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A three-dimensional spatial characterization of the crossed-hands deficit

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ABSTRACT

To perceive the location of touch in space, we integrate information about skin-location with information about the location of that body part in space. Most research investigating this process of *tactile spatial remapping* has used the so-called *crossed-hands deficit*, in which the ability to judge the temporal order of touches on the two hands is impaired when the arms are crossed. This posture induces a conflict between skin-based and tactile external spatial representations, specifically in the left-right dimension. Thus, it is unknown whether touch is affected by posture when spatial relations other than the right-left dimension are available. Here, we tested the extent to which the crossed-hands deficit is a measure of tactile remapping, reflecting tactile encoding in three-dimensional space. Participants judged the temporal order of tactile stimuli presented to crossed and uncrossed hands. The arms were placed at different elevations (up-down dimension; Experiments 1 and 2), or at different distances from the body in the depth plane (close-far dimension; Experiment 3). The crossed-hands deficit was reduced when other sources of spatial information, orthogonal to the left-right dimension (i.e., close-far, up-down), were available. Nonetheless, the deficit persisted in all conditions, even when processing of non-conflicting information in the close-far or up-down dimensions was enough to solve the task. Together, these results demonstrate that the processing underlying the crossed-hands deficit is related to the encoding of tactile localization in three-dimensional space, rather than related uniquely to the cost of processing information in the right-left dimension. Furthermore, the persistence of the crossing effect provides evidence for automatic integration of all available information during the encoding of tactile information.

1. Introduction

Localizing touch in space is essential for spatially-coordinated action. To swat away a fly on our arm, we need to know not just where on the arm the fly landed, but also the posture of the arm in space. Thus, tactile localization (caused in this case by the insect) entails the transformation of the location of touch in a reference frame that is skin-based (a touch *on the right arm*) to one that is defined by coordinates in external space (a touch *on the right side of space*) and the subsequent integration of these two reference frames. It has been proposed that the external reference frame, in which tactile events are encoded after remapping, relies strongly on a visually-based representation of space (Begum Ali, Cowie, & Bremner, 2014; Ley, Bottari, Shenoy, Kekunnaya, & Röder, 2013; Röder, Rösler, & Spence, 2004). However, this proposal leaves open how this representation for touch in a three-dimensional space is characterized and the way the different dimensions interact.

Tactile remapping has been generally studied by manipulating limb posture, especially by crossing the arms. In this posture, a touch on the right hand (in skin-based coordinates), is located in left space, creating an incongruence between reference frames in the right-left dimension (Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001; for a review see Heed, Buchholz, Engel, & Röder, 2015). A well-known consequence of this conflicting information is the impairment in the ability to report the order of two stimuli, one applied to each hand, when hands are crossed (Heed & Azañón, 2014; Shore et al., 2002; Yamamoto & Kitazawa, 2001). In such instances, the order of two stimuli might be correctly computed, but it is inaccurately reported because of the incorrect localization of the stimuli in space (Badde, Heed, & Röder, 2016; Overvliet, Azañón, & Soto-Faraco, 2011; Roberts & Humphreys, 2008). This result has been interpreted as evidence that posture is taken into account automatically, even if this impairs task performance (Azañón, Camacho, & Soto-Faraco, 2010; Kitazawa, 2002; Yamamoto & Kitazawa, 2001). In the remapping literature, this idea has been extrapolated indirectly to all postures, to the extent that it is generally assumed that tactile remapping (or the encoding of touch in external space) is a general

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step in tactile processing (Azañón & Soto-Faraco, 2008; Kitazawa, 2002; Overvliet et al., 2011; Röder et al., 2004).

The crossing effect has been suggested to result, amongst other models, from either an impairment of coordinate transformation (Yamamoto & Kitazawa, 2001) or a conflict in the integration of disparate spatial information (Badde, Röder, & Heed, 2015; Badde et al., 2016; Heed et al., 2015). Regardless of the interpretation of the origin of the effect, all these studies assume that the deficit indexes an automatic triggering of spatial transformations during tactile processing. And the aim of this transformation is the generation of a tactile location estimate in external space (Azañón, Stenner, Cardini, & Haggard, 2015; Heed, Backhaus, & Röder, 2012; Heed et al., 2015). Although the deficit is in the right-left dimension, the final estimate should code location in three-dimensional space and certainly not only in the right-left dimension. To our knowledge, however, no studies have shown that spatial relations in dimensions other than the left-right dimension have any effect at all on TOJ judgements. Indeed, Yamamoto and Kitazawa found that crossing the hands with one hand close to the body and another further apart did not appear to influence the deficit (Yamamoto & Kitazawa, 2001). Thus, although it is generally assumed that touch is localized with respect to all three axes of space, this has not been experimentally demonstrated.

