Dynamic tuning of tactile localization to body posture

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Summary:

Localizing touch in space is essential for goal-directed action. Because body posture changes, the brain must transform tactile coordinates from an initial skin-based representation to external space by integrating information about current posture [1–3]. This process, referred to as tactile remapping, generally results in accurate localization, but accuracy drops when skin-based and external spatial representations of touch are conflicting, e.g., after crossing the limbs [1, 4]. Importantly, frequent experience of such postures can improve localization [5, 6]. This suggests that remapping may not only integrate current sensory input but also prior experience [7, 8]. Here, we demonstrate that this can result in rapid changes in localization performance over the course of few trials. We obtained an implicit measure of tactile localization by studying the perceived temporal order of two touches, one on each hand. Crucially, we varied the number of consecutive trials during which participants held their arms crossed or uncrossed. As expected, accuracy dropped immediately after the arms had been crossed. Importantly, this was followed by a progressive recovery if posture was maintained, despite the absence of performance feedback. Strikingly, a significant improvement was already evident in the localization of the second pair of touches. This rapid improvement required preceding touch in the same posture and did not occur merely as a function of time. Moreover, even touches that were not task-relevant led to improved localization of subsequent touch. Our findings show that touches are mapped from skin to external space as a function of recent tactile experience.

Results and Discussion

Our ability to localize touch on body parts that are crossed is often inaccurate. This deficit is very consistent across individuals and exceptionally difficult to overcome [5, 6]. Correctly localizing touches on crossed fingers, for example, requires that this posture is maintained over a long period of time, in the order of months [5]. Conversely, when everyday life activities require frequent crossing of the arms, e.g., while playing the piano, the crossed-hands deficit is reduced [9]. These examples suggest that localizing touch in space may not proceed in the same uniform way every time a touch is encountered but change with prolonged experience of certain postures [5, 6, 9]. In contrast to this prevailing view, we demonstrate a much quicker and more short-lived improvement in tactile localization when the limbs are crossed.

We studied the perceived temporal order of two touches, one applied on each hand, while the arms were crossed or uncrossed. Tactile temporal order judgements (TOJ) are an established, implicit index of tactile localization [1, 10, 11]. When the arms are crossed, as compared to uncrossed, tactile TOJ are impaired [1, 4]. One explanation invokes an automatic transformation of touch from a skin-centred to an external spatial frame of reference that takes posture into account [12–15]. When the arms are crossed, these two reference frames are in conflict, which leads to impaired localization performance and consequently inaccurate TOJ [4, 16, 17]. We report four experiments examining whether posture-dependent deficits in tactile localization diminish with successive experience. Importantly, we varied the number of trials for which posture remained constant following a postural change. In Experiment 1, we confirm that the crossed-hands deficit is reduced when this posture is sustained, as compared to when posture changes frequently. In Experiments 2 and 3, we demonstrate that this improvement in tactile localization develops rapidly after crossing the arms, over the course of very few trials, and that it depends on spatial information derived from recent touch, rather than on time. Finally, in Experiment 4, we show that recent tactile experience improves the localization of subsequent touch even when touch is task-irrelevant.

