence on tactile localization may prevail when touches are applied nearby. Unfortunately, it is difficult to test the distal distance hypothesis without running into these issues. Increasing the distal distance from a crossed point also increases the horizontal distance between homologous regions of the arms and, thereby, between the two touches in the TOJ task. Horizontal distance is known to affect TOJ (Gallace & Spence, 2005; Roberts et al., 2003; Shore et al., 2005). Thus, varying the distal distance while holding the horizontal distance constant is anatomically only possible when crossing the hands at the wrist, as in our study. On the other hand, interleaving conditions from trial to trial would probably not minimize expectations about the location of touch: If both the location of the crossed point and the location of the stimulated body area are constant, crossing the limbs would always be linked to receive touches on the crossed portion of the limb. Irrespective of these issues, we can argue that the crossed deficit is similar regardless of the stimulated body site, when holding horizontal distance constant.

Conclusion

We found that crossing the limbs affects tactile perception in a metrically precise way and alters localization of touches equally and only distal to the point of crossing. We demonstrated that the process of remapping tactile events into external space is based on a detailed, metric description of the external spatial positions of the relevant elements in the kinematic chain of the limb, not just on a coarse assessment of end-point location. When the representation of the limbs as crossed or uncrossed with respect to touch is less precise, tactile localization is biased as if touch was originated from the uncrossed portion of the limb.

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Received June 9, 2015
Revision received November 12, 2015
Accepted December 13, 2015 ■

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