This is a fundamental issue that needs to be addressed before assuming that the crossed-hands deficit is a valid index of tactile remapping in 3D space. Note that crossing body parts is the most popular paradigm in the tactile remapping literature, as crossing the limbs produces large effects. Very few studies have investigated remapping along other dimensions (see Azañón, Longo, Soto-Faraco, & Haggard, 2010 for a task that varied the up-down dimension, though not using TOJs), or in the left-right dimension without inducing a conflict (see for exceptions, e.g., Gillmeister & Forster, 2012; Shore, Gray, Spry, & Spence, 2005). Thus, it is not clear to what extent the crossed-hands deficit is a reflection of remapping in three-dimensional space, the result of confusion specifically in the left-right axis, or a combination of the two. It is true that, by definition, the presence of a crossed-hands deficit implies that posture has been taken into account. But the extent of the deficit and the underlying processing might not reflect the computation of a location estimate in volumetric external space, but the processing of a conflict in a particularly salient spatial dimension.

There are, in fact, some reasons for thinking that it is the presence of a conflict between reference frames in the left-right dimension, rather than tactile remapping in 3D space, what underlies the crossed-hands deficit. First, there is no comparable effect of an influence of posture when no conflict between reference frames is involved. For instance, some results show that TOJs are slightly better when uncrossed hands are placed far apart rather than close together (Roberts, Wing, Durkin, & Humphreys, 2003; Shore et al., 2005). In this situation, no conflicting information about touch is present. Thus, one could argue that this positive result indicates that touch is remapped in external space (i.e., taking posture into account) in non-conflicting situations. However, even if a default transformation takes place when the arms are uncrossed, the effects observed in these studies are small (<20 ms; as compared to hundreds of ms in the crossed-hands studies; Roberts et al., 2003; Shore et al., 2005), not always present (see Kuroki, Watanabe, Kawakami, Tachi, & Nishida, 2010) and occur only under certain stimulation protocols (Shore et al., 2005). Second, the crossed-hands deficit is based on the processing of right-left spatial information, which is known to produce larger perceptual effects than when dealing with any other spatial dimension (Corballis & Beale, 1970; Farrell, 1979; Nicoletti & Ulmita, 1984). The left-right dimension is unique in being the axis in which our bodies are bilaterally symmetric (Corballis & Beale, 1970). Thus, the left-right position of touches on the skin might be uniquely confusable, since every location has an exact contralateral homologue, especially in light of known interactions between touches on homologous fingers (e.g., Tamè, Pavani, Papadelis, Farnè, & Braun, 2015). Moreover, the left-right axis is known to rely on distinct neural mechanisms. For example, left-right confusion is among a constellations of symptoms typically reported in Gerstmann's syndrome (Benton, 1959; Roeltgen, Sevush, & Heilman, 1983), which has been linked to lesions in the left inferior parietal lobe.

In the present study, we tested the extent to which the crossed-hands deficit reflects remapping in three-dimensional space, and not uniquely on the right-left dimension. Specifically, we aimed at modulating the crossed-hands deficit by adding other sources of spatial information, orthogonal to the conflicting left-right information. Note that in all previous studies, stimuli differed along a single spatial dimension (see Yamamoto & Kitazawa, 2001, Fig. 5, for an exception). Thus, typically, one hand would be placed to the right and the other to the left of the body, and both would be aligned in all other spatial dimensions. Here, we asked blindfolded participants to make TOJs of stimuli presented to crossed and uncrossed hands that were placed at different elevations (up-down dimension), or at different distances from the body in the depth plane (close-far dimension). If the effects observed when the hands are crossed are related to the encoding of touch in three-dimensional space, then the crossed-hands deficit should reflect the encoding of touch also in the depth and vertical planes. Thus, non-conflicting spatial information in the depth and vertical planes could be used to solve the task, hence ameliorating (or eliminating) the deficit. If, on the contrary, the crossed-deficit simply reflects the by-product of a conflict in the right-left dimension, then adding extra-spatial information should be irrelevant.

2. Methods

2.1. Participants

Forty-eight healthy volunteers participated in the study, 16 in each of the three experiments (Experiment 1: M = 27.06 years; SD = 8.32; 10 female; Experiment 2: M = 25.56 years; SD = 4.70; 10 female; Experiment 3: M = 26.56 years; SD = 6.29; 14 female). Participants were right-handed as assessed by the Edinburgh Inventory (Experiment 1: M = 87.72, SD = 13.82; Experiment 2: M = 93.31, SD = 14.14; Experiment 3: M = 91.71, SD = 13.90) and reported normal tactile sensitivity. They were naïve as 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 ethical committee.