In Experiment 1, two taps were presented, one to each hand, at different stimulus onset asynchronies (SOA). Participants were required to identify which stimulus was presented second by pressing a button with the corresponding hand. The posture of the arms, which could be crossed or uncrossed, either remained constant throughout an entire block of trials (blocked condition) or changed after one to three trials (interleaved condition; see procedure in Figure 1a). A 2x2 ANOVA *Hand posture* x *Posture change schedule* showed that the just noticeable difference (JND) was larger when the arms were crossed as compared to uncrossed ($F(1,11)=10.4$, $p=0.008$; Figure 2b), replicating a well-established crossed-hands deficit [1, 4]. Importantly, the crossed-hands deficit (difference between JNDs in the two postures) was reduced almost by a factor of two in the blocked as compared to the interleaved condition (mean crossed-hands deficit: 68 and 122 ms, respectively; interaction: $F(1,11)=6.0$, $p=0.033$). Planned t-tests showed that performance in the crossed hands posture tended to be better when posture remained constant, as compared to when posture changed frequently ($t(11)=2.2$, $p=0.048$, Bonferroni-corrected threshold at 0.025), but no difference was observed for the uncrossed posture ($t(11)=1.2$, $p=0.25$). Importantly, the improvement occurred in the absence of performance feedback, indicating that subjects did not simply change their responses based on the outcome of the previous trial [18]. Experiment 1 shows that tactile localization in the crossed posture improves when that posture is maintained or, conversely, becomes less accurate when posture is variable, but no such effect occurs when the hands are uncrossed. This suggests that the improvement in the crossed posture arises downstream of primary somatosensory processing, which is identical for both postures, possibly at a stage at which tactile coordinates are transformed from skin-based to external space.

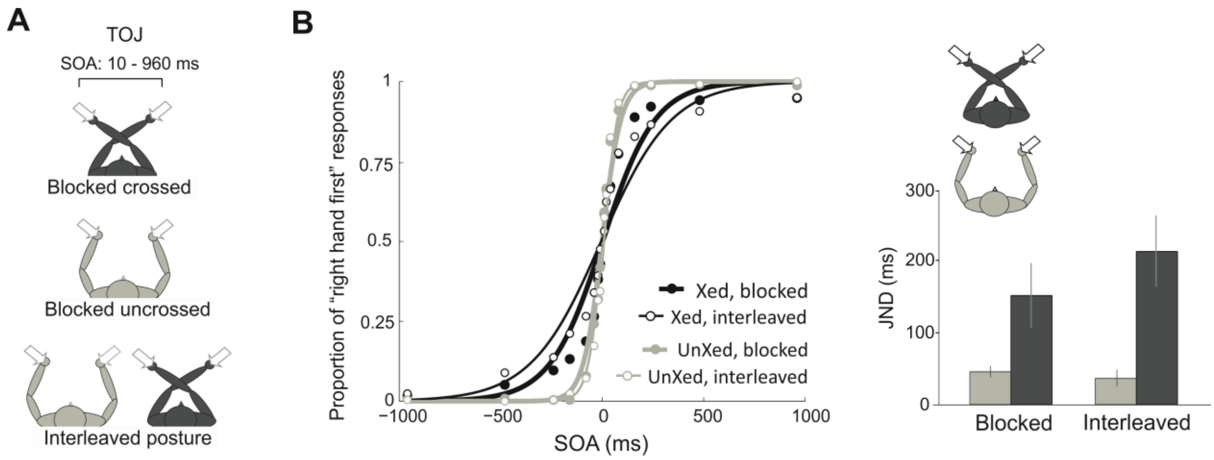

Figure 1. Procedure and Results of Experiment 1.

(A) Procedure of Experiment 1. On each trial, participants crossed or uncrossed their hands or maintained one of the two postures, as instructed by the words "cross" or "parallel" on a computer screen. Two 10 ms taps were delivered 1.0 ±0.5 secs after the end of this movement (or, if posture was maintained, 2 ±0.5 secs after the instruction on the screen) via solenoid tappers attached to the dorsal surface of the middle phalanx of each ring finger. Participants indicated which hand was stimulated second by pressing a button with that hand (without time restriction). Both arms were occluded from view and no performance feedback was given (see Supplemental Information for details of the set-up). Stimuli were presented at SOAs of ±10, ±20, ±40, ±80, ±160, ±240, ±480 and ±960 ms (negative values indicate that the left-hand was leading). In the continuous conditions, posture of the hands, either crossed or uncrossed, was kept constant for the duration of each block. In the interleaved condition, the position of the hands alternated, with a maximum of 3 repetitions in the same posture. Four blocks of 320 trials each were tested (two in the interleaved condition; order counterbalanced).