2.2. Procedure

On each trial, a touch was applied to the dorsal surface of the middle phalanx of each ring finger. 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, UK). Stimuli were presented at varying stimulus onset asynchronies (SOAs; ±960, ±480, ±220, ±110, ±70, ±40, ±20 ms), with a similar range to previous experiments (Azañón & Soto-Faraco, 2007; Azañón et al., 2015). Negative values indicate that the left hand was stimulated first. Participants were required to identify which stimulus was presented first by pressing a button with the corresponding hand, as accurately as possible with no time restriction. In a 2×2 factorial design, the hands of the participant could be either uncrossed or crossed over the body midline, and spatially aligned or not. In Experiments 1 and 2, spatial alignment refers to the distance of the hands in the vertical dimension (i.e., up-down). That is, whether both hands are close to each other (aligned) or far from each other (misaligned) in the vertical dimension. In Experiment 3, alignment refers to the disposition of both hands in the depth dimension (i.e., close-far from the body). Participants were blindfolded and white noise was presented continuously through headphones.

Prior to the start of the experiment, participants performed two practice blocks of 14 trials each, with hands crossed and uncrossed (with the hands aligned in the vertical and depth plane), using a selection of long SOAs (from 100 ms to 1.25 s). If the participant was able to report the correct order of the stimuli in more than 70% of the trials in each posture, the experiment started. If, however, the participant did not pass this threshold in one posture, the block was repeated (with a limit of 4 block repetitions) until the threshold was reached (two participants failed to reach this criterion after 4 blocks and did not continue). Stimulus presentation was controlled using Matlab Data Acquisition Toolbox and Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007), running on a PC computer.

2.2.1. Experiment 1

This experiment included four conditions in a 2×2 factorial design, where the arms of the participants could be either crossed or uncrossed over the body midline and the right arm could be either far above or close to the table. The different conditions are illustrated in Fig. 1 (left panel). The left arm rested on the table with the fingers placed on a platform 3 cm above the table. To avoid contact between the arms when they were crossed, the right arm was placed 9 cm above the table in the aligned condition and 27 cm in the misaligned condition. Hence, the vertical distance between the stimulated ring fingers was 6 and 24 cm in the aligned and misaligned conditions, respectively. The Euclidean distance between the two tactile stimulators was kept constant at ~30 cm across conditions. Each condition was presented twice in blocks of 84 trials (which correspond to 12 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 participant. We added 6 practice trials randomly assigned from the same pool of SOAs, at the beginning of each block. Participants were blindfolded in this and the following experiments.

2.2.2. Experiment 2

This experiment was similar to Experiment 1, except that the horizontal distance between the two ring fingers was kept constant at ~30 cm (see Fig. 1, right panel). In Experiment 1, the Euclidean distance between the touches was constant and therefore the horizontal distance between the two ring fingers varied, with shorter horizontal distances in the misaligned as compared to the aligned conditions. Some studies have found that changes in the horizontal distance between two touches affect tactile TOJ performance (Gallace & Spence, 2005; Roberts et al., 2003; Shore et al., 2005). Thus, we designed Experiment 2 to ensure that any pattern of results in Experiment 1 could not be explained by the difference in the horizontal distance across conditions. As in Experiment 1, the right arm rested on top of a platform 27 cm above the left arm in the misaligned condition, and 9 cm above in the aligned condition.

2.2.3. Experiment 3

In Experiment 3, we tested the influence of additional spatial information in the depth plane on the crossed-hands TOJ deficit. In this experiment, the participant's arms could be crossed or uncrossed, with the right arm placed closer to the body, as compared to the left (see Fig. 2) or both aligned at the same distance from the body. The distance in depth from the two ring fingers was 20 and 0 cm in the misaligned and aligned conditions, respectively. In both crossed conditions, the arms were touching each other at the crossing point. The horizontal distance between the fingers was ~17 cm across conditions.

2.3. Analyses

We present two different dependent variables, the just-noticeable difference (JND), a measure of precision, and the proportion correct responses. To calculate the JND, the proportion of right hand first responses across all SOAs was fitted to a logistic regression model for each participant and posture separately (using a generalized linear model fit function, glmfit in Matlab), as when plotted, performance resembled a typical psychophysical, S-shaped curve (see Heed & Azañón, 2014). The point of each curve at which the proportion of right-first responses was 25 and 75%, respectively, were projected onto the SOA axis. The difference in SOA between these two projections, divided by 2, was used as a measure of sensitivity to the tactile temporal order, with steeper slopes (and lower JND values) indicating better performance. This value denotes the SOA at which the two tactile stimuli need to be presented for the participant to make 75% correct responses. Thus, the difference in JND between uncrossed and crossed conditions can be used as an index of the crossed-hands deficit. Individual JNDs were submitted to an ANOVA with posture and alignment as within-subject factors. This was followed by planned two-tailed *t*-test comparisons across conditions. We also conducted an across-experiment comparison to explore possible differences in the strength of the interaction between Experiments 1–2 and 2–3, using mixed repeated-measures ANOVA. To quantify the magnitude of the effects we report, we provide partial eta squared values for F-tests, which assesses the proportion of variance accounted for by that effect, partialling out the effects of other main effects and interactions. For *t*-tests, we provide Cohen's dz, which givens the standardized mean difference between conditions (Lakens, 2013).

JND analyses implicitly assume that the response profile across SOAs follows a specific distribution. To circumvent this assumption, we also computed the average of the proportion correct responses for each SOA (i.e. accuracy; Cadieux, Barnett-Cowan, & Shore, 2010). Unlike JNDs, this measure has the disadvantage to be blind to differences between SOAs.

2.4. Exclusion criteria

Seven participants (three in Experiment 1, two in Experiment 2, and two in Experiment 3) were asked to leave before the end of the experiment (<5 blocks), for the following reasons: Four participants consistently responded at chance levels at the largest SOA (960 ms) in one or more conditions. Two participants were overtly not engaging in the task, denoted by their attitude and the frequent errors in the longest SOA in both postures. One participant persistently reported not feeling the taps in the crossed conditions.

To confirm that the exclusion criteria did not bias our results, we analyzed the partial data of these participants on the two crossed conditions (at least one block of which was available for all participants), collapsing across the three experiments. The mean JND in the crossed-aligned condition was 717 ms and 410 ms in the misaligned condition, and this difference was not significant ($t(6) = 1.79$, $p = 0.12$; absolute JNDs were computed, to avoid the negative JND of two subjects; analyses of accuracy were also not significant, means of 57% and 59%, respectively, $t(6) = 0.41$, $p = 0.70$). When excluding two participants with negative JND values, the average JND was 731 and 292 ms in the crossed aligned and misaligned conditions, respectively, and this difference approached significance levels ($t(4) = 2.32$, $p = 0.08$). The results