(B) Results of Experiment 1. The proportions of "left hand second" responses (i.e., "right hand first") across all SOAs were fitted with logistic functions, for each subject and condition separately. The just noticeable difference (JND; corresponding to the semi-interquartile range) was calculated as a measure of sensitivity to tactile temporal order (TOJ). The logistic fits to the group-averaged data are shown (**left panel**). Fourteen volunteers were tested (mean age 25 years, SD=5.4; 7 female). Data from two participants were excluded because of poor model fit (R2 < 0.4 in one or more conditions; remaining sample: n=12; mean age 26 years; SD=5.4; 7 female). The mean JND for each condition is shown in the **right panel**. Error bars represent SEM. There was no significant change in the point of subjective equality across conditions. Experiment 1 shows that the crossed hands deficit is reduced when posture is maintained.

Experiment 2 investigated in greater detail the dynamics with which tactile localization changes after crossing the arms. The core experimental data were sequences of four successive TOJ trials after each change in arm posture. Shorter or longer sequences were included to reduce predictability ('fillers' in Figure 2a). Only two SOAs were used, one for each posture. These SOAs were preselected by an adjustment procedure to produce a target level of performance for each individual (~79% correct [19]; ~70% in the following experiments; mean crossed = 142 ms; uncrossed = 41 ms). We used signal detection theory to obtain d' as an index of sensitivity to the temporal order (complementary analyses of percent correct are shown in the Supplemental Information). We computed four separate d'-values for consecutive trials following a posture change. As shown in Figure 2b, sensitivity increased across the course of the four trials, but only in the crossed-hands posture (*Posture* x *Trial Order* interaction, $F(3,33)=4.8$, $p=0.007$; main effect of *Trial Order* $F(3,33)=9.6$, $p<0.001$). This interaction was better explained by a linear effect of Trial Order ($F(1,11)=10.6$, $p=0.008$) than by quadratic or cubic effects (both $p>0.32$). We therefore calculated linear trends across subjects and trials, separately for the crossed and the uncrossed postures. A one-sample t test of the linear slope against zero reflected a significant increase in sensitivity for the crossed posture (mean slope: 0.32 increase in d' per repetition; $t(11)= 5.2$, $p<0.001$), but not for the uncrossed posture (mean slope: 0.04; $p=0.44$; Bonferroni-corrected threshold at 0.025). Importantly, the linear increase in the crossed condition was also significant when excluding the first trial after a posture change ($t(11)=2.5$, $p=0.029$, threshold at 0.05), excluding the possibility that the trend was explained by a drop in sensitivity immediately after movement.