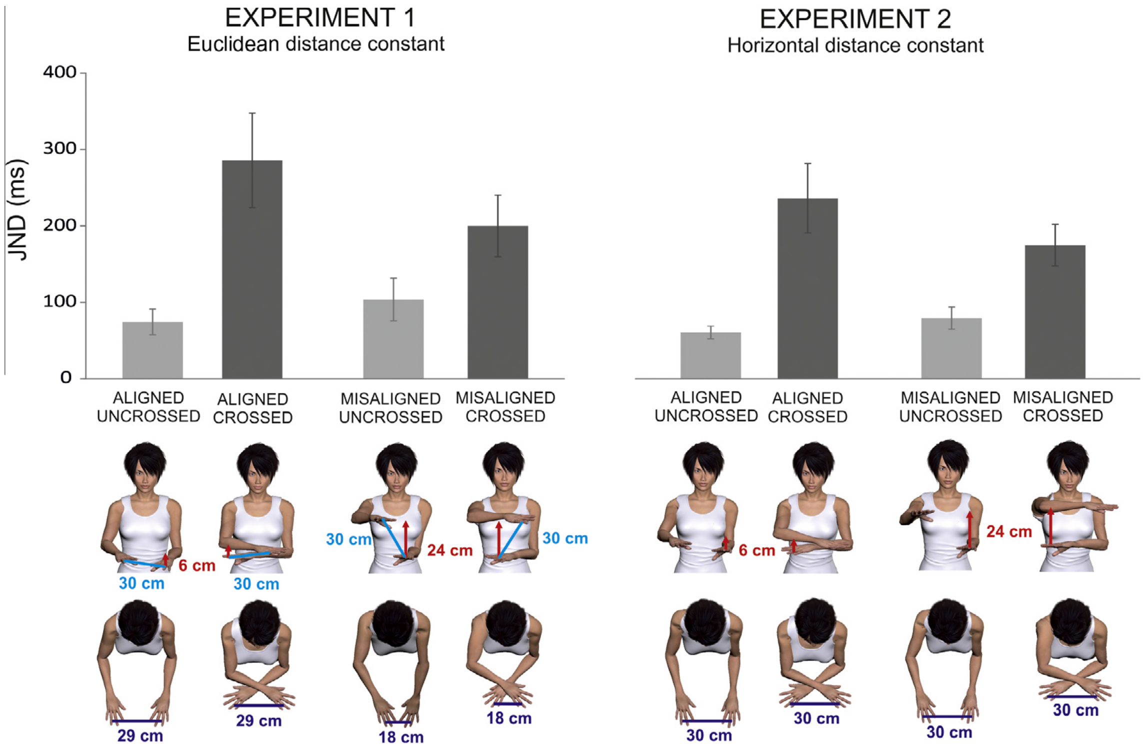

Fig. 1. Methods and results of Experiments 1 and 2. Mean just-noticeable difference (JND) in the aligned and misaligned conditions (vertical plane) with crossed and uncrossed limbs. Dark grey bars represent data from the crossed conditions; light grey bars represent data from the uncrossed conditions. Error bars represent standard error of the mean. Female figures depict the different positions of the arms in the front and aerial views of the same postures. Red lines and numbers indicate the vertical distance between the ring fingers; light blue depict the Euclidean distance, and dark blue the horizontal distance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

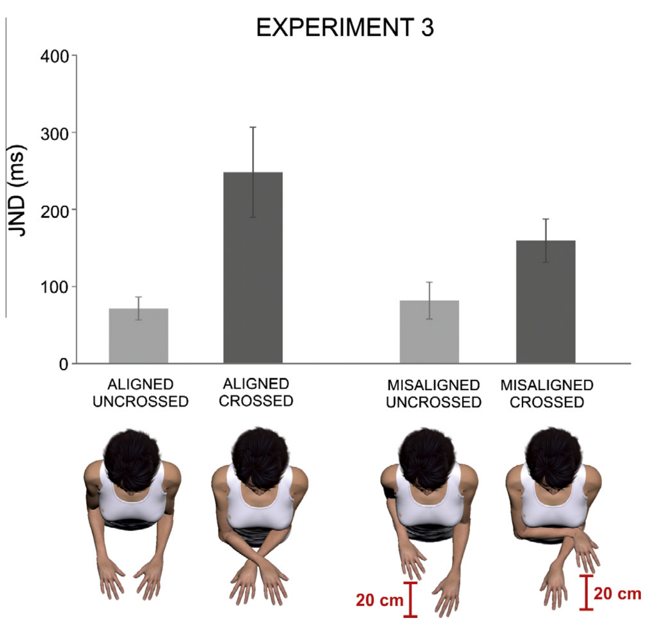

Fig. 2. Methods and results of Experiment 3. Mean just-noticeable difference (JND) in the aligned and misaligned conditions (depth plane) with crossed and uncrossed limbs. Dark grey bars represent data from the crossed conditions; light grey bars represent data from the uncrossed conditions. Error bars represent standard error of the mean. Female figures depict the different positions of the arms in the aerial view. Red lines and numbers indicate the distance in depth between the ring fingers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the partial data suggest no differences across crossed conditions, or, in any case, a trend to observe better performance in the crossed-misaligned condition. Thus, the data of the excluded participants mimics the overall results of the study.

These exclusion criteria was chosen to avoid data that cannot be properly fitted using psychometric curves. Even so, the data of two participants that completed the experiment were excluded on the basis of poor model fit (R^2 below 0.5; $R^2 = 0.1$ and 0.4, for the two outliers respectively; Experiment 3), and the data were replaced with that from two new participants. Interestingly, the two outliers performed inside the normal rage in the crossed-misaligned condition (JNDs of 550 ms and 469 ms), but not in the crossed-aligned condition (JNDs of 6991 ms and 1989 ms; see footnote in the Results section of Experiment 3), which mimics again the overall results of the study. The overall fit of the data in the three experiments was high ($R^2 = 0.936$, SD = 0.06). The data of 16 participants were used in each experiment.

3. Results

3.1. Experiment 1

In Experiment 1 we investigated whether information about the location of a touch in the vertical (up-down) dimension could be used to prevent the crossed-hands deficit. We expected that elevating one of the hands would reduce the crossed-hands deficit. A repeated measures ANOVA with the within-subject factors of *Posture* and *Alignment* showed that the JND was larger when the arms were crossed as compared to uncrossed (main effect of posture: $F(1,15) = 11.93$, $p = 0.004$, $\eta p^2 = 0.44$; Fig. 1, left panel), replicating a well-established crossed-hands deficit (Shore et al., 2002; Yamamoto & Kitazawa, 2001). Moreover, the crossed-hands deficit (difference in performance in the two postures) was reduced by a factor of two in the misaligned as compared to the aligned condition (mean crossed-hands deficit: 96.79 and 211.36 ms, respectively) as denoted by the interaction *Posture* × *Alignment*: $F(1,15) = 10.27$, $p = 0.006$, $\eta p^2 = 0.41$). However, despite this reduction, a reliable crossed-hands deficit emerged in both conditions (planned *t*-test comparisons – misaligned: $t(15) = 2.81$, $p = 0.01$, $dz = 0.70$; aligned: $t(15) = 3.61$, $p < 0.003$, $dz = 0.90$). A similar pattern of results was obtained when the proportion of correct responses over all SOA was calculated (main effect of *Posture*: $F(1,15) = 26.47$, $p < 0.001$, $\eta p^2 = 0.64$; interaction: $F(1,15) = 6.49$, $p = 0.02$, $\eta p^2 = 0.30$).

The results of Experiment 1 show that the crossed-hands deficit is reduced – but not eliminated – when an extra spatial cue is available, in this case, the location of touch in the vertical axis. This result suggests that information about the external location of touch in the vertical (up-down) dimension is processed and used to reduce the deficit.

3.2. Experiment 2

In Experiment 1 we manipulated the elevation of the right hand, leaving constant the Euclidean distance between the touches. This manipulation has the disadvantage that the horizontal distance between both hands differs across conditions. Thus, the hands of the participants were closer to each other (in the horizontal dimension) in the misaligned condition and further apart in the aligned condition. Increasing the horizontal distance between two touches might reduce the crossed-hands deficit (Gallace & Spence, 2005; Roberts et al., 2003; Shore et al., 2005). It is unlikely, however, that the results of Experiment 1 could be explained by these differences, as we found that the crossed-hands deficit in the aligned condition, where the hands were further appart in horizontal space, was indeed increased, rather than reduced. On the other hand, ambiguity about whether touches are presented from a crossed or an uncrossed portion of a limb has been found to reduce the deficit in a recent study (Azañón, Radulova, Haggard, & Longo, 2016). Thus, a second possibility is that a short horizontal distance in the misaligned (elevated) crossed posture, where each hand is close to the crossing point (in the horizontal dimension), could have increased the uncertainty about whether the taps were actually presented from crossed hands (see the crossed-misaligned posture in the aerial view; Fig. 1, left panel). Despite the fact that all the conditions were blocked and participants were explicitly aware of the crossed position of the hands, ambiguity could have been originated at the time of remapping each individual tactile stimulus or could have influenced the weighting of anatomical and external information.

In Experiment 2, we controlled for this possibility by keeping the horizontal distance between the hands constant to ~30 cm. The different elevations of the right hand were as in Experiment 1. We found a similar pattern of results in Experiment 2 to those observed in the previous experiment. The JND was again larger when the arms were crossed as compared to uncrossed, as shown by a main effect of *Posture* ($F(1,15) = 25.68$, $p < 0.001$, $\eta p^2 = 0.63$; Fig. 1, right panel). Again, the crossed-hands deficit was reduced, almost by half, in the misaligned as compared to the aligned condition (mean crossed-hands deficit: 95.39 and 175.69 ms, respectively), and this was denoted by the significant interaction ($F(1,15) = 6.18$, $p = 0.025$, $\eta p^2 = 0.29$). Note that again, the crossed-hands deficit was still present in both conditions (planned *t*-test comparisons; misaligned, $t(15) = 5.38$, $p < 0.001$, $dz = 1.35$; aligned, $t(15) = 4.34$, $p < 0.001$, $dz = 1.08$). A similar pattern of results was obtained when the proportion of correct responses over all SOAs was calculated (main effect of *Posture*: $F(1,15) = 38.88$, $p < 0.001$, $\eta p^2 = 0.72$; interaction: $F(1,15) = 4.90$, $p = 0.043$, $\eta p^2 = 0.25$).

We also conducted a mixed ANOVA across the two Experiments, with *Horizontal Distance* (constant, variable) as a between-subjects factor. We found that the main effect of Posture (JND: $F(1,30) = 31.01$, $p < 0.001$, $\eta p^2 = 0.51$; Accuracy: $F(1,30) = 62.18$, $p < 0.001$, $\eta p^2 = 0.68$) and the interaction were significant (JND: $F(1,30) = 16.35$, $p < 0.001$, $\eta p^2 = 0.35$; Accuracy: $F(1,30) = 11.08$, $p = 0.002$, $\eta p^2 = 0.27$). Importantly, the between-subjects factor of *Horizontal Distance* did not interact with any of the variables (JND: all $p > 0.48$; Accuracy: $p > 0.78$).