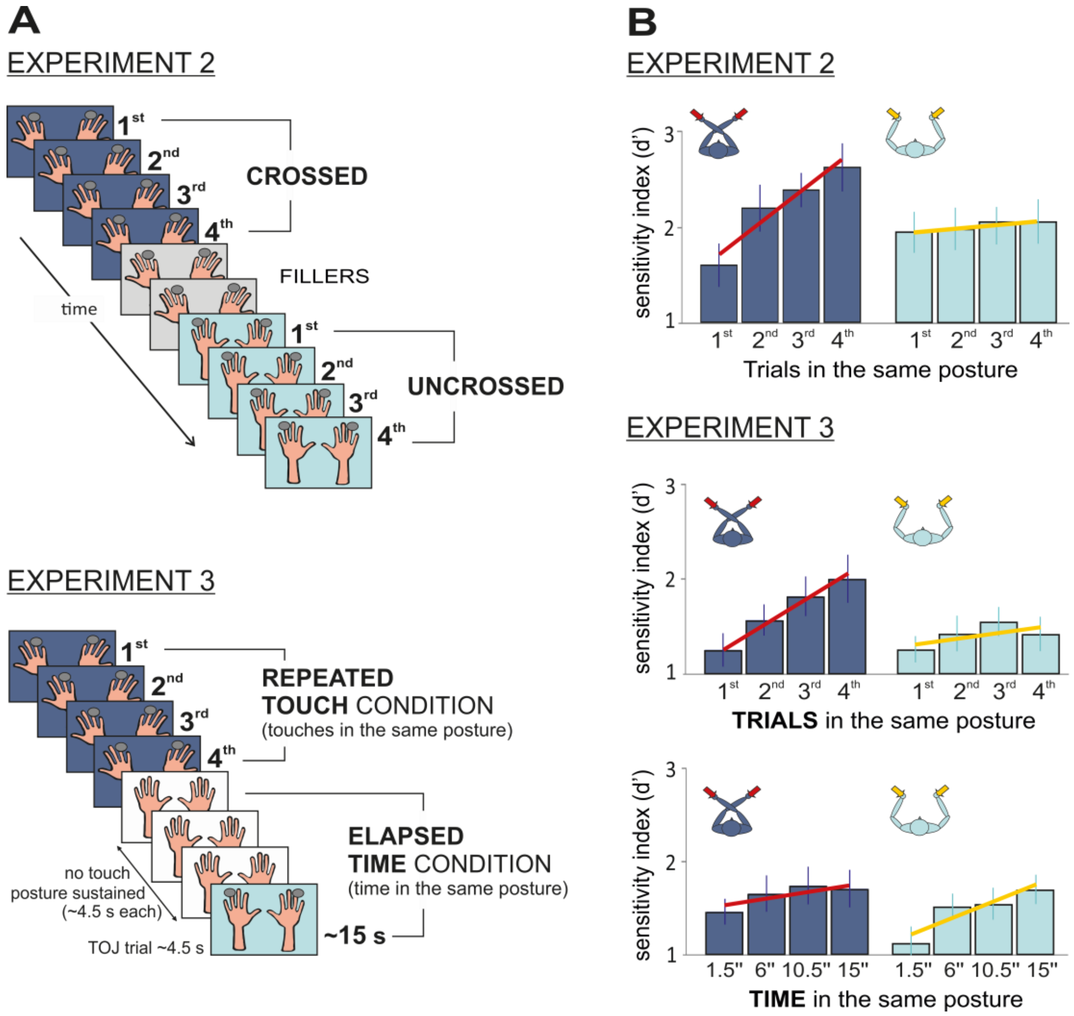

Figure 2. Procedure and Results of Experiments 2 and 3.

<u>(A) Procedure of Experiments 2-3</u>. In Experiment 2 (**top panel**) participants completed a sequence of four TOJ trials after a change of posture (to reduce predictability, posture changed after 1,2 or 6 trials in ~40% of sequences; these 'filler' trials are shown in **grey**, ~25% of all data). Only two SOA per subject were used, one for each posture (the same SOA were used for left-then-right and right-then-left stimulation). These were individually preselected to match performance in the two postures by a staircase procedure prior to the main experiment in which posture changed on every trial [19] (see Supplemental Information). On each trial, participants performed the same task as in Experiment 1. 12 Participants (mean age 23 years, SD=2.9; 4 female) completed eighty trials for each of the four trial positions (1st, 2nd, 3rd and 4th trial after a posture change). A total of ~860 trials were tested in 10 blocks. In Experiment 3 (**bottom panel**), participants performed the same task as in Experiment 2 (*repeated-touch condition*) plus a control condition (*elapsed-time condition*), in which touches were delivered only on the first, second, third or fourth trial. These trials were preceded by trials of identical duration but without touch (computed online as the average duration of the preceding TOJ trials in that posture; ~4.5 s), in which participants were merely required to keep the hands still. Sequences of trials from both conditions were pseudorandomly interleaved and the type of trial was visually cued at the beginning of each trial. An example of a "fourth" trial in the timing condition is illustrated here. 14 participants (n=14; mean age 24 years, SD=4.1; 7 female) completed 72 trials (36 right-then-left sequences) for each posture, condition and trial position. A total of 2124 trials (including 5% of fillers) were tested in 18 blocks, completed in separate sessions on different days (2 to 4).