3.3. Experiment 3

In Experiment 3, we tested the influence on the crossed-hands TOJ deficit of additional spatial information about the location of touch in the depth plane, orthogonal to the right-left conflicting dimension. The distance from the two ring fingers in depth (close-far) space was 20 and 0 cm in the misaligned and aligned conditions, respectively (see Fig. 2).

A repeated-measures ANOVA with the within-subject factors of *Posture* and *Alignment* showed larger JNDs when the arms were crossed as compared to uncrossed ($F(1,15) = 23.24$, $p < 0.001$, $\eta p^2 = 0.61$; Fig. 2). The crossed-hands deficit was numerically reduced by more than half in the misaligned condition as compared to the aligned condition (mean crossed-hands deficit: 77.62 and 176.67 ms, respectively). The interaction, however, was not significant, although a trend was observed ($F(1,15) = 3.87$, $p = 0.068$, $\eta p^2 = 0.21$). Despite this reduction, a reliable crossed-hands effect was observed in both conditions (misaligned: $t(15) = 4.32$, $p < 0.001$, $dz = 1.08$; aligned: $t(15) = 3.65$, $p = 0.002$, $dz = 0.91$). A similar pattern of results was obtained when the proportion of correct responses over all SOAs was calculated, instead of JNDs, this time with a significant interaction ($F(1,15) = 7.77$, $p = 0.014$, $\eta p^2 = 0.34$; main effect of *Posture*: $F(1,15) = 36.71$, $p < 0.001$, $\eta p^2 = 0.71$; main effect of *Alignment*, $F(1,15) = 4.94$, $p = 0.042$, $\eta p^2 = 0.25$).[1]

We also computed a mixed repeated measures ANOVA across Experiments 2 and 3 to see if there were differences in the strength of the interaction between experiments. We chose Experiment 2 as in both experiments the horizontal distance was kept constant. We found that the main effect of *Posture* (JND: $F(1,30) = 48.90$, $p < 0.001$, $\eta p^2 = 0.62$; Accuracy: $F(1,30) = 75.59$, $p < 0.001$, $\eta p^2 = 0.72$) was significant. The main effect of *Alignment* (JND: $F(1,30) = 4.65$, $p = 0.039$, $\eta p^2 = 0.13$; Accuracy: $F(1,30) = 5.75$, $p = 0.023$, $\eta p^2 = 0.16$) was driven by the interaction *Posture* × *Alignment* (JND: $F(1,30) = 8.98$, $p = 0.005$, $\eta p^2 = 0.23$; Accuracy: $F(1,30) = 12.34$, $p = 0.001$, $\eta p^2 = 0.29$). The interaction *Posture* × *Alignment* × *Experiment* was not significant (JND and Accuracy, both $Fs < 0.1$), which suggests that the interaction was similar across experiments.

4. Discussion

This study examined to what extent the crossed-hands deficit reflects the processing of tactile location in three-dimensional space. We found that the crossed-hands deficit was reduced when other sources of spatial information, orthogonal to the left-right dimension, were available; namely, when the stimuli could be differentiated also in terms of elevation or depth. These results suggest that the processing underlying the crossed-hands deficit is

[1] The addition of the two outliers (see Methods section) to the analyses produced a similar interaction ($n = 18$, $F(1,17) = 10.97$, $p = 0.004$, $\eta p^2 = 0.39$). This was the case even when the outliers but not their replacement were included in the analyses ($n = 16$, $F(1,15) = 9.07$, $p = 0.009$, $\eta p^2 = 0.38$). Note that only data about accuracy in these participants can be analyzed because of the impossibility to fit their data to a psychometric curve in the crossed-aligned condition.

related to the encoding of the location of touch in three-dimensional space, rather than related uniquely to the cost of processing information in the right-left dimension. Further, the persistence of the crossing effect indicates that anatomical and external left-right locations of touch are used for the localization responses even when non-conflicting information alone (up-down or close-far) is enough to solve the task. These results provide evidence for automatic integration of all available information during the encoding of tactile information.