(B) Main results of Experiment 2-3. Group-mean sensitivity index as a function of trial position in Experiment 2 (**top**) and 3 (**bottom**). Signal detection theory was used to investigate modulations of tactile temporal order sensitivity, indexed by d' [45, 46]. Correct "right-second" responses were classified as hits (H) and incorrect "right-second" responses were classified as false alarms (FA, defining H and FA on the bases of "left-second" responses yields identical results, see [45, 46]). d' was calculated as d'=Z(H)-Z(FA), where Z represent the z-transform of these rates. **Dark blue** bars represent data from the crossed condition, while **light blue** bars represent data from the uncrossed condition. The **red** and **yellow lines** represent the linear fit (see Supplemental Information), and error bars represent the SEM. Note that a direct comparison between d' in crossed and uncrossed postures is not informative because the SOA used for each posture differs (to match performance, see explanation in (A)). We did not find any effect on response bias (criterion) across conditions in any of the Experiments. Experiments 2-3 show that tactile localization in the crossed posture improves as a function of repeated touch, not as a function of time.

These results confirm the findings of Experiment 1, showing that tactile localization improves when posture is sustained, specifically in the unfamiliar crossed posture. Furthermore, Experiment 2 reveals how rapidly this improvement unfolds: a single TOJ trial was sufficient to improve localization of subsequent touch ($t(11)=2.9$, $p=0.013$, Bonferroni-corrected threshold at 0.017). In addition, Experiment 2 shows that tactile localization performance is reset to a lower level after each posture change. This resetting explains the lack of overall improvement by the end of the experiment: Neither the linear trend across the four consecutive trials after a posture change, nor the four separate d'-values for each of these trials differed between the first and the second half of the experiment (Supplemental Information). As in Experiment 1, the modulatory effect was observed only when the hands were crossed (see [6]), even though performance was matched to produce a similar error rate in both postures. This makes any ceiling effect an unlikely explanation for the lack of improvement in the uncrossed condition in Experiment 1.

Does this improvement occur as a function of time or does it depend on tactile stimulation? Several studies have shown that limb position sense decays over time, even at intervals as short as a few seconds [20–22]. This decay could potentially improve performance in the crossed-hands condition specifically, since impaired performance in this condition is due to interference from a proprioceptive signal in an external spatial reference frame. Alternatively, the effect could depend on accumulating spatial information with each successive touch. We tested these alternative explanations in Experiment 3. In one condition, subjects performed the same task as in Experiment 2 (*repeated-touch* condition). In the other condition (*elapsed-time* condition), touches were delivered only on the first, second, third or fourth trial of a given sequence (counted from the last posture change). The other preceding trials of that sequence had the same duration as the touch-trial but contained no touches (Figure 2a, bottom panel). Thus, time intervals between posture changes were identical in both conditions, whereas the number of touches was different. The presence or absence of upcoming touches was cued at the beginning of each trial.

The results of Experiment 3 show that sampling of tactile information is necessary for an improvement in tactile localization, while mere time spent in a new posture has no effect (Figure 2b, bottom panel). An ANOVA with the factors *Condition* (repeated-touch vs. elapsed-time) x *Posture* x *Trial Order* revealed a significant triple interaction ($F(3,39)=5.4$, $p=0.003$; a main effect of *Trial Order* was also significant ($F(3,39)=12.2$, $p<0.001$). That is, whereas participants' performance differed when hands were crossed vs. uncrossed in the repeated-touch condition (*Posture* x *Trial Order* interaction, $F(3,39)=3.5$, $p=0.024$), no effect of posture was found in the elapsed-time condition ($p=0.26$). As in Experiment 2, the relationship among the three factors was better explained by a linear effect of Trial Order ($F(1,13)= 24.3$, $p<0.001$) than by quadratic or cubic effects (both $F<1$). We therefore calculated the linear trends across trials, and analysed them directly, as in Experiment 2. A planned comparison of trends in the crossed condition that tested the "touch or time" hypothesis showed that the linear increase was significantly larger in the repeated-touch condition than in the elapsed-time condition (mean slopes: 0.25 vs 0.08; $t(13)=2.4$, $p=0.030$, threshold at 0.05). We further tested the linear trend in each condition against the null hypothesis of zero slope (Bonferroni-corrected threshold at 0.013). We found a significant increase in the crossed/repeated-touch condition ($t(13)=5.3$, $p<0.001$), but not in the uncrossed/repeated-touch condition ($t(13)=1.1$, $p=0.29$) nor in the crossed/elapsed-time condition ($t(13)=1.5$, $p=0.16$). That is, no improvement was observed when participants maintained the crossed posture without receiving any touch. Unexpectedly, there was a linear increase in performance in the uncrossed/elapsed-time condition ($t(13)=4.4$, $p=0.001$). This increase, however, was explained by a transient improvement from trial one to trial two with no further improvement across following trials. Indeed, when excluding trial one from the analyses, only the increase in the crossed/repeated-touch condition remained significant ($t(13)=3.0$, $p=0.010$; all others $p>0.15$). The fact that tactile stimulation was required to improve subsequent sensitivity indicates that tactile localization changes as a function of recent tactile information and not because proprioceptive information decays over time.

Remarkably, this improvement in tactile spatial localization occurred even when preceding touches were task-irrelevant, as demonstrated in Experiment 4. Participants uncrossed the arms every *two* or *four* trials and received two touches on each trial. Uncrossed TOJ trials (mostly single trials) were included as fillers to ensure posture switches. Importantly, only the last trial of each sequence (of either two or four trials) required an explicit temporal order judgement, as indicated by a cue at the beginning of that trial (Figure 3a). In the preceding trials, a rapid series of visual pictograms was presented on a screen, which overlapped in time with the tactile stimulation on that trial. In these combined visuo-tactile trials, participants were asked to detect consecutive repetitions of pictures and to respond exclusively to this visual task while ignoring the touches (mean performance 84% across subjects; visual performance did not differ across trial order in the sequence; $p>0.47$). If tactile localization processes can benefit from prior touch even if that touch is currently task-irrelevant, we would expect a similar increase in sensitivity following a postural change as in Experiments 2 and 3. We found that sensitivity was larger for the fourth as compared to the second trial ($t(9)=3.7$, $p=0.005$; Figure 3b). Comparing data from Experiment 4 vs. Experiment 2, where preceding touches had been task-relevant, we found a similar degree of improvement between the second and the fourth trial in both experiments (*Experiment* x *Position* (second vs. fourth) ANOVA, interaction: $F<1$). An additional experiment (Supplemental Information, Experiment S1) confirmed that there was no improvement by task-irrelevant touch when the arms were uncrossed. Tactile localization therefore benefited from recent tactile-spatial information even when there was no explicit requirement to localize the preceding touch. In addition, Experiment 4 largely excludes the possibility that the progressive improvement across trials in Experiments 1 to 4 can be explained by task-switching costs [23], as the increase in performance in Experiment 4 cannot be accounted for by post-switch decisions (see Supplemental Information for a more detailed discussion).