Our results show that information about elevation and depth interacts with information about the right-left dimension. Intriguingly, this contrasts with previous research that has shown that the addition of non-spatial information, such as when the stimuli differ in the identity of the stimulated body part, has little if any effect on the deficit (Schicke & Roder, 2006; Shore et al., 2002). For instance, TOJ crossing effects are comparable when same or different fingers of each hand are stimulated (Shore et al., 2002), or even when stimuli are applied to one hand and to one foot, while they are crossed with each other (Schicke & Roder, 2006). Moreover, the effect of crossing the arms when stimuli differs in frequency or duration is comparable to any standard crossing effect (see Figs. 1 and 5 in Roberts & Humphreys, 2008; though see Badde et al., 2015, where TOJ crossing effects are reduced when location, but also non-spatial characteristics of the stimuli, are reported in a dual task). These results are quite surprising, as one could imagine solving the task using the identity of the body part, the frequency or the duration of the stimulus that has been stimulated first. These previous results suggest that the automatic encoding of tactile location is pretty encapsulated from many other forms of sensory information. The fact that in our study the addition of spatial information about elevation and depth was able to modulate the deficit suggests that the deficit reflects automatic remapping into a representation of volumetric 3D space in which left-right position is integrated with other spatial dimensions.

Nevertheless, it is important to note the persistence of the deficit: the deficit was ameliorated – but still present – in all conditions. Thus, the crossed-hands deficit persists even when information orthogonal to the left-right dimension is available and sufficient to solve the task. One possible explanation is that processing in the left-right dimension might be more salient than processing in other dimensions (Nicoletti & Ulmita, 1984). The left-right dimension is the axis in which our bodies are symmetric (Corballis & Beale, 1970) and people often have difficulty telling which is left and which is right (Corballis & Beale, 1970; Hirnstein, Ocklenburg, Schneider, & Hausmann, 2009). Many studies have shown that it takes longer to make locational discriminations when the relevant spatial dimensions are described by the terms right and left as compared to up or down, even in the absence of verbal responses (Corballis & Beale, 1970; Farrell, 1979; Nicoletti & Ulmita, 1984). Moreover, disorders of spatial orientation and spatial compatibility effects are more acute in the right-left dimension (Corballis & Beale, 1970; Howard & Templeton, 1966), as they are in neurological deficits related to spatial attention (such as in neglect, Bisiach & Vallar, 1988). Thus, it is possible that a general attentional bias in favour of right/left axis might have been the cause of the prevalence of the deficit. Another interpretation is related to the weight that the processing of conflicting information is given in the brain. It is possible that any type of conflicting spatial information is more salient than non-conflicting information, independent of the dimension in which it is present. If this were the case, then inducing a conflict in the vertical or depth dimensions should produce a similar deficit than when crossing the hands. A third possibility is that decisions are based by default on all available information, regardless of whether or not it is conflicting. Indeed, there is some evidence for this proposal. For instance, in the study of Azañón and Soto-Faraco (2007), the sight of uncrossed or crossed rubber hands on top of the occluded real hands provided additional, though irrelevant, information about the location of the tactile stimuli. However, participants integrated this information, as TOJ crossing effects were modulated by the posture of the rubber hands. In Badde, Röder, and Heed (2014), TOJs for tactile stimuli to the fingers were influenced by whether stimuli were applied to the same or different hands, with the latter providing additional information which benefitted performance. Finally, in Azañón et al. (2015) information about the localization of preceding touches influenced TOJ performance in subsequent trials, even when the preceding tactile information was task irrelevant.

Finally, the modulation of the crossed-hands deficit appeared to be greater when information about elevation (Exp 1 and 2), rather than depth (Exp 3), was available, though this difference was not significant. The idea that the vertical dimension might be more salient or might produce a more reliable proprioceptive estimate about the location of the arm than the depth dimension is an interesting point for further experiments to explore (see Van Beers, Wolpert, & Haggard, 2002, for differences in proprioception between azimuth and depth). Indeed, Yamamoto and Kitazawa (2001) found that crossing the hands produces a similar response regardless of the distance in depth between the hands. Close inspection of their Fig. 5E–F (see Yamamoto & Kitazawa, 2001), however, reveals that performance was likely slightly worse when only information in the left and right space was available.

In summary, we show that the crossed-hands deficit is reduced when other sources of spatial information, orthogonal to the left-right dimension, are available. Thus, we show that the crossed-hands deficit also occurs in the vertical and depth planes, generalizing previous results to 3D space. Our results provide novel insights into the mechanisms by which the brain instantiates spatial transformations during tactile localization. First, the present results provide the first experimental evidence that tactile localization occurs in 3D space. Second, it validates the crossed-hands deficit as a measure of tactile remapping. Third, the fact that the deficit persisted even when non-conflicting information about the location of touch was available, provides evidence for an automatic integration of all available information. This also suggests that selective attention to a single spatial dimension is not possible without automatic processing of other dimensions. It also bears in mind the extent to which the crossed-hands deficit reflects the encoding of touch in external space vs. the processing in the left-right dimension specifically. Finally, and more generally, the present study provides first experimental insight into the characterization of the space coded in tactile localization and how the different spatial dimensions interact.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2016.09.007.

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