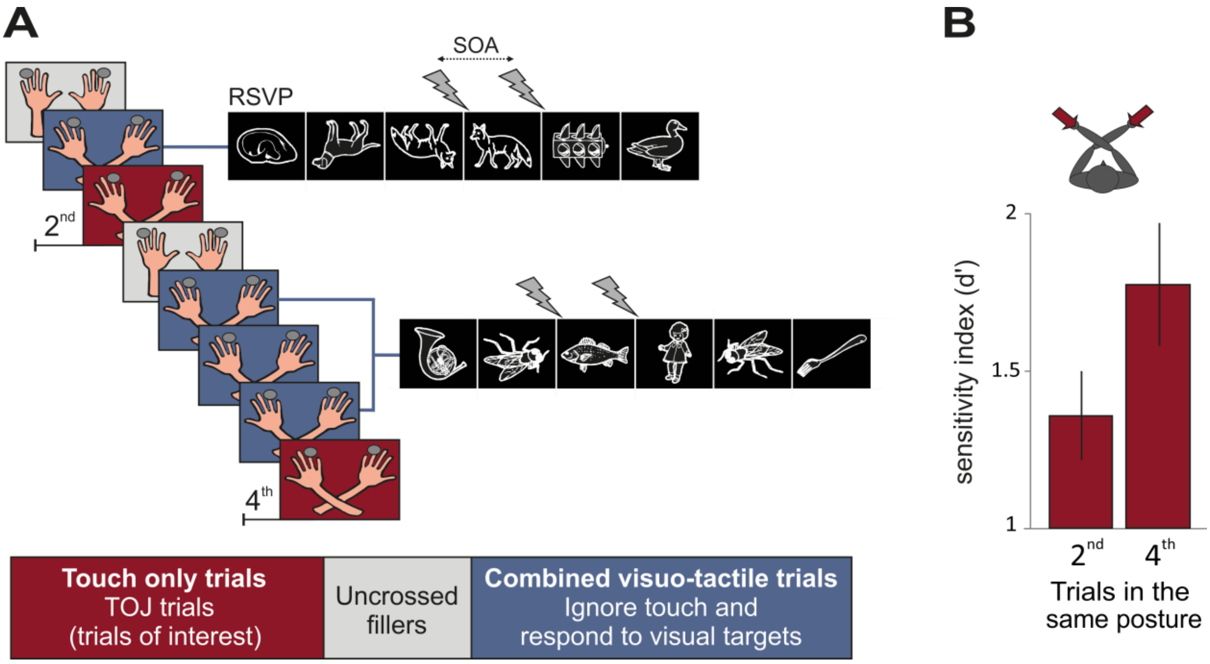

Figure 3. Procedure and Results of Experiment 4.

<u>(A) Procedure of Experiment 4</u>. Participants uncrossed their hands every two or four trials and received two touches on each trial, with an individually adjusted SOA (see Supplemental Information). The last trial of each sequence required a TOJ (touch only trials, red). In the preceding trials (one or three, depending on the sequence), a rapid series of six pictures [47] was presented on a computer screen, overlapping in time with the presentation of the two taps on that trial (blue). In these combined visuo-tactile trials, participants were required to detect consecutive repetitions of pictures, regardless of their orientation, and ignore touch (see Supplemental Information). Posture and task-relevant modality (touch or vision) were visually cued at the beginning of each trial. Uncrossed TOJ trials were included to ensure a switch in posture, but were not analysed (72% were single trials, depicted in grey). 10 participants (mean age=21 years; SD=3.5; 8 female) completed 80 touch-only trials per condition in 10 blocks for a total of 700 trials (uncrossed fillers, 31%).

<u>(B) Main results of Experiment 4</u>. Group-mean d' in the last trial of each sequence. Error bars represent the SEM. Experiment 4 shows that tactile localization improves in the crossed hands posture even when preceding touches are task-irrelevant.

Taken together, our results demonstrate a mechanism by which the brain updates spatial transformations during multisensory, tactile-proprioceptive, integration. Classical models of coordinate transformation are based on *current* sensory states, e.g., on a "snapshot" of proprioceptive, visual, tactile and kinaesthetic information at the time of tactile stimulation [24, 25]. Here, we demonstrate that tactile localization also relies on spatial information from *preceding* touches. We show that tactile localization in the unfamiliar, crossed posture improves rapidly due to postural and tactile information integrated in the process of remapping recent stimuli. Importantly, this improvement in tactile localization requires neither performance feedback nor explicit localization of these preceding tactile events.

Our findings raise the interesting question how the brain achieves this improvement. A modulation at an early, somatotopic stage of tactile processing is unlikely given the consistent absence of improvement in the uncrossed posture across experiments (see also Supplemental Information, Experiment S1). Since skin-based somatotopic coordinates do not change when the hands are crossed, early modulations should influence performance similarly in both postures [4, 26]. A modulation at a later stage, during the coordinate transformation between skin and external space, is therefore more likely. Accordingly, we discuss two potential mechanisms of improvement at this later stage, based on current theories of tactile remapping. It is often assumed that the crossed-hands deficit results from a conflict between two concurrently available, opposing representations of touch (in an anatomical and a visually-based external reference frame) [1, 4, 11, 27, 28]. Within this framework, the observed improvement in tactile localization could be explained in analogy to mechanisms of conflict monitoring in cognitive control [29, 30]. Specifically, after touch in the crossed posture is localized in external space, a higher-level system could signal a conflict between reference frames and adjust the relative weighting of reference frames, thereby reducing conflict during the remapping of subsequent touch. This would agree with a recent proposal that each location estimate reflects a weighted sum of information from different reference frames, and that these weights are subject to top-down modulation [17, 31].

According to an alternative view, the presumed conflict between reference frames is due to common limb postures dominating information about less usual postures [1, 32–36]. According to this view, tactile localization is influenced by a prior expectation that a tactile sensation originates from where the touched limb is typically located in external space - e.g. from the right side of space for the right hand [33]. The improvement in tactile localization observed here could therefore reflect a progressive adjustment of a prior postural model due to repeated co-occurrence of touch with a proprioceptive signature of an uncommon, crossed posture [5]. Similar experience-dependent mechanisms have been proposed to explain the development of crossmodal neurons [37, 38], specifically the emergence of a visually-based spatial map for touch [9, 13, 32].

We found no evidence of a general improvement across the course of the experiment. Instead, performance was reset every time posture changed from uncrossed to crossed. This could suggest that the brain initializes a fixed, default localization process every time the hands are crossed. Following the two alternative accounts discussed above, this could correspond to a re-setting of weights for each reference frame or to a re-setting of a prior model of tactile localization. For example, transfer of learning across sequences of crossed postures that are interleaved with uncrossed postures might be overridden by strong proprioceptive feedback during movement [39]. Indeed, it has been shown that tactile localization is influenced by the next posture even before movement execution, during the planning of an imminent movement [40, 41]. The different time scales of the rapid, but short-lasting improvement in our study and the slow, but long-lasting training (or exposure) effects in previous studies [5, 6, 9] may indicate that the two phenomena rely on distinct mechanisms: a fast, state-specific adjustment that occurs in the absence of performance feedback [7] and a slow, reusable learning that depends on continuous experience and feedback, and might result in permanent structural changes [37].

In conclusion, we demonstrate a dynamic tuning of tactile localization as a function of posture which progressively updates spatial coordinate transformations on the basis of previous sensory experience, touch by touch. Most studies on tactile spatial processing assume that remapping is relatively stable and uniform [1, 4, 42]. Contrary to this assumption, we show that tactile remapping dynamically changes at very short time scales. These rapid dynamics might complement other mechanisms underlying long-lasting, plastic changes in body representation and tactile remapping that occur with training, development, ageing and injury [6, 43, 44].

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Author contributions

E.A., P.H, M.P.S. and F.C. conceived the study. E.A. and F.C. collected the data. E.A. conducted the statistical analyses. E.A., M.P.S. and P.H. wrote the paper with input from F.C.